

doi.org/10.3114/fuse.2018.02.09

## A preliminary overview of the corticioid *Atractiellomyces* (*Pucciniomycotina*, *Basidiomycetes*)

V. Spirin<sup>1,2,\*</sup>, V. Malysheva<sup>3</sup>, G. Trichies<sup>4</sup>, A. Savchenko<sup>5</sup>, K. Pöldmaa<sup>5</sup>, J. Nordén<sup>6</sup>, O. Miettinen<sup>1</sup>, K.-H. Larsson<sup>2</sup>

<sup>1</sup>Botany Unit (Mycology), Finnish Museum of Natural History, P.O. Box 7, FI-00014 University of Helsinki, Finland

<sup>2</sup>Natural History Museum, University of Oslo, P.O. Box 1172, Blindern, 0318 Oslo, Norway

<sup>3</sup>Komarov Botanical Institute, Russian Academy of Sciences, Prof. Popova str. 2, 197376 St. Petersburg, Russia

<sup>4</sup>5, Empasse des Écoles, F-57700 Neufchef, France

<sup>5</sup>Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, EE-51005 Tartu, Estonia

<sup>6</sup>Norwegian Institute for Nature Research, Gaustadalléen 21, 0349 Oslo, Norway

\*Corresponding author: viacheslav.spirin@helsinki.fi

### Key words:

corticioid species  
phylogeny  
rust fungi  
taxonomy

**Abstract:** The taxonomy of the corticioid fungi from the class *Atractiellomyces* (*Pucciniomycotina*, *Basidiomycetes*) currently addressed to the genus *Helicogloea*, is revised based on morphological and nuclear ribosomal DNA (ITS and LSU) data. The genus is restricted to 25 species with semitranslucent, gelatinous basidiocarps lacking differentiated cystidia and clamps on hyphae, of which 11 are described as new to science. The asexual genus *Leucogloea* is placed as a synonym of *Helicogloea s. str.* Since the type species of *Saccoblastia*, *S. ovispora*, is combined to *Helicogloea*, a new genus, *Saccosoma*, is introduced to encompass *Saccoblastia farinacea* and six related species, one of which is described as new. In contrast to *Helicogloea* in the strict sense, the basidiocarps of *Saccosoma* are arid, not gelatinized, and hyphae are clamped. The third lineage of the corticioid *Atractiellomyces* is represented by the *Bourdotigloea vestita* complex. Species of *Bourdotigloea* are devoid of clamps but often possess well-differentiated cystidia, as well as long, cylindrical-fusiform basidiospores. *Bourdotigloea* encompasses nine species, of which six are described here as new.

Published online: 23 October 2018.

## INTRODUCTION

The *Atractiellomyces* is a class among the rust fungi (*Pucciniomycotina*), with about 50 species (Aime *et al.* 2014, Toome-Heller 2016). The presence of saccate probasidia and unique ultrastructural elements (attractosomes), as well as absence of a yeast stage are the main diagnostic features of this group. The *Atractiellomyces* encompasses representatives with pycnidoid (*Basidiopycnis*, *Basidiopycnides*), gasteroid (*Atractiella*, *Phleogena*) and corticioid (*Helicogloea*, *Saccoblastia*) fructifications, as well as a number of asexual taxa (*Hobsonia*, *Infundibura*, *Leucogloea*, *Proceropycnis*) (Bauer *et al.* 2006, Oberwinkler *et al.* 2006, Aime *et al.* 2014, 2018). For now, most of them are considered saprotrophic, inhabiting plant remnants or beetle galleries in decaying wood (Bauer *et al.* 2006, Oberwinkler *et al.* 2006), with a few taxa detected in orchid mycorrhiza (Kottke *et al.* 2010) or associated with tree roots (Bonito *et al.* 2017). However, the genus- and species-level taxonomy of the class remains extremely poorly resolved, and DNA data available in public repositories are fragmentary. In this paper, we revise the taxonomy of the *Atractiellomyces* species producing effused, crust-like (corticioid) basidiocarps currently addressed to the genus *Helicogloea s. lat.*, using morphological and DNA methods.

