# Five new species of *Biatora* from four continents

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**Abstract:** Printzen, C., Halda, J. P., McCarthy, J. W., Palice, Z., Rodriguez Flakus, P., Thor, G., Tønsberg, T. & Vondrák, J. 2016. Five new species of *Biatora* from four continents. – Herzogia **29**: xx–xx.

*Biatora australis* and *B. hafellneri* from South America, *B. pacifica* from East Asia, *B. radicicola* from central and northern Europe and the Caucasus, and *B. terrae-novae* from Newfoundland are described as new to science. The phylogenetic position of four of these species is reconstructed using ITS and mrSSU sequence data. Revised identification keys for the *Biatora vernalis* group and *Biatora* species with non-septate ascospores and blue or green apothecial pigments are also provided.

**Zusammenfassung:** Printzen, C., Halda, J. P., McCarthy, J. W., Palice, Z., Rodriguez Flakus, P., Thor, G., Tønsberg, T. & Vondrák, J. 2016. Fünf neue *Biatora*-Arten aus vier Kontinenten. – Herzogia **29**: xx–xx.

*Biatora australis* und *B. hafellneri* aus Südamerika, *B. pacifica* aus Ostasien, *B. radicicola* aus Mittel- und Nordeuropa und dem Kaukasus sowie *B. terrae-novae* von Neufundland werden als neu für die Wissenschaft beschrieben. Die phylogenetische Stellung von vier dieser Arten wird mittels ITS- und mrSSU-Sequenzdaten rekonstruiert. Die Arbeit enthält auch revidierte Bestimmungsschlüssel für die *Biatora-vernalis*-Gruppe und *Biatora*-Arten mit unseptierten Sporen und blauen oder grünen Apothecienpigmenten.

**Key words:** East Asia, Europe, ITS, lichens, mrSSU, Newfoundland, Patagonia.

## Introduction

To date, the genus *Biatora* comprises about 40 species of mostly inconspicuous, crustose lichens inhabiting organic substrata (bark, wood, bryophytes and plant debris). The phylogenetic relationships within the genus were recently studied by Printzen (2014), who distinguished six more or less well supported species groups and a number of taxa that could not be assigned to any of these groups with certainty. Printzen (2014) included several so far undescribed species into the phylogenetic analysis. Two of these species, *Biatora radicicola* and *B. terrae-novae*, are formally described here.

*Biatora* was once thought to be restricted to temperate, boreal and arctic regions of the Northern Hemisphere (Printzen & Lumbsch 2000). Revisions of southern South American lecideoid lichens showed that this view had to be altered, and that *B. rufidula* extended its distributional range to the Southern Hemisphere (Rodriguez-Flakus & Printzen 2014). Further studies have now revealed the existence of two more South American species, *B. australis* and *B. hafellneri*, that are apparently new to science and are also described here.

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One reason for the steady increase of described *Biatora* species over the last 20 years (e.g. Printzen & Tønsberg 1999, 2003, 2004, Spribille et al. 2009, Tønsberg 2002) is more focused collecting activities. Most *Biatora* species prefer boreal coniferous and mixed forests. Considering the high diversity of conifers in East Asia and the fact that research activities in the past were largely focused on Europe and North America, an even higher number of undetected species can be expected in East Asia. Here we also describe a further species, *B. pacifica* from Japan, South Korea and the Russian Far East. In addition, we present updated determination keys for the *Biatora vernalis* group and *Biatora* species with aseptate to 1-septate ascospores and blue or green apothecial pigments.

Morphological differences between *Biatora* species can be very subtle, even if these species appear not as closely related in phylogenetic trees (Printzen 2014). In order to estimate the distinctness of the newly described taxa and, if possible, their phylogenetic position, we used DNA sequences of the internal transcribed spacer region (ITS) of the ribosomal RNA, the proposed universal barcoding marker for fungi (Schoch et al. 2012) as well as the small subunit of the mitochondrial ribosomal RNA (mrSSU).

## Materials and Methods

This study is mainly based on material collected by the authors on field trips in Argentina, Canada, the Czech Republic, Ecuador, Finland, Japan, Russia, South Korea and Ukraine and deposited in BCRU, BG, CANL, FR, KRAM, PRA, QCA, UPS and the private herbaria of F. Berger, J. P. Halda and J. Malíček. Additional material was obtained from BP and M.

Specimens were either hand-sectioned or sectioned with a Hyrax S-30 microtome with KS 34 cryostat (Zeiss) and mounted in water, Lugol's solution or lactophenol cotton blue (LCB). Spore measurements were made on sections mounted in water. Measurements of ascomatal structures in LCB followed Printzen (1995). Spore measurements are given as (smallest single measurement-) smallest mean-largest mean (-largest single measurement). Spot test reactions were carried out on hand sections of thalli and apothecia under the microscope. Lichen substances were identified by TLC (Culberson & Kristinsson 1970) and later modifications.

We sequenced the internal transcribed spacer region and a part of the mitochondrial small subunit of the ribosomal RNA to infer the phylogenetic position and ascertain the distinctiveness of the newly described species. Methods of DNA extraction, PCR and DNA sequencing and editing followed Printzen (2014). We performed NCBI BLAST searches (Johnson et al. 2008) to identify similar sequences in Genbank and compiled three separate datasets around the newly generated sequences of (1) *B. terrae-novae*, (2) *B. radicicola* and (3) *B. australis* and *B. hafellneri* based on the infrageneric groups found by Printzen (2014) and using *Mycobilimbia tetramera* (De Not.) Vitik. et al. as outgroup. Sequences used in the analyses are listed in Table 1. Alignments were created and regions of uncertain alignment identified using the GUIDANCE2 server (URL: http://guidance.tau.ac.il/ver2/, Landan & Graur 2008; Sela et al. 2015). We selected the default settings with MAFFT as the alignment algorithm and the 6-mer alignment method. Regions with GUIDANCE scores below 0.9 (ITS) or 0.93 (mrSSU) were removed from the analyses. Maximum likelihood bootstrap trees on concatenated datasets were reconstructed with raxMLGUI version 0.9 beta 2 (Stamatakis 2006; Silvestro & Michalak 2010) under a GTRGAMMA model with separate partitions for the ITS1, 5.8S, ITS2 regions and mrSSU using the ML + rapid bootstrap option. Newly generated DNA sequences were submitted to Genbank (Table 1).

**Table 1**: Collections used for DNA sequencing and GenBank accession numbers. Accession numbers in bold indicate newly generated sequences.

| Species | Origin | ITS | mrSSU |
|---|---|---|---|
| *Biatora aegrefaciens* | USA: Alaska, Mitkof Island, T. Tønsberg 30212 (BG) | KF650956 | - |
| *Biatora alaskana* | USA: Alaska, Borough of Sitka, C. Printzen 5229 (FR) | KF650957 | KF662404 |
| *Biatora alaskana* | Russia: Khabarovskiy Krai, 33.7 km (air line) due W of Lazarev, 52°13.452'N, 141°00.419'E, B. Kanz, T. Spribille, L. Yakovtchenko & C. Printzen 11552 (FR) | - | **KX389598** |
| *Biatora alaskana* | Japan: Gumma, Honshu, Katashina mura, 25 km WNW of Nikko City, 36.82225°N, 139.36333°E, G. Thor 32399 (UPS) | **KX389591** | **KX389603** |
| *Biatora appalachensis* | USA: North Carolina, Graham Co., C. Printzen 6661 (FR) | KF650959 | - |
| *Biatora australis* | Argentina: Tierra del Fuego, Antártida e Islas del Atlántico Sur, 54°50'39.6"S, 68°34'23.9"W, P. Rodriguez Flakus 2473 & A. Flakus (BCRU) | **KX389594** | **KX389597** |
| *Biatora bacidioides* | Turkey: Rize Prov., B. Kanz & C. Printzen s.n. (FR) | - | KF662406 |
| *Biatora beckhausii* | Norway: H. Holien 6744 (TRH) | AF282071 | KF662407 |
| *Biatora britannica* | Genbank | AY032897 | - |
| *Biatora* cf. *chrysantha* | Japan: Gumma, Honshu, Katashina mura, 25 km WNW of Nikko City, 36.82086°N, 139.37642°E, G. Thor 32429 (UPS) | - | **KX389599** |
| *Biatora chrysantha* | Czech Republic: W-Bohemia, Šumava Mts., Z. Palice & C. Printzen s.n. (FR) | AJ247569 | KF662408 |
| *Biatora chrysanthoides* | USA: Washington, Clallam Co., C. Printzen 5318 (FR) | KF650960 | KF662409 |
| *Biatora cuprea* | Sweden: Torne Lappmark, Jukkasjärvi par., B. Kanz & C. Printzen 5437 (BG) | KF650961 | KF662410 |
| *Biatora efflorescens* | Czech Republic: S-Bohemia, Šumava Mts., Z. Palice s.n. (FR) | AJ247555 | - |
| *Biatora ementiens* | Sweden: Torne Lappmark, B. Kanz & C. Printzen 5440 (BG) | KF650962 | KF662411 |
| *Biatora fallax* | Czech Republic: S-Bohemia, Šumava Mts., Z. Palice s.n. (FR) | AJ247548 | KF662412 |
| *Biatora fallax* | Czech Republic: S Bohemia, Šumava Mts, 48°57'08.6"N, 13°47'52.4"E, J. Maliček & Z. Palice 19135 (FR) | **KX389592** | **KX389604** |
| *Biatora fallax* | Czech Republic: S Bohemia, Šumava Mts, České Žleby, 48°53'49.6"N, 13°48'01.5"E, F. Berger & Z. Palice 20009 (FR) | **KX389593** | **KX389605** |
| *Biatora flavopunctata* | USA: Washington, Clallam Co., C. Printzen 5327 (FR) | KF650963 | KF662413 |
| *Biatora globulosa* | Sweden: S. Ekman 3142 (BG) | AF282073 | KF662414 |
| *Biatora hafellneri* | Argentina: Rio Negro, Bariloche, Parque Nacional Nahuel Huapi, 41°20'32.7"S, 71°34'39.2"W, P. Rodriguez Flakus 3038 & A. Flakus (FR–holotype) | **KX389595** | - |
| *Biatora helvola* | Finland: Etelä-Savo, M. Kuusinen s.n. (BG) | KF650964 | - |
| *Biatora hemipolia* | USA: Washington, Kittitas Co., T. Tønsberg 25091 (BG) | AF282072 | AF282072 |
| *Biatora hertelii* | Portugal: Madeira, Rabaçal, B. Kanz & C. Printzen s.n. (FR) | AJ247536 | KF662416 |
| *Biatora hypophaea* | USA: Oregon, Linn Co., C. Printzen s.n. (BG) | KF650966 | - |
| *Biatora kodiakensis* | USA: Alaska, Kodiak Island Borough, T. Tønsberg 29371(BG) | KF650967 | KF662417 |
| *Biatora ligni-mollis* | Czech Republic: S-Bohemia, Novohradské hory Mts., J. Malíček & Z. Palice 14609 (FR) | KF650968 | KF662418 |
| *Biatora longispora* | USA: Massachussetts, Berkshire Co., P. May 5409 (hb. May) | KF650969 | KF662419 |
| *Biatora longispora* | Japan: Tochigi, Honshu, Shimotsuke Prov., Nikko City, 36.79972°N, 139.48311°E, G. Thor 32461 (UPS) | - | **KX389602** |
| *Biatora* cf. *longispora* | Japan: Tochigi, Honshu, Shimotsuke Prov., Nikko City, 36.76592°N, 139.44706°E, G. Thor 32100 (UPS) | **KX389590** | **KX389601** |
| *Biatora meiocarpa* | Genbank | AM292667 | AM292710 |
| *Biatora nobilis* | USA: Washington, T. Tønsberg 29057 (BG) | KF650970 | KF662421 |