The genus *Helicogloea* was described by Patouillard (in Patouillard & Lagerheim 1892) with a single species, *H. lagerheimii*, based on Lagerheim's collection from Ecuador. In the protologue, Patouillard compared the new genus with

*Platygloea* and *Helicobasidium*; however, he overlooked saccate probasidia characteristic for this species and the genus as a whole. This seems to have been a reason to abandon *Helicogloea* in favour of *Saccoblastia*, another genus described three years later from Brazil (Möller 1895). Möller introduced his genus for two new species, *S. ovispora* and *S. sphaerospora*, with excellent descriptions and illustrations of basidial morphology. He emphasized the importance of saccate probasidia as the main generic feature. Four new species were added to *Saccoblastia* by Bourdot & Galzin (1909), Coker (1928) and Linder (1929). Bourdot & Galzin (1928) assumed that Möller's generic description refers to species with floccose basidiocarps, and therefore separated *Saccoblastia sebacea*, having gelatinous fructifications, to a newly introduced section *Saccogloea*.

Baker's study (1936) was a crucial moment in the taxonomic history of the genus. She conducted cytological investigations of all species then addressed to *Saccoblastia* and showed that they all are microscopically similar. Baker studied the original specimen of *H. lagerheimii*, the type species of *Helicogloea*, and proved that it possesses saccate probasidia. Therefore, the genus name *Saccoblastia* was replaced by the older epithet *Helicogloea*. Donk (1966) raised objections to such a wide genus concept and proposed to limit *Helicogloea* to gelatinous species only (i.e. section *Saccogloea*) while species with floccose, non-hygroscopic basidiocarps were retained in *Saccoblastia*. Donk's arguments were accepted by Jülich (1976), Wojewoda (1982) and Kisimova-Horovitz *et al.* (2000). Phylogenetic studies by Aime *et al.* (2006) and Bauer *et al.* (2006) demonstrated that

*Helicogloea* and *Saccoblastia* sensu Donk are not congeneric and belong to different lineages within *Atractiellomycetes*. In the latter study, *Platygloea vestita* was detected as closely related to *Saccoblastia*. Finally, Aime et al. (2018) introduced two new monotypic genera, *Neogloea* (typified with *Helicogloea variabilis*) and *Bourdotigloea* (typified with *P. vestita*).

Here we reinstate *Helicogloea* s. str. with 25 accepted species closely related to the type species, *H. lagerheimii*, and describe 11 of them as new. Identity of the generic type of *Saccoblastia*, *S. ovispora*, is clarified, and this species is transferred to *Helicogloea* s. str. As a consequence, a new genus, *Saccosoma*, is introduced to encompass *Saccoblastia* sensu Donk, i.e. species with arid basidiocarps. Identity of *Bourdotigloea vestita* and eight related species is discussed, and six of them are described as new to science.

## MATERIAL AND METHODS

### Specimens

Types and specimens from fungaria H, O, LE, TU, TAAM, CWU, PC, HBG, K, C, S, NY, CFMR, BPI, FH, TENN, TRH, PDD, as well as from private collections of Gérard Trichies (GT), Nicolas Küffer (NK) and Ilya Viner (IV), were studied. Microscopic routine follows Miettinen et al. (2018). All measurements and line drawings were made from microscopic slides prepared in Cotton Blue, using oil immersion and phase contrast illumination ( $\times 1250$  magnification). In almost all cases, 20 subhymenial and 20 subicular (if differentiated) hyphae, 20 basidia and 30 basidiospores per specimen were measured. For presenting basidiospore and basidial measurements, 5 % extreme values from both ends of variation are given in parentheses. For hyphal diameter measurements, the 20 % tails are put in parentheses. The following abbreviations are used in descriptions below: L – mean basidiospore length, W – mean basidiospore width, Q' – length / width ratio, Q – mean length / width ratio.