| **Species** | **Origin** | **ITS** | **mrSSU** |
|---|---|---|---|
| *Biatora ocelliformis* | Germany: Bavaria, Niederbayern, C. Printzen s.n. (FR) | KF650972 | - |
| *Biatora oligocarpa* | USA: Alaska, Kodiak Island Borough, T. Tønsberg 29571 ( BG) | KF650973 | KF662423 |
| *Biatora pallens* | Sweden: Lule Lappmark, Jokkmokk par., U. Nordin 2161 (BG) | KF650975 | KF662425 |
| *Biatora pausiaca* | USA: Washington, Clallam Co., T. Tønsberg 28017 & C. Printzen (BG) | KF650976 | KF662426 |
| *Biatora pontica* | Turkey: Trabzon Prov., C. Printzen 6114 (BG) | KF650977 | KF662427 |
| *Biatora printzenii* | USA: North Carolina, Swain Co., C. Printzen 6837 (BG) | KF650978 | KF662428 |
| *Biatora pycnidiata* | Canada: Newfoundland, Ferryland District, C. Printzen 5497 (BG ) | KF650979 | KF662429 |
| *Biatora radicicola* | Czech Republic: E-Bohemia, Nové Město, J. Halda 4104 (FR–holotype) | KF650980 | - |
| *Biatora radicicola* | Ukraine: Eastern Carpathians, Khust, Velyka Uhol'ka, 48°17'52"N, 23°39'59"E, F. Berger 29335 (hb. Berger) | **KX389587** | - |
| *Biatora radicicola* | Ukraine: Eastern Carpathians, Khust, Velyka Uhol'ka, 48°17'48"N, 23°42'15"E, J. Vondrák 14388 (PRA) | **KX389586** | **KX389606** |
| *Biatora radicicola* | Ukraine: Eastern Carpathians, Khust, Velyka Uhol'ka, 48°17'52"N, 23°39'59"E, Z. Palice 19970 (PRA) | **KX389588** | **KX389607** |
| *Biatora rufidula* | USA: Washington, Pierce Co., C. Printzen 5055 (FR) | KF650981 | KF662430 |
| *Biatora sphaeroidiza* | Sweden: Uppland, Alsike par., Z. Palice s.n. (FR) | KF650982 | - |
| *Biatora subduplex* | Sweden: Torne Lappmark, Jukkasjärvi par., B. Kanz & C. Printzen 5436 (FR) | KF650983 | KF662431 |
| *Biatora tacomensis* | USA: Washington, Lewis Co., C. Printzen 5015 (FR) | - | KF662420 |
| *Biatora terrae-novae* | Canada: Newfoundland, Fortune Bay-Hermitage District, C. Printzen 5758 (BG) | KF650971 | KF662422 |
| *Biatora terrae-novae* | Canada: Newfoundland, Port-au-Port Peninsula, 48.52544°N, 59.21586°W, J. McCarthy 2361 (FR–holotype) | **KX389589** | **KX389600** |
| *Biatora toensbergii* | USA: Washington, Pierce Co., C. Printzen 5053 (FR) | KF650984 | KF662432 |
| *Biatora vacciniicola* | USA: Alaska, City and Borough of Juneau, T. Tønsberg 27486 (BG) | KF650985 | KF662433 |
| *Biatora vernalis* | Genbank | AF282070 | AM292711 |
| *Biatora veteranorum* | Czech Republic: S-Bohemia, Novohradské hory Mts., J. Malíček & Z. Palice 14753 (FR) | KF650986 | KF662434 |
| *Cliostomum corrugatum* | Sweden: Skåne, Trolle-Ljungby par., S. Ekman 3115 (BG) | - | AY567722 |
| *Cliostomum griffithii* | Genbank | AF282076 | GU138667 |
| *Lecania croatica* | Turkey: Trabzon Prov., C. Printzen 5946 (BG) | KF650949 | KF662397 |
| *Lecania cyrtella* | Sweden: S. Ekman 3017 (BG) | AF282067 | AY567720 |
| *Lecidea albohyalina* | Sweden: Hälsingland, F. Jonsson 6:29 (hb. Mellansel) | KF650950 | KF662398 |
| *Lecidea sphaerella* | Czech Republic: S-Bohemia, Šumava Mts., Z. Palice 4621 (FR) | KF650952 | KF662400 |
| *Mycobililmbia pilularis* | Norway: Lindås, T. Tønsberg 39665 (BG) | KF650954 | KF662402 |
| *Mycobilimbia carneoalbida* | Finland: Uusima Prov., C. Printzen & M. Kuusinen s.n. (FR) | AJ247573 | **KX389596** |
| *Mycobilimbia epixanthoides* | Finland: Uusima Prov., C. Printzen & M. Kuusinen s.n. (FR) | KF650953 | KF662401 |
| *Mycobilimbia tetramera* | Norway: Lindås, T. Tønsberg 39665 (BG) | KF650955 | KF662403 |

## Results and Discussion

We were unable to obtain DNA sequences from *Biatora pacifica*. The size of the final datasets before and after removal of uncertain alignment positions can be found in Table 2. The phylogenetic tree in figure 1A shows that *B. australis* forms a well supported clade with *Biatora ligni-mollis* T.Sprib. & Printzen (boorstrap support 89 %). The exact position of *B. hafellneri* on this tree remains uncertain. We place it in *Biatora* mainly because of anatomical similarities and because, according to our BLAST search, the most similar sequences in GenBank belong to *Biatora*. *Biatora radicicola* is a very variable species. The tree in figure 1B shows that three more individuals sequenced by us are conspecific with the type of *B. radicicola* but leave its exact position within *Biatora* uncertain. Its placement within this genus was, however, already demonstrated in PRINTZEN (2014) based on a three-gene dataset. The position of *B. terrae-novae* within the *B. vernalis* group is relatively well supported (Fig. 1C) as well as its distinctness from *B. fallax* Hepp. Both species are morphologically very similar to each other (see below), but the sister group relationship between *B. fallax* and the arctic *B. cuprea* (Sommerf.) Fr. is very well supported and excludes any possiblity that *B. fallax* and *B. terrae-novae* could be regarded as conspecific.

**Table 2**: Sizes of dataset (in base pairs) before and after removal of uncertain alignment positions with GUIDANCE2.

| Data Set | ITS, complete | ITS after GUIDANCE | mrSSU, complete | mrSSU after GUIDANCE | ITS+mrSSU complete | ITS + mrSSU after GUIDANCE |
|---|---|---|---|---|---|---|
| *Biatora vernalis* group | 518 | 349 | 853 | 829 | 1371 | 1178 |
| *Biatora* species with dark apothecia | 506 | 352 | 841 | 820 | 1347 | 1173 |
| *Biatora* complete | 495 | 361 | 867 | 763 | 1362 | 1124 |

## The Species

***Biatora australis*** Rodr.Flakus & Printzen **sp. nov.** [MycoBank 817314] (Fig. 2)

**Type:** Ecuador. Prov. Chimborazo, Parque Nacional Sangay, El Altar, fragment of a *Gynoxys* forest on the crest descending E of Laguna de Collantes, elev. 4150 m, 01°40'10"S, 78°25'45"W, on bark of *Gynoxys*, 26 August 1999, Z. Palice 3711 (holotype: PRA; isotypes: FR, KRAM, and QCA).

**Description: Thallus** whitish, greyish-white to greyish-green, endosubstratal or very thin; soredia and isidia absent; **Hypothallus** not clearly developed; **Cortex** 5–25 µm high, of short-celled hyphae; **Algal layer** 40–80 µm high, interalgal hyphae mostly short-celled and forming an almost plectenchymatous matrix; **Photobiont** chlorococcoid, cells (sub)globose, 7–16 µm in diameter; **Apothecia** single or in groups of up to five, 0.2–0.55 mm in diameter, rounded or slightly deformed, sessile with constricted base; disc moderately to strongly convex (especially in old apothecia), yellowish to pale brown, epruinose, matte, margin lacking from the beginning or thin and barely prominent in young apothecia but soon excluded, paler or sometimes concolorous with disc; **Proper exciple** strongly gelatinized, laterally 20–50 µm, basally 30–65 µm wide, colourless, in major part inspersed with colourless to pale ochre crystals dissolving in KOH, composed of radiating hyphae, lumina 0.5-0.8 µm (apically up to 1 µm) wide; **Hypothecium** 40–100 µm high, colourless, of strongly gelatinized hyphae with 1–2 µm wide lumina; **Subhymenium** 10–45 µm high, colourless; **Hymenium** 40–50 µm high, colourless; **Epihymenium** 5–8 µm high, colourless or pale ochre due to an epipsamma composed of the same