*Specimens examined (sequenced collections are marked by an asterisk):*

- Bourdotigloea cerea*. **Norway**, Oppland, Sel, Sagåa Nat. Res., *Picea abies*, 13 Sep. 2016, *Spirin 11057\** (O, **holotype**).
- B. concisa*. **France**, Moselle, Fontoy, dead *Stereum rugosum* on *Alnus glutinosa*, 27 Feb. 2011, *Trichies 11015\** (H, **holotype**), Ottange, dead *Hymenochaete tabacina* on rotten wood, 7 May 2001, *Trichies 01096* (GT, H). **UK**, England, East Sussex, Buckhurst Park, *Fagus sylvatica*, 20 Feb. 1923, *Pearson* (herb. Bourdot 35590) (PC 0706701).
- B. dura*. **Norway**, Oppland, Nord-Fron, Liadalane Nat. Res., *Betula pubescens*, 12 Sep. 2016, *Spirin 11054\** (O, **holotype**), *Alnus incana*, 29 Sep. 2017, *Spirin 11645\** (O).
- B. grisea*. **Norway**, Møre og Romsdal, Nettet, Eikesdalen, *A. incana*, 28 Sep. 2017, *Spirin 11624\** (O), *11629\** (O, **holotype**).
- B. lanea*. **Norway**, Østfold, Aremark, *P. abies*, 25 Oct. 2011, *J. Nordén 9962\** (O, **holotype**).
- B. longispora*. **Russia**, Leningrad Reg., Boksitogorsk Dist., Chagoda, *Pinus sylvestris*, 19 Aug. 2018 *Spirin 12192* (H). **USA**, North Carolina, Macon Co., Highlands, decorticated pine (?) wood, together with *Tulasnella allantospora*, 23 Jun. 1953, *Olive* (NY); Oregon: Lane Co., Lorane, *Pseudotsuga menziesii*, 22 Oct. 1938 *Doty 522* (NY, **lectotype**).