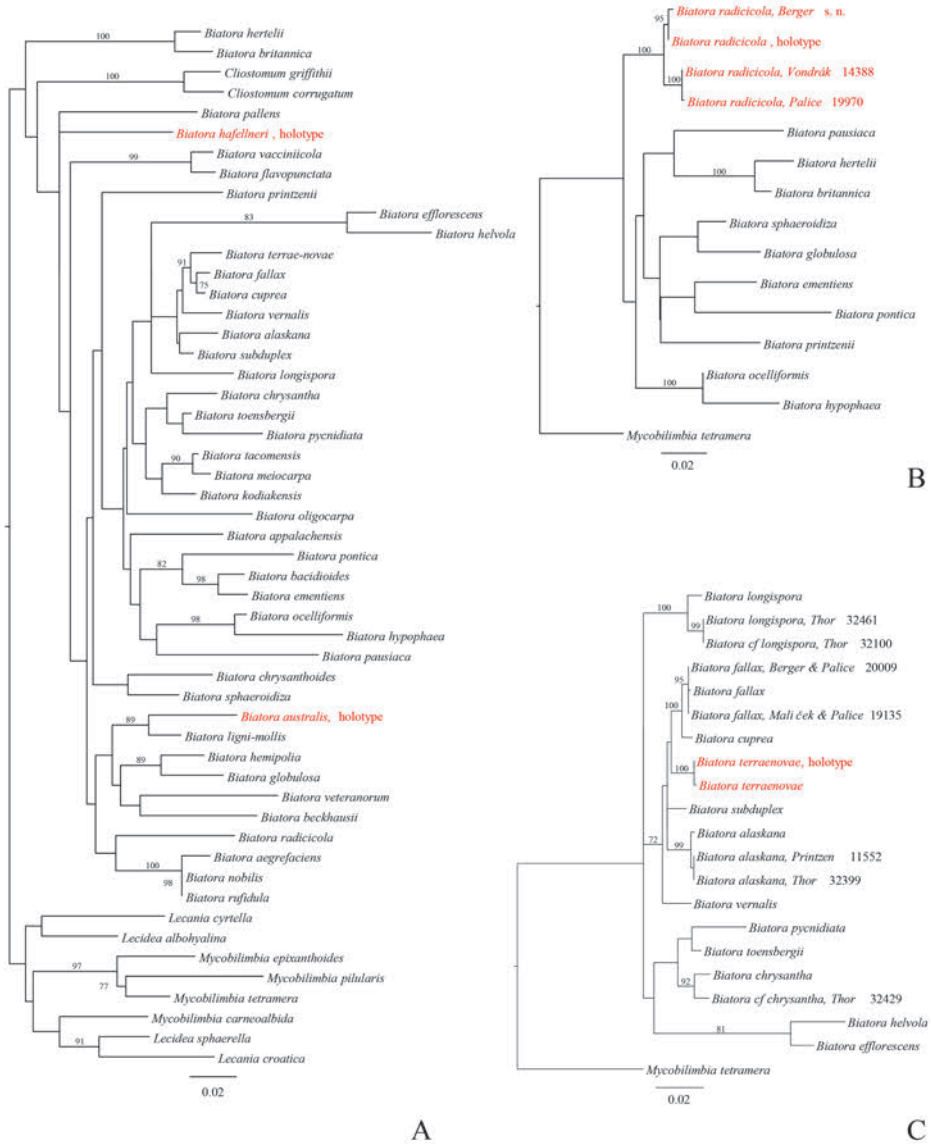


**Fig. 1**: Maximum likelihood trees. **A** – Phylogenetic positions of *Biatora australis* and *B. hafellneri*. **B** – Distinctness of *B. radicicola*. **C** – Distinct phylogenetic position of *B. terrae-novae* relative to *B. fallax*. Numbers adjacent to branches indicate bootstrap support values above 70 %.

granules as found in the exciple; **Paraphyses** simple to branched and rarely anastomosing, lumina 0.5–0.7 µm (apically 0.7–1.5 µm) wide, colourless; **Asci** of *Biatora*-type, 8-spored; **Ascospores** colourless, simple or 1-septate (rarely up to 3-septate), narrowly ellipsoid, sometimes slightly curved, (10–)13.3–15.0(–20) × (2.5–)2.9–3.6(–4.0) µm (n=60); **Pycnidia**: not seen.

**Chemistry:** Probably lobaric acid. No substances detected by TLC but apothecia (in the Ecuadorian specimen) KC+ violet.

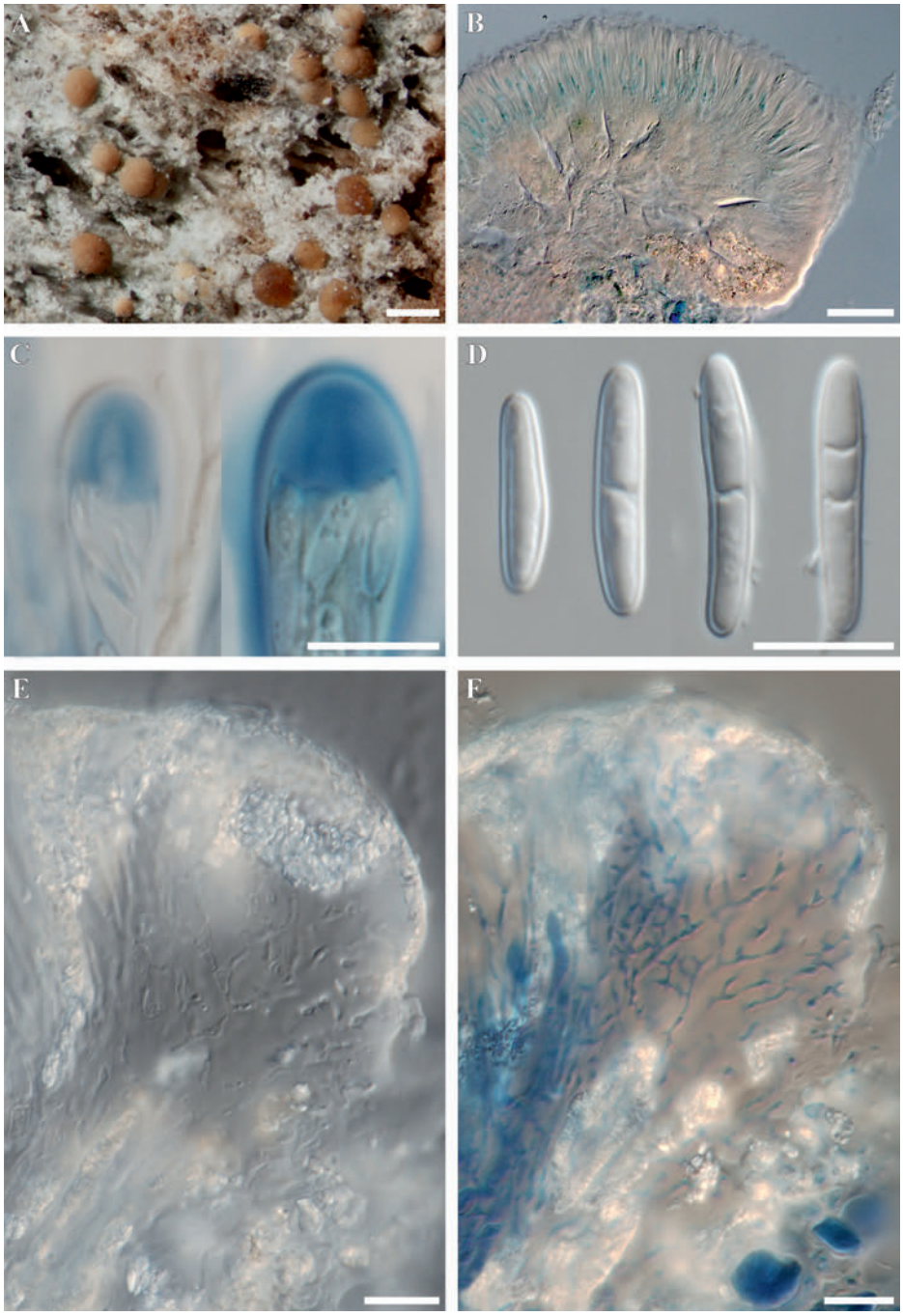


**Fig. 2**: *Biatora australis* (Rodriguez Flakus 2473 & Flakus). **A** – Thin, whitish thallus with pale, yellowish brown, emarginate apothecia. **B** – Transverse section through apothecium. **C** – Asci showing amyloid *Biatora*-like ascus apex (mounted in K/I). **D** – Ascospores. **E, F** – Sections through exciple composed of radiating, highly conglutinated hyphae and partly inspersed by crystals visible in polarized light (F mounted in LCB). – Scales: A = 0.5 mm; B = 50 µm; C– D = 10 µm; E– F = 25 µm.

**Etymology:** The specific epithet refers to the occurrence of this species in South America.

**Ecology and distribution:** *Biatora australis* is currently known from two localities in Argentina and Ecuador. Both collections grew on somewhat rotten bark, the Argentinian one in Magellanic subpolar forest, the Ecuadorian one on *Gynoxys* at 4150 m elevation. Interestingly, a similar distributional pattern is shared by the habitually and ecologically similar *Myrionora pseudocyphellariae* (Etayo) S. Ekman & Palice co-occuring at the Ecuadorian locality (Palice et al. 2013). It might be assumed that both species are more common but overlooked because of their small apothecia and immersed thallus.

**Notes:** The chemical identity of the crystals in the exciple and epihymenium are still somewhat unclear. They are reminiscent of the lobaric acid crystals in apothecia of *B. ligni-mollis*, *Myrionora albidula* (Willey) R.C.Harris, *M. pseudocyphellariae* or *Scoliciosporum pruinosum* (P.James) Vězda (see Tønsberg 1998, Palice et al. 2013) and we observed the characteristic KC+ violet reaction in the Ecuadorian collection. With its minute, strongly convex apothecia, *B. australis* resembles few other species of *Biatora*. The holotype and isotype of *B. alborufidula* (Hedl.) S.Ekman & Printzen have ascospores that are on average narrower than 3 µm and a shallower hymenium of 30–35 µm. This species also lacks crystals in the exciple and epihymenium. *Biatora troendelagica* Holien & Printzen has a sorediate thallus producing divaricatic acid and ascospores rarely exceeding 10 µm in length. *Biatora ligni-mollis* appears to be the closest relative (Fig. 1) and has been found on similar substrata (but mostly on soft, rotten wood). It has mostly larger apothecia, usually abundant emergent pycnidia, narrower ascospores, 1.8–2.8 µm wide, and produces lobaric acid.

**Additional specimen examined: Argentina**. **Tierra del Fuego,** Antártida e Islas del Atlántico Sur, Ushuahia, Tierra del Fuego National Park, near Roca Lake, Magellanic subpolar forest, elev. 25 m, 54°50'39.6"S, 68°34'23.9"W, on bark, 21 September 2012, P. Rodriguez Flakus 2473 & A. Flakus (FR).