- B. multifurcata*. **Norway**, Aust-Agder, Grimstad, Sæveli Nat. Res., *Quercus robur* (fallen branch) and dead *Fuscoporia ferrea*, 2 Nov. 2017, *Spirin 11785\** (O, **holotype**).
- B. sebacinoides*. **USA**, Louisiana, Caddo Parish, Shreveport, dead *Exidia glandulosa* on branch of *Quercus* sp., 4 Jul. 1947, *Olive* (NY, **lectotype**).
- B. vestita*. **France**, Aveyron, Bouisson, *Vulleminia comedens* on *Alnus* sp., 19 Feb. 1914, *Galzin 19039* (PC 0706695), *Genista tinctoria*, 24 Dec. 1916, *Galzin 21380* (PC, **lectotype**); Moselle: Neufchef, fallen log (conifer?), 7 Mar. 2009, *Trichies 09017\** (GT, H).
- Bourdotigloea* sp. **USA**, Iowa, Iowa City, drift wood, 8 Jul. 1934, *Rogers 305* (FH 00486509), without host indication, 19 May 1936, *Martin* (FH 00486507, TENN 010594).
- Helicobasidium inconspicuum*. **Austria**, Niederösterreich, Wienerwald, *Quercus* sp., 18 Aug. 1907, *Höhnel* (FH, **lectotype**).
- Helicogloea angustispora*. **USA**, North Carolina: Macon Co., Highlands, on very rotten frondose stump, 29 Aug. 1950, *Olive* (TENN, **lectotype**).
- H. aquilonia*. **Finland**, Etelä-Häme, Nokia, Pitkäniemi, *Sorbus aucuparia*, 10 Aug. 2010, *Söderholm 4241\** (H). **Germany**, Niedersachsen, Lüchow-Dannenberg, *Quercus* sp., 12 Oct. 2003, *Hechler A3.050* (HBG); Sachsen-Anhalt, Sangerhausen, Grillenberg, *Fagus sylvatica*, 8 Sep. 1995, *Hechler 95.066* (HBG). **Norway**, Vest-Agder, Lyngdal, Fladstad, *Q. robur*, 1 Nov. 2017, *Spirin 11755* (O); Hedmark, Løten, Korpreiret i Øksna, hardwood, 26 Sep. 1997, *Høgholen 56/97\** (O F87681); Oppland, Nord-Fron, Liadalane Nat. Res., *Ulmus glabra* (with *Heteroradulum deglubens*), 29 Sep. 2017, *Spirin 11655* (O), Sel, Sagåa Nat. Res., *Salix caprea*, 13 Sep. 2016, *Spirin 11072* (O) (infected by *Achroomyces chlamyospora*); Rogaland: Sokndal, *Tilia cordata* (?), 22–25 Jul. 1971, *Ryvarden 7377* (O F104774); Nordland, Vega, Sundsvoll, on *Ulota phyllantha* and underlying wood, 2 Jul. 1972, *Degelius\** (O). **Russia**, Leningrad Reg., Boksitogorsk Dist., Vozhani, *Populus tremula*, 1–2 Oct. 2016, *Spirin 11163\** (H, **holotype**), 11179 (H), Podporozhie Dist., Oksozero, *S. aucuparia*, 16 Sep. 2017, *Spirin 11457* (H); Nizhny Novgorod Reg.: Lukoyanov Dist., Razino, *P. tremula*, 22 Jul. 2018, *Spirin 11966* (H).
- H. burdsallii*. **USA**, Arizona, Santa Cruz Co., Coronado Nat. Forest, *Fraxinus velutina*, 12 Aug. 1971, *Burdsall 6017\** (CFMR, **holotype**), 6026 (CFMR); California, Napa Co., Sage Creek, *Umbellularia californica* (?), 25 Nov. 1979, *Wells 2803* (BPI).
- H. caroliniana*. **USA**, North Carolina, Orange Co., Chapel Hill, *Quercus* sp., 4 Feb. 1920, *Couch 4078* (BPI, **lectotype**).
- H. compressa*. **Russia**, St. Petersburg, Primorsky Dist., North Coast of Neva Mouth Nat. Res., *P. tremula* (?), 8 Oct. 2013, *Arslanov* (LE 313253\*). **USA**, Tennessee, Sevier Co., Greenbrier, decayed log, 30 Sep. 2015, *Pöldmaa* (TU119718B, culture strain TFC202060\*).
- H. crassitexta*. **Russia**, Krasnoyarsk Reg., Ermakovskoe Dist., Sayano-Shushensky Nat. Res., *Pinus sibirica*, 17 Aug. 2015 *Malysheva* (LE 312773\*, **holotype**).
- H. dryina*. **Finland**, Perä-Pohjanmaa, Rovaniemi, Pisavaara, *P. abies*, 1 Sep. 1960, *Kujala & J. Eriksson* (H). **Norway**, Akershus, Nannestad, *P. abies*, 8 Oct. 2011, *Svantesson 786\** (O, **holotype**), *P. abies*, 9 Oct. 2011, *Svantesson 802* (O), *Botryobasidium subcoronatum* on *P. abies*, 9 Oct. 2011, *Svantesson 808* (O); Oppland, Jevnaker, *P. abies*, 6 Oct. 2011, *J. Nordén 9729* (O); Østfold, Aremark, *P. abies*, 24 Oct. 2011, *Svantesson 1005* (O), *B. subcoronatum* on *P. abies*, 25 Oct.