***Biatora hafellneri*** Rodr.Flakus & Printzen **sp. nov.** [MycoBank 817315] (Fig. 3)

**Type:** Argentina. Río Negro, Bariloche, Parque Nacional Nahuel Huapi, Mascardi Lake, Valdivian temperate forest, 841 m, 41°20'32.7"S, 71°34'39.2"W, on bark, 06 October 2012, P. Rodriguez Flakus 3038 & A. Flakus (holotype: FR-0261090; isotype: BCRU).

**Description: Thallus** composed of yellowish to greyish green, irregularly globose to isidioid granules, 0.08–0.1 mm wide, that usually break into soredia; **Soralia** greyish green, not clearly delimited; **Hypothallus** greyish white, between areoles and along the margin, but not forming a clearly delimited prothallus; **Cortex** consisting of a single layer of hyphae, ca. 3 µm high; algal layer 35–75 µm high; **Photobiont** chlorococcoid, cells (sub)globose, 5–10 µm in diameter; **Apothecia** single or in groups of up to three, on average 0.4 mm (max. 0.8 mm) in diameter, rounded to slightly irregular in outline, sessile, with a weakly constricted base, disc weakly to moderately convex (in old apothecia), pale brown, orange-brown to dark brown, matte, epruinose, margin level with disc, thin and excluded with age, slightly paler or sometimes concolorous with disc, matte, proper exciple laterally 35–85 µm, basally 95–150 µm wide, colourless to yellowish orange, particularly near hymenium of strongly gelatinized, radiating hyphae with lumina 0.5–1.0 µm (apically 1–2 µm) wide; **Hypothecium** 40–125 µm high, colourless to slightly yellowish orange, of strongly gelatinized hyphae with lumina 0.5–1.0 µm wide; **Subhymenium** 20–45 µm high, colourless or slightly darker than hypothecium; **Hymenium** 65–80 µm high, colourless to pale yellowish orange; **Epihymenium** 4–10 µm high, colourless to orange-brown; **Paraphyses** simple to weakly branched (mostly near the tips) and rarely anastomosing, colourless, lumina 0.7–1.0 µm wide, apically not thickened. **Asci** of *Biatora*-type, 8-spored; **Ascospores** colourless, simple or rarely 1-septate, ellipsoid, (12.0–)15.7–16.2(–20.0) × (3.5–)5.6–5.7(–7.0) µm, length/width index (1.8–)2.8–2.9(–5.4) µm (n=30); **Pycnidia**: not seen.

**Chemistry:** No substances detected by TLC, all spot tests negative.

**Etymology:** Named in honour of Josef Hafellner for his outstanding contributions to the systematics of crustose lichens.

**Ecology and distribution:** The third species of *Biatora* reported from the Southern Hemisphere where it was collected in two localities in the Parque Nacional Nahuel Huapi in Argentina, growing on bark of trees in Valdivian temperate forest.

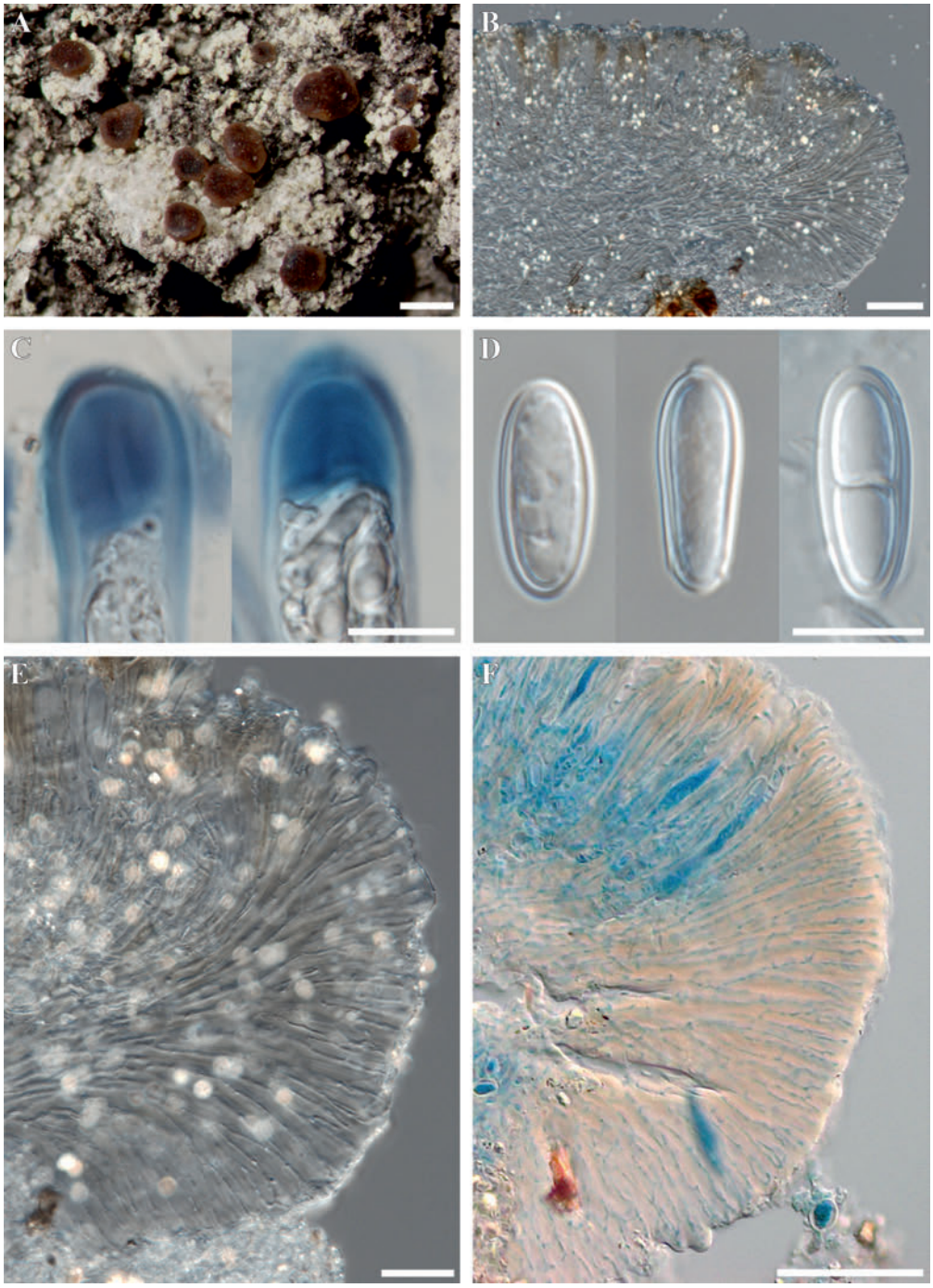


**Fig. 3**: *Biatora hafellneri* (holotype). **A** – Granular thallus with dark brown, thinly marginate apothecia. **B** – Transverse section through apothecium. **C** – Asci showing amyloid Biatora-like ascus apex (mounted in K/I). **D** – Ascospores. **E, F** – sections through exciple showing radiately arranged, highly conglutinated hyphae (F mounted in LCB). – Scales: A = 0.5 mm; B = 50 µm; C–D = 10 µm; E–F = 25 µm.

**Notes:** *Biatora hafellneri* is unlikely to be confused with other species of *Biatora*. The only other sorediate *Biatora* that does not produce secondary substances is *B. oligocarpa* Printzen & Tønsberg, which has discrete soralia of up to 0.4 mm diameter and pinkish beige apothecia. It is further distinguished by smaller ascospores of 11–15.5 ×3.5–4.5 µm and apically thickened paraphyses with lumina of up to 3 µm. Similar looking species of *Mycobilimbia* have 2–4-septate ascospores. The phylogenetic position of *B. hafellneri* within *Biatora* is so far unresolved (Fig. 1).

**Additional specimen examined: Argentina**. **Río Negro,** Bariloche, Parque Nacional Nahuel Huapi, cascada de los duendes cerca al lago Gutiérrez, Valdivian temperate forest, elev. 819 m, 41°10′46.4"S, 71°24′51.5"W, 4 October 2012, P. Rodriguez-Flakus 2701 & A. Flakus (FR).

***Biatora pacifica*** Printzen, Tønsberg & G.Thor **sp. nov.** [MycoBank 817316] (Fig. 4)

**Type:** Russia. Sakhalin province (Сахалинская область), Nevelsky district (Невельский район), Moneron island, stand of *Abies* with young growth shaded by old trees, 46°16'07.0"N, 141°14'11.8"E, elev. 150-200 m, on bark at base of old *Abies sachalinensis*, 14 July 2004, C. Printzen 9098, B. Kanz, A. Taran & S. Tchabanenko (holotype: FR-0261024; isotypes to be distributed in 'Printzen: Lichenes corticoli et lignicoli exsiccati').

**Description: Thallus** relatively thick and tartareous (resembling that of a *Pertusaria*), irregularly warted, rarely areolate; areoles 0.1–0.25 mm in diameter, matte or slightly glossy, whitish to greenish grey; soredia and isidia absent; **Hypothallus** not observed; cortex 10–35 µm high; **Algal layer** (35–)60–200 µm high, interalgal hyphae mostly short-celled and forming an almost plectenchymatous matrix; **Photobiont** chlorococcoid, cells (sub)globose, 5–13 µm in diameter; **Apothecia** usually abundant, single, more rarely forming small clusters of two to four, on average 0.42–0.80 mm (max. 0.60–1.6 mm) in diameter, rounded or quite frequently deformed and with undulate margins, broadly adnate with unconstricted or only slightly constricted base; disc flat to weakly, rarely moderately convex, dark grey or olive brown, sometimes with a bluish hue, rarely light olive, matte or somewhat glossy; margin level with disc, persistent or rarely excluded in older apothecia, lighter than disc, usually white or pale grey, matte or slightly glossy; proper exciple laterally 40–70 µm, basally 25–75 µm wide (but sometimes not extending below hymenium and appearing as a continuation of the hymenium without asci), colourless outside, sometimes olive brown within and near hymenium, of radiating hyphae with individual gelatinous sheaths that separate in squash preparations, lumina 1–2 µm, apically unthickened, gelatinous sheaths 3.5–8.0 µm wide; **Hypothecium** (0–)25–90(–140) µm high, colourless, pale olivaceous, mostly mottled blue (pontica-blue, Meyer & Printzen 2000), of strongly gelatinized hyphae with lumina 1.5–4.0 µm wide; **Subhymenium** 25–100 µm high, of same colour or slightly darker than hypothecium; **Hymenium** 35–50 µm high, pale yellow or olive green (often in vertical strips); **Epihymenium** not distinguished; **Paraphyses** simple (very few branched and anastomosing), colourless, lumina 1.0–1.5 µm (apically 1–2 µm) wide, surrounded by individual gelatinous sheaths of 2–4 µm (apically 4–6 µm) width, that often extend into the subhymenium and sometimes also separate in squash preparations; **Asci** of *Biatora*-type, with 8 ascospores; **Ascospores** often sparse, colourless [rarely dark red due to encrustation with pontica-red (!)], simple or rarely 1-septate, narrowly ellipsoid, (8.0–)9.6–12.1(–14.0) × (2.5–)3.0–3.5(–4.0) µm (n = 125); **Pycnidia**: half or entirely immersed in thallus warts, with conspicuous beige or orange-brown ostioles surrounded by a pale rim, globular or somewhat angular, 100–150(–250) µm in diameter, walls colourless to pale ochre; **Conidia** bacilliform, 5.3–8.0 × 0.5–0.7 µm.

**Chemistry:** One xanthone (major) "pacifica unknown" in Rf-classes A 6, B 6, C 6, traces of unidentified xanthones in Rf-classes A 5–6, B 6, C 5–6 detected by TLC. Apothecial tissues with pontica-blue and an unidentified olive-green pigment reacting C+ pale mauve, K+ red (particularly after pretreatment with HCl).

**Etymology:** Named because of its occurrence along the Pacific coast of East Asia.

**Ecology and distribution:** *Biatora pacifica* has been collected along the Pacific coasts of Russia, Japan and Korea. On Sakhalin and Hokkaido it appears to be a lowland species occurring in mixed coniferous forests between sea level and elevations of about 600 m. In South Korea it has been collected from 700 to about 1600 m above sea level. So far, the species has been collected on bark of *Abies*

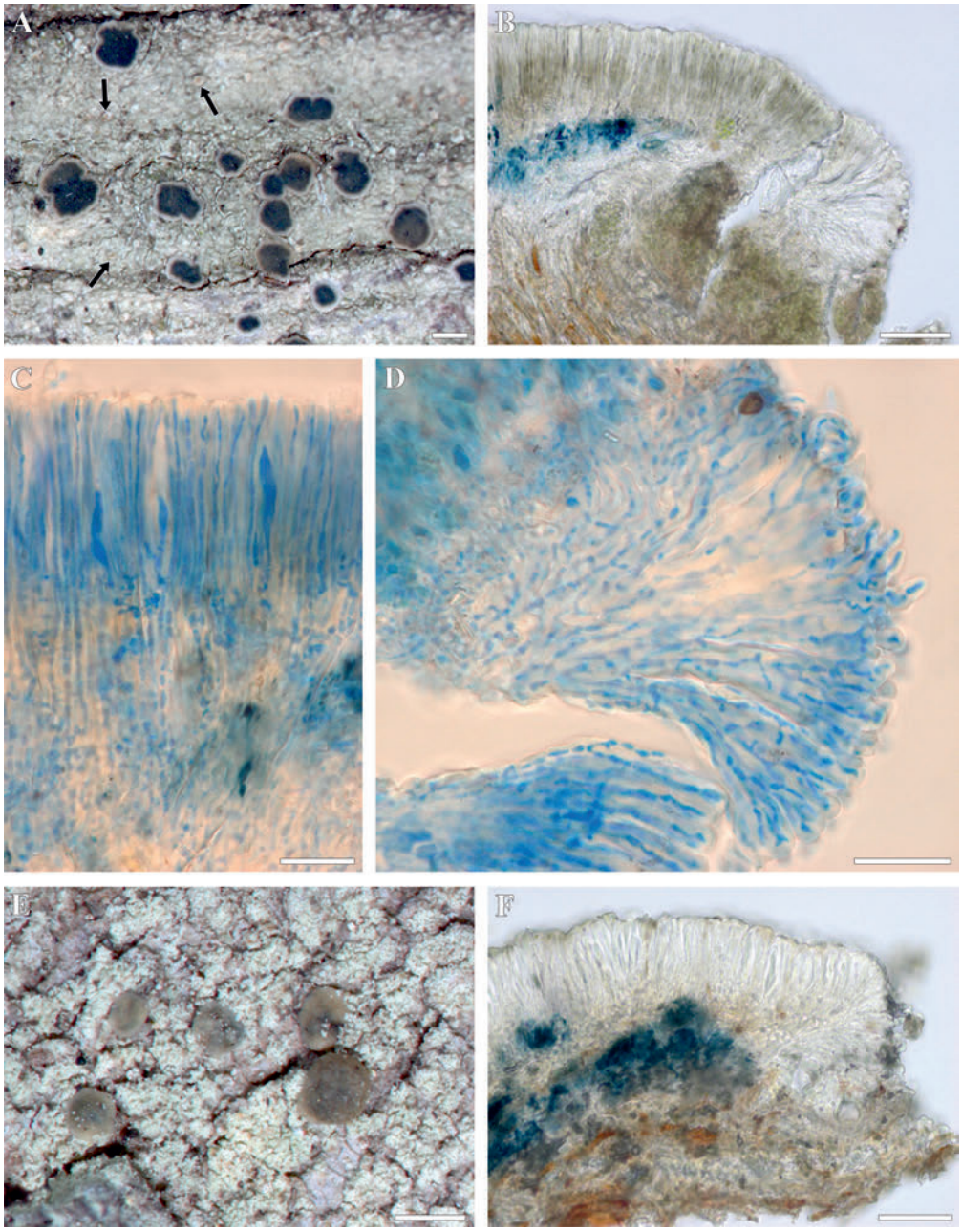


**Fig. 4**: *Biatora pacifica* (holotype, A–D) and *B. pontica* (FR-0076434, E–F). **A** – Thallus with adnate, dark grey apothecia, pycnidia indicated by arrows. **B** – Transverse section through apothecium showing ascogenous hyphae surrounded by pontica-blue. **C** – Hymenium with parallel paraphyses extending into the hypothecium. **D** – Excipular hyphae with free ends and individual gelatinous sheaths (C and D mounted in LCB). **E** – Sorediate thallus with light greyish apothecia. **F** – transverse section through apothecium showing ascogenous hyphae surrounded by pontica-blue. – Scales: A, E = 0.5 mm; B, F = 50 µm; C–D = 10 µm.

*koreana*, *A. sachalinensis*, *Acer mono*, *A. palmatum*, *Alnus* spp., *Magnolia* sp., *Quercus crispula*, *Q. dentata*, *Salix* sp. and unidentified dead deciduous trees.

**Notes:** *Biatora pacifica* resembles the recently described *Ivanpisutia oxneri* S.Y.Kondr., L.Lőkös & J.-S.Hur (Kondratyuk et al. 2015). KOLRI did not respond to a loan request so that we were unable to study type material of this species. In three collections from BP, one of them a paratype, the thallus reacted P+ red and probably contained argopsin (although the protologue of *I. oxneri* states that the species contains no secondary compounds). These collections also had smaller ascospores of (8.0–)9.8–9.9(–12.0) × (2.3–)2.7(–3.0) µm and are hence not conspecific with *B. pacifica*. *Biatora pacifica* appears to be the esorediate counterpart of *B. pontica* Printzen & Tønsberg (Fig. 4E–F) with a similar chemistry, including various unidentified xanthones and *pontica*-blue surrounding ascogenous hyphae, sometimes also clusters of algal cells, in the subhymenium and hypothecium. This hypothesis, however, awaits verification, as we were so far unable to obtain any DNA sequences from *B. pacifica*.

**Additional specimens examined (paratypes): Japan**. [**Hokkaido Prefecture,**] Hokkaido, Kitami Prov., Shari-gun, Shari-cho, Shiretoko Nat. Park, NW slope of Shiretoko Peninsula c. 10 km NE Utoro town, along the trail from Iwaobetsu hot-spring hotel (Onsen) to Mt Rausu-dake, 44.10233°N, 145.10129°E, 12 July 2010, A. Frisch 10/Jp450 (UPS); ibid., 44.1065°N, 145.09207°E, G. Thor 23672 & A. Frisch (UPS); ibid., 44.10606°N, 145.09406°E, 14 July 2010, A. Frisch 10/Jp661 (UPS); ibid., 44.10675°N, 145.09517°E, 14 July 2010, A. Frisch 10/Jp670 (UPS); ibid., 44.1065°N, 145.09207°E, 10 July 2010, G. Thor 23691 (UPS); ibid., 44.106278°N, 145.093°E, 11 July 2010, G. Thor 23911 (UPS); ibid., 44.10164°N, 145.10086°E, G. Thor 24214 (UPS); ibid., 44.10617°N, 145.09228°E, G. Thor 23742 (UPS); c. 7 km NE Utoro village, S of the small road to Iwaobetsu hot spring (Onsen), 44.10053°N, 145.06217°E, 16 July 2010, A. Frisch 10/944 (UPS); ibid., N of the small road to Iwaobetsu hot-spring hotel (Onsen), 44.11203°N, 145.08436°E, 15 June 2010, G. Thor 25039 (UPS); Rishiri-to Island, Rishiri-gun, Rishirifuji-cho, Oniwaki area, at Oniwaki mountain trail at the parking area 3 km NW of Oniwaki city and 1 km to the W, 45°09'N, 141°17'E, elev. 280–420 m, on *Salix* sp., 2 June 1995, G. Thor 13980 (UPS); Teshio Prov., Teshio-gun, Toyotomi-cho, 35 km NNW of the small town Teshio at the coast, along small road 2.5 km from the coast, 45°12'N, 141°36'E, elev. 10-20 m, on deciduous tree, 30 May 1995, G. Thor 13701 (UPS); ibid., T. Tønsberg 22218 (BG); Rishiri-Rebun-Sarobetsu National Park, 23 km NNW of the small town Teshio at the coast, Wakasakanai area, S the road from the coast to the town Toyotomi, 1 km from the coast, 45°05'N, 141°39'E, 30 May 1995, T. Tønsberg 22136 (BG); 25 km NNW of small town Teshio at coast, Wakasakanai area, 1 km N of road from coast to town Toyotomi, 800 m from coast, 45°06'N, 141°38'E, 30 May 1995, G. Thor 13659 (UPS); Tomamae-gun, Shosambetsu-mura, 15 km ENE the small town Haboro at the coast, near the road, 44°23'N, 141°53'E, 28 May 1995, G. Thor 13547 (UPS); ibid., 29 May 1995, T. Tønsberg 22058 (BG); Rumoi-gun, Obira-cho, 25 km ENE the small town Obira at the coast, Kawakami area, 44°06'N, 141°58'E, 28 May 1995, T. Tønsberg 22038a (BG); 21 km ENE of the small town Obira at the coast along the E (and upper) trail from the parking area to Tengunotaki Water Fall, 44°04N, 141°55' E, 28 May 1995, G. Thor 13491 (UPS). – **Russia**. **Sakhalin province (**Сахалинская область**),** Nevelsky district (Невельский район), Moneron Island (SW of Sakhalin island), 46°15'36.6"N, 141°14'54.3"E, 13 July 2004, C. Printzen 8973, 8996 (FR); ibid.; 46°16'07.0"N, 141°14'11.8"E, 14 July 2004, C. Printzen 9075 (FR). – **South Korea**. **Gangwon-do,** Yangyang-gun, Ser-myun, Osaeck-ri, the southern part of the massif Sorak Mts, Sorak-san National Park, the south slope of Mt. Dachong, along the trail from the shelter c. 500 m WNW the top of Mt. Dachong to the village at Hangyeryong Pass, c. 1-3 km SW the shelter, 38°07.10'–06.45'N, 128°27.25'–26.00'E, 20 October 2006, G. Thor 20389 (UPS); **Jeju-do,** Cheju Island, along Eorimok trail on the NW slope of Mt Halla, from the timberline below the Witsae Oreum Shelter to the Eorimok Nat. Park Office, 33.38333°N, 126.51667°E, 24 May 2001, G. Thor 17168 (UPS).

***Biatora radicicola*** Printzen, Palice & J.P.Halda **sp. nov.** [MycoBank 817317] (Fig. 5)

**Type:** Czech Republic. Bohemia, Nové Město n. Metují, ad merid. a pago Peklo versus (2 km), ad ripam fluminis Metuje (dextra ripa), 50°22'08.05"N, 16°11'05.27"E, elev. 361 m, ad corticem radicis (*Carpinus betulus*), 21 April 2000, Josef P. Halda 4104 (holotype: FR-0261019; isotype: hb. Halda).

**Description: Thallus** crustose, effuse, irregularly cracked, surface usually smooth but sometimes with minute warts (reminiscent of goose pimples), dull green grey to olive green, sometimes with beige or ochre specks; soredia and isidia absent; **Hypothallus** not observed; cortex 5–25 µm high, of short-celled hyphae; algal layer 40–80 µm high, interalgal hyphae mostly short-celled and forming an almost plectenchymatous matrix; **Photobiont** chlorococcoid, cells (sub)globose, 5–12 µm in diameter; **Apothecia** usually abundant, single, more rarely forming small clusters of two to five, on average 0.23–0.39 mm, max. 0.8 mm in diameter, rounded or slightly deformed, broadly adnate or

sessile with slightly constricted base; disc flat, rarely slightly convex in older apothecia, black, rarely dark blue-grey or a piebald mixture of olive, grey and beige hues, matte or rarely with a velvety gloss; margin weakly prominent in young apothecia, persistent or rarely excluded in older ones, black, usually weakly glossy; proper exciple well developed and gelatinized, laterally 25–55 µm, basally 40–70 µm wide, pigmentation very variable with turquoise cinereorufa-green (K+ lighter green, N+ violaceous) and an uncharacterized brown pigment in varying concentrations, usually in more or less periclinal stripes interrupted by unpigmented areas (Fig. 4), turquoise pigmentation usually darker near hymenium, brown pigmentation usually concentrated around the border between exciple and hypothecium or hymenium, turning olive where both pigments mix, in extreme cases exciple almost entirely black but for a slightly lighter zone stretching from the hypothecium into the center of the exciple, composed of radiating, branched and anastomosing hyphae, lumina 1–2 µm (apically 1–3 µm) wide; **Hypothecium** 35–110 µm high, colourless or with a faint greyish haze, of strongly gelatinized hyphae with lumina 1–2 µm wide; **Subhymenium**: 25–45 µm high, colourless or more often with a greyish brown or greenish grey central layer; hymenium (30–)40–50(–60) µm high, colourless or pale emerald to olive green, particularly near the base, sometimes (in well-lit sites?) with unevenly distributed tiny turquoise crystals or their aggregates, ca 0.3–1.0(–3.0) µm; **Epihymenium** 5–10 µm high, with amorphous pale olive to almost black pigment and/or turquoise pigment granules in irregular patches, very rarely colourless; **Paraphyses** mostly simple, a few branched and anastomosing, lumina 0.7–1.0 µm (apically 1–2) µm wide, unpigmented or rarely with darker gelatinous sheaths near the apices; **Asci** of *Biatora*-type, with 8 ascospores; **Ascospores** colourless, simple or rarely 1-septate, narrowly ellipsoid, (6.0–)8.3–10.4(–13.5) × (2.5–)2.9–3.5(–4.3) µm (n=59); **Pycnidia** not observed.

**Chemistry:** No secondary metabolites detected by TLC. Apothecial tissues with cinereorufa-green (MEYER & PRINTZEN 2000) and an unidentified brownish pigment.

**Etymology:** Named for its preferred substratum, tree roots.

**Ecology and distribution:** So far, *B. radicicola* is only known from a few localities in Central Europe and two single collections from Finland and the Caucasus. The species is confined to sheltered and humid microhabitats, usually growing at the very bases of trees, most frequently on exposed roots, sometimes below overhangs (along river banks). Most specimens come from woodlands along smaller rivers or rivulets in the submontane belt (Fig. 5E). Here, *B. radicicola* may tolerate short-term flooding and at least in some cases specimens were subjected to occasional water spraying. Specimens from these habitats are usually not accompanied by other lichens and, except for the type specimen, are generally not well developed. Besides this, the species was also found in well-lit montane forests dominated by beech and with rather specific ecological conditions. The stand in Moravia consisted of dwarfed and 'L'-shaped trees on a steep slope due to frequent avalanches. The locality in the eastern Carpathians was situated at the transition between an old-growth beech forest and 'Polonina' grassland along a secondarily lowered timberline and influenced by occasional cattle-grazing. The locality in the Caucasus is a mixed humid high-montane primeval forest of *Abies nordmanniana*, *Fagus orientalis* and *Acer trautvetteri*. In montane habitats the prolonged snow cover is likely one of the chief determinants for the occurrence of this taxon. Unlike most other species of *Biatora*, *B. radicidola* appears to be a slightly nitrophytic or at least nitrogen-tolerant species. The shade-tolerant and acidophytic *Coenogonium pineti* (Ach.) Lücking & Lumbsch as well as the nitrophytic *Candelariella efflorescens* R.C.Harris & W.R.Buck and *Physcia dubia* (Hoffm.) Lettau were recorded as associated lichens in Ukrainian collections. The 'lowland' habitats along rivers are periodically enriched by alluvial nutrients. The species is shade-tolerant but in the Carpathians it was also growing in relatively well-lit sites. Specimens from these habitats are much better developed, with more intensely pigmented apothecia and thicker and paler thalli. *Biatora radicicola* may be overlooked in many localities because of its highly specific ecology and its superficial similarity with a poorly developed *Lecidella* (Fig. 5A). As a niche specialist, it is implicitly a rare species. Moreover, its typical habitat, the lower sections of small streams, are endangered by human activities such as water regulation. The new species should be classified in national Red Lists.

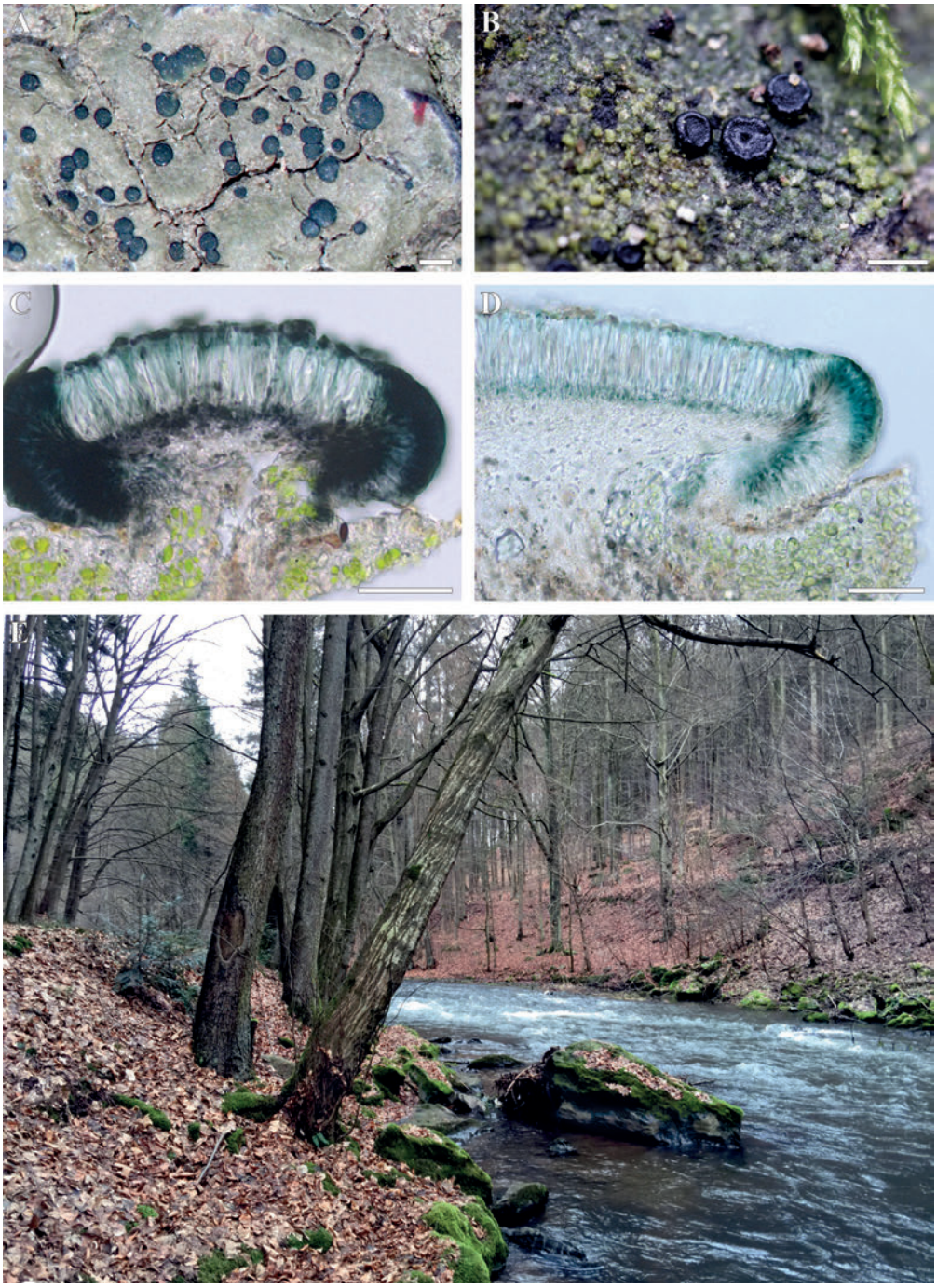


**Fig. 5**: *Biatora radicicola*. **A** – Smooth thallus with black apothecia (holotype). **B** – Thallus and apothecia under natural conditions at the type locality. **C, D** – Transverse sections through apothecia showing variable pigmentation (C, Vondrák 14142; D, holotype). **E** – Type locality. – Scales: A–B = 0.5 mm; C–D = 50 µm.

**Notes:** "*Biatora radicicola*" was already used as a provisional name in the phylogenetic analysis by PRINTZEN (2014) in which the species occupied an isolated and unsupported position between the *ocelliformis*-group and a clade combining the *hertelii*- and *vernalis*-groups. Accordingly, its relationships within the genus are so far unresolved. Morphologically, the vivid pigmentation of the exciple and the marginate, black apothecia remind of a *Bacidia* or *Lecidella*, but asci of the *Biatora*-type, narrowly ellipsoid, mostly non-septate ascospores, and strongly conglutinate paraphyses serve to distinguish *B. radicicola* from members of these genera. Most *Biatora*-species with dark apothecia are either sorediate (*B. britannica* Printzen, Lumbsch & Orange, *B. pontica*) or contain argopsin or xanthones [*B. hertelii* Printzen & Etayo, *B. hypophaea* Printzen & Tønsberg, *B. pacifica*, *B. ocelliformis* (Nyl.) Arnold, *B. sphaeroidiza* (Vain.) Holien & Printzen]. *Biatora bacidioides* Printzen & Tønsberg and *B. beckhausii* (Körb.) Tuck. can be distinguished by their multiseptate, bacilliform or filiform ascospores. The most similar species seems to be *B. globulosa* (Flörke) Fr., which however has a shallower hymenium that rarely exceeds 30 µm in height, narrower ascospores (2.0–3.0 µm) and less vividly pigmented apothecial tissues (mostly only blackish-green epihymenium and outer layer of the exciple). The apothecia of both species are similar in size, but in *B. globulosa* the margin is soon excluded.

**Additional specimens examined (paratypes): Czech Republic**. **North Moravia,** Jeseníky Mts, Malá kotlina corrie, rather steep-sloped remnant of beech forest with some *Acer pseudoplatanus* and *Picea abies*, elev. ca 1150 m, on bark of a dwarf *Fagus sylvatica*, 22 September 2001, Z. Palice 1227 (PRA); **E Bohemia,** Orlické hory Mts., Klášterec n. Orl., near the [river] Divoká Orlice, elev. 500-550 m, on exposed root of *Acer pseudoplatanus* near the water, 20 April 1996, Z. Palice s. n. (PRA); Orlické hory Mts, nature reserve "Zemská brána", at river bank of the [river] Divoká Orlice, elev. ca. 500 m, on exposed, periodically inundated roots of *Picea* in boulder underhang, 9 March 1997, Z. Palice s. n. (PRA); ibid., elev. 550 m, on base of *Acer pseudoplatanus*, 9 March 1997, Z. Palice s. n. (PRA). – **Finland**. [**Northern Ostrobothnia,**] Kuusamo, Kuusamo par., Oulanka National Park, ca 10 km WNW of Oulangan biological station, Maaninkajoki brook (a left hand side tributary of Aventojoki river), 66°24'25"N, 29°07'30"E, elev. 200 m, at the very base of *Salix* at brook-bank periodically inundated, 29 August 1997, Z. Palice 1289 (PRA). – **Ukraine**. [**Zakarpattia Oblast,**] Eastern Carpathians, Khust, Velika Uholka, beech forest at artificial treeline on a ridge 2 km SSW-SW of Mt Menchul, 48.297948°N, 23.666583°E, elev. 1200–1215 m, on bark at base of *Fagus sylvatica*, 17 May 2015, F. Berger 29335, J. Malíček 8266, Z. Palice 19631, 19970 & J. Vondrák 14142, 14387 (hb. Berger, Malíček, PRA); ibid., beech forest at artificial tree line on SE slope of Mt Menchul [1501 m], 48°17'48"N, 23°42'15"E, elev. 1220 m, on bark of *Fagus*, 12 May 2015, J. Vondrák 14388 (PRA). – **Russia**. **Republic of Adygea,** Caucasus, ca. 6.5 km S of Guzeripl' village, Mt. Abago [2628], montane mixed primeval forest at NW-facing slope of point 1778, 43°56'10"N, 40°08'48.4"E, elev. 1720 m, on bark at foot of *Fagus orientalis*, 12 June 2016, Z. Palice 21105 (PRA, FR, LE, BG).

***Biatora terrae-novae*** Printzen & J.W.McCarthy **sp. nov.** [MycoBank 817318] (Fig. 6)

**Type:** Canada. Newfoundland and Labrador, Newfoundland, Port-au-Port Peninsula, between Cape St. George and Mainland, route 460, Route de mon grand-père Trail, 48.52544°N, 59.21586°W, elev. 204 m, mature *Abies balsamea-Picea glauca*-feathermoss stand near stream through limestone ravine, on moss at base of *Abies balsamea* stem, 21 May 2013, J. McCarthy 2361 (holotype: FR-0261091; isotype: CANL).

**Description: Thallus** granular-warted, areoles more or less isodiametric and moderately convex to semiglobose, surface light green or greenish grey, turning beige in the herbarium, matte; soredia and isidia absent; **Hypothallus** whitish, between areoles and at thallus margin; cortex 10–30 µm high, of short-celled hyphae; algal layer 30–120 µm high; **Photobiont** chlorococcoid, cells (sub)globose, 6–10 µm in diameter; **Apothecia**: abundant, single or in clusters of two to five, on average 0.53–0.57 mm, max. 0.8 mm in diameter, rounded or slightly deformed, sessile with a strongly constricted base; disc weakly to strongly convex (older apothecia almost globose), ochre to reddish brown, matte or rarely with a velvety gloss; margin level with disc or weakly prominent in very young apothecia, soon excluded, whitish or slightly lighter than disc, not or weakly glossy; proper exciple well developed and gelatinized, laterally (25–)65–95 µm, basally 120–300 µm wide, colourless or faintly yellowish, composed of radiating, poorly branched and anastomosing hyphae with cylindrical 1.0–1.5(–3.0) µm (apically 1.0–3.0 µm) wide lumina; **Hypothecium** (85–)150–350 µm high, colourless or faintly yellowish, of strongly gelatinized hyphae with 1–4 µm wide lumina; **Subhymenium** 70–95 µm high, colourless or faintly yellowish; **Hymenium** 50–65 µm high, colourless; **Epihymenium** not distinguished; **Paraphyses** simple, rarely weakly branched and anastomosing, unpigmented, lumina 0.7–1.5 µm

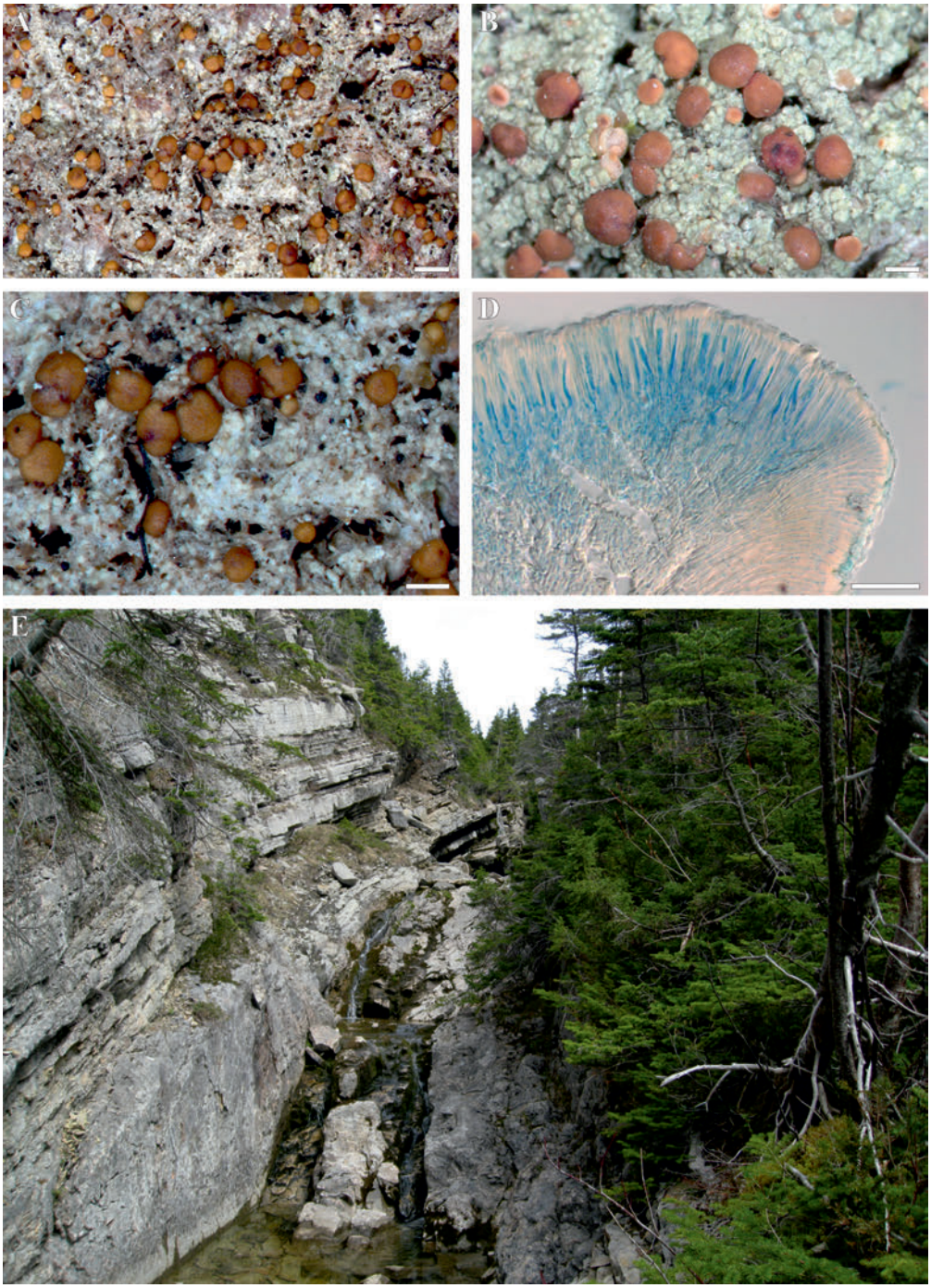


**Fig. 6**: *Biatora terrae-novae*. **A–C** – Thallus with strongly convex apothecia (A, C = Printzen 5758; B = holotype). **D**– Transverse sections through apothecium mounted in LCB. **E** – Type locality. – Scales: A = 1 mm; B–C = 0.5 mm; D = 50 µm.

wide, apically (1.0–)1.5–3.0 µm wide; **Asci** of *Biatora*-type, with 8 ascospores; **Ascospores** colourless, simple or rarely 1-septate, narrowly ellipsoid, (7.0–)10.5–13.6(–17.0) × (3.0–)3.9–4.0(–4.5) µm (n=35); **Pycnidia** not observed.

**Chemistry:** Argopsin (major), ± norargopsin (minor).

**Etymology:** The species is so far only known from Newfoundland.

**Ecology and Distribution:** So far, *Biatora terrae-novae* has only been collected on bark of *Abies* and *Picea* in lowland coniferous forests in Newfoundland.

**Notes:** With its light green thallus and its relatively large, ochre to orange-brown apothecia with a constricted base, *Biatora terrae-novae* looks like a typical member of the *Biatora vernalis* group and closely resembles *B. vernalis* (L.) Fr. in the field. It can be distinguished from this species, *B. subduplex* (Nyl.) Printzen and *B. alaskana* Printzen & Tønsberg by the P+ red thallus (argopsin). Argopsin is also produced by the morphologically similar *B. fallax*, which is distinguished by the additional production of gyrophoric acid and more finely dissected and sometimes sorediate thallus areoles. The chemically and morphologically similar *B. pycnidiata* Printzen & Tønsberg, the most common species of *Biatora* in Newfoundland, has flatter and more adnate apothecia, a thinner thallus of 50–100 µm and usually produces lots of conspicuous pycnidia with gaping ostioles. Although the morphological and chemical differences among *B. fallax*, *B. pycnidiata* and *B. terrae-novae* are extremely small, the phylogenetic tree in PRINTZEN (2014) and the one in Fig. 1 show that *B. pycnidiata* is only remotely related to the other two species. The closest relative of *B. fallax* is *B. cuprea* that only occurs in arctic habitats and forms areolate, white and very firm crusts over detritus and bryophytes.

**Additional specimens examined (paratypes): Canada**. **Newfoundland and Labrador,** Newfoundland, Burin Peninsula, Fortune Bay-Hermitage District, 3.5 km N of English Harbour East, S of Rd between Grand Le Pierre and English Harbour East, 47°39.90'N, 54°52.56'W, elev. 100–150 m, 5 October 2000, C. Printzen 5758 (BG); Cook's Brook, 9 September 1897, A. Waghorne 836 (M).

**Table 3**: Differences between *Biatora terrae-novae*, *B. fallax* and *B. pycnidiata*.

| Species | Spores size | Thallus height | Pycnidia | Exciple | Hymenium | Hypothecium + subhymenium | Chemistry |
|---|---|---|---|---|---|---|---|
| *B. terrae-novae* | (7.0–)10.6–13.6(–17.0) × (3.0–)3.9–4.0(–4.5) | (125–)150–175 µm | not seen | laterally 25-95, basally 120-300 µm | 50–55(–65) µm | 250–320–440 | argopsin |
| *B. fallax* | (8.5–)10.8–13.9(–19.5) × (3.0–)3.7–4.5(–5.5) µm | 200–400 µm | not seen | laterally 35-90, basally 100-280 µm | 40–55 µm | 200–250–350 | argopsin, gyrophoric acid |
| *B. pycnidiata* | (8.5–)12.1–15.6(–19.0) × (3.0–)3.6–4.4(–5.5) µm | 50–100 µm (sometimes endosubstratal) | frequent, with gaping ostiole | laterally 35-95, basally 30-150 µm | 40–55 µm | 70–170–320 | argopsin |

## Key to species of the *Biatora vernalis* group

**1** Thallus sorediate ..... **2**

**1*** Thallus esorediate ..... **5**

**2** Thallus of minute, densely crowded squamules, mostly vivid to dark green in fresh collections, mostly esorediate; soredia, if present, scattered and poorly delimited ..... ***B. fallax***

**2*** Thallus not as above, thin and not subsquamulose, with punctiform soralia or sorediate in most parts ..... **3**

**3** Thallus and soralia P+ red, C-, containing argopsin..... ***B. efflorescens***

**3*** Thallus and soralia P-, C+ pink, with gyrophoric acid, argopsin absent ..... **4**

**4** Apothecia in section C+ pink; ascospores (mean of 10) 9.3–10.7 × 3.2–3.3 µm; Norway and Pacific Northwest of North America ..... ***B. chrysanthoides***

**4*** Apothecia in section C-; ascospores (mean of 10) 11.9–15.6 × 3.8–5.9 µm; widely distributed ..... ***B. chrysantha***

**5** On mosses, soil or detritus ..... **6**
**5*** On bark or rotten wood of shrubs and trees ..... **8**

**6** Thallus greenish grey; in boreal and temperate forests and woodlands; mostly on bryophytes, rarely directly on bark ..... ***B. vernalis***
**6*** Thallus whitish grey; in arctic-alpine habitats, rarely descending into the subalpine zone ..... **7**

**7** Thallus P+ red, containing argopsin ..... ***B. cuprea***
**7*** Thallus P-, argopsin absent ..... ***B. subduplex***

**8** Ascospores mostly simple, but 3- to 5-septate ones frequently intermixed, (16.5–)20.9–24.9(–29.5) × (4.0–)4.8–5.8(–6.5) µm..... ***B. alaskana***
**8*** Ascospores simple to 1-septate, smaller ..... **9**

**9** Thallus P+ red, containing argopsin ..... **10**
**9*** Thallus P-, argopsin absent ..... **13**

**10** Thallus of minute, densely crowded squamules, mostly higher than 100 µm, vivid to dark green in fresh collections; apothecia usually strongly convex ..... **11**
**10*** Thallus rimose, up to 100 µm thick, usually some shade of white or grey; apothecia weakly to moderately convex ..... **12**

**11** Thallus C+ pink (reaction can be very faint), with gyrophoric acid; uncommon but widespread; on rotten bark and wood in *Picea abies* forests ..... ***B. fallax***
**11*** Thallus C-, gyrophoric acid absent; so far only known from Newfoundland; on healthy bark, sometimes overgrowing bryophytes ..... ***B. terrae-novae***

**12** Thallus usually with numerous, conspicuous semi-immersed pycnidia; conidia 6–8(–10) µm long; eastern North America ..... ***B. pycnidiata***
**12*** Thallus usually without pycnidia; conidia, if present 7.5–10 µm long; western North America and Norway ..... ***B. toensbergii***

**13** Ascospores (mean of 10) 16.5–21.6 × 3.5–4.1 µm, 3.5–7 times as long as broad; apothecial sections C- ..... ***B. longispora***
**13*** Ascospores (mean of 10) 10.2–14.2 × 3.4–4.5 µm, 2–4.5 times as long as broad; apothecial sections C+ pink ..... ***B. helvola***

## Key to species of *Biatora* with aseptate or 1-septate spores and blue or green apothecial pigments

**1** Thallus sorediate ..... **2**
**1*** Thallus esorediate ..... **4**

**2** Thallus and soredia P-; apothecia, if present, with blue and red, K+ purple pigments in the subhymenium ..... ***B. pontica***
**2*** Thallus and soredia P+ red; pigments in apothecial sections not reacting K+ purple..... **3**

**3** Soralia 0.4–0.85 mm in diameter, strongly convex, C+ pink, with gyrophoric acid and argopsin; apothecia greyish ochre, without blue tinge; ascospores 2.5–3.5 µm wide; Great Smoky Mountains ***B. printzenii***
**3*** Soralia 0.15–0.30 mm in diameter, usually level with thallus, C-, containing only argopsin; apothecia bluish grey; ascospores 3.0–4.5 µm wide; British Isles ..... ***B. britannica***

**4** On bryophytes and detritus in the Arctic ..... ***B. ementiens***
**4*** On bark of trees and shrubs in boreal and temperate regions..... **5**

5 Thallus and apothecial sections C+ orange, containing thiophanic acid and asemone ... ***B. sphaeroidiza***
**5*** Thallus C- ..... **6**

**6** Thallus P+ red, containing argopsin ..... **7**
**6*** Thallus P-, containing either xanthones or no secondary metabolites ..... **10**

**7** Hymenium N+ orange to reddish, after pretreatment with K violaceous in HCl; hymenium 45–60 µm high; only known from laurisilva on Madeira ..... ***B. hertelii***

**7*** Hymenium N+ violaceous, red or purple, blue in HCl (after pretreatment with K); hymenium 30–45 µm high, widespread in the boreal forest zone ..... **8**

**8** Ascospores (mean of 10) up to 3 µm wide ..... ***Ivanpisutia oxneri***
**8*** Ascospores (mean of 10) 3 or more µm wide ..... **9**

**9** Subhymenium with a brown pigment ..... ***B. hypophaea***
**9*** Subhymenium lacking brown pigment (but hypothecium sometimes appearing dark due to air bubbles!) ..... ***B. ocelliformis***

**10** Epihymenium, hymenium and/or exciple with dark green, turquoise or nearly black pigmentation, N+ violaceous (cinereorufa-green) ..... **11**
**10*** Epihymenium, hymenium and/or exciple with olivaceous or dull green pigmentation, not turning violaceous in N ..... **12**

**11** Ascospores 2–3 µm wide; exciple colourless within ..... ***B. globulosa***
**11*** Ascospores wider; exciple green, turquoise or nearly black within ..... ***B. radicicola***

**12** Ascospores 2.8–4.0 µm wide; subhymenium with specks of pontica-blue; a range of unknown substances (xanthones?) detected by TLC ..... ***B. pacifica***
**12*** Ascospores 3.5–6.5 µm wide; subhymenium without specks of pontica-blue; no substances detected by TLC ..... ***B. pausiaca***

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