- 2011, *J. Nordén 9966* (O); Telemark, Nome, *P. abies*, 20 Oct. 2011, *J. Nordén 9934* (O), 25 Oct. 2016, *Spirin 11197* (O); Møre og Romsdal, Sunndal, 20 Aug. 1991, *Torkelsen 313/91* (O); Sør-Trøndelag, Meldal, Urvatn, *P. abies*, 27 Sep. 1991, *Bendiksen & Høiland 11a-46* (O F149951). **Sweden**, Jämtland, Krokomb, *B. subcoronatum* on *P. abies*, 12 Sep. 2011, *J. Nordén 9108* (O); Småland, Vetlanda, *P. abies*, 3 Nov. 2010, *J. Nordén 7745\** (O), *Botryobasidium* sp. on *P. abies*, 2–3 Nov. 2010, *J. Nordén 7740, 7746* (O), 3 Nov. 2010, *Botryobasidium obtusisporum* on *P. abies*, 3 Nov. 2010, *J. Nordén 7749, 8001* (O, H), Vimmerby, *P. abies*, 4 Nov. 2010, *J. Nordén 7909* (O), *Sistotrema coroniferum* and *Botryohypochnus isabellinus* on *P. abies*, 4 Nov. 2010, *J. Nordén 7911* (O), *Botryobasidium* sp. on *P. abies*, 5 Nov. 2010, *J. Nordén 8029* (O).
- H. eburnea*. **Kenya**, Taita-Tavet, Taita Hills, Chawia, decayed hardwood log, 17 Nov. 2017, *Savchenko 171127/1127A\** (H, **holotype**).
- H. exigua*. **Canada**, Ontario, Toronto, Holland River Marsh, *Populus* sp., 6 May 1936, *Linder* (FH 00486504). **France**, Moselle, Moyeuve-Petite, vallée du Conroy, *Betula pendula*, 25 Aug. 2002, *Trichies 02123* (GT, H). **USA**, Michigan, Marquette Co., Big Bay, *Acer saccharum*, 6 Aug. 1974, *Burdsall 8162\** (CFMR, **holotype**).
- H. irregularis*. **French Polynesia**, Tahiti, Papeari, Harrison Smith Estate, old stem of bamboo, 13 Jun. 1956, *Olive* (NY 00834140, **holotype**).
- H. intermedia*. **Panama**, Chiriquí Prov, Rio Chiriquí, 3 Jul. 1935, *Martin 2423* (FH 00304773).
- H. lagerheimii*. **Ecuador**, Baños, Chorrera de Agoyan, rotten branch, Jan. 1892 *Lagerheim* (FH, **lectotype**). **USA**, California, Napa Co., Robert L. Stevenson Memorial State Park, hardwood, 19 Dec. 1965, *Wells 1711-2\** (BPI 719891).
- H. lunula*. **New Zealand**, Wairarapa, Pigeon Bush Res., decorticated branch, 1 Jan. 2006, *Paulus & Steer* (PDD 88360\*, **holotype**).
- H. microsaccata*. **Russia**, Primorie, Ussuriisk Dist., Ussuri Nat. Res., deciduous tree (fallen branch), 15 Aug. 2011, *Malysheva* (LE 262936\*, **holotype**).
- H. ovispora*. **Brazil**, Santa Catharina, Blumenau, rotten wood, *Möller 767* (HBG, **lectotype**).
- H. pellucida*. **Canada**, Ontario, Nipissing, Temagami, *Fraxinus* sp., 7 Aug. 1936, *Jackson* (FH 00486502 ex TRTC 10518). **Norway**, Møre og Romsdal, Nesset, Eikesdalen, *U. glabra*, 28 Sep. 2017, *Spirin 11617* (O). **Russia**, Nizhny Novgorod Reg., Lukoyanov Dist., Razino, *A. glutinosa*, 10 Aug. 2016, *Spirin 10610\** (H, **holotype**), *U. glabra*, 24 Jul. 2018, *Spirin 12025* (H). **Ukraine**, Donetsk Reg., Slovyansk Dist., Svyati Gori Nat. Res., *P. tremula*, 19–20 Oct. 2009, *Ordynets & Akulov* (CWU 4000\*, 4186). **USA**, Massachusetts, Middlesex Co., Wakefield, *Malus* sp., 5 Nov. 1941, *Linder* (FH 00486501); North Carolina, Macon Co., Highlands, hardwood, 20 Aug. 1952, *Olive* (TENN 43239).
- H. sebacea*. **Denmark**, Nørrejylland, Aalborg, Solbjerg Enge, *Betula* sp., 24 Aug. 2011, *Heilmann-Clausen 11-066\** (C). **Estonia**, Viljandimaa, Pääsma, *U. glabra*, 18 Sep. 2018, *Spirin 12372, 12379, 12383* (H, TU). **France**, Allier, St. Priest, *Cerasus* (?) (very rotten wood), 26 Nov. 1908, *Bourdot 5882* (PC, **lectotype**); Meurthe-et-Moselle, Val de Briey, *Fraxinus excelsior*, 23 Jan. 2003, *Trichies 03004* (GT, H); Moselle, Thionville, Beuvange-sous-Saint-Michel, hardwood (*Populus nigra* or *Salix fragilis*), 9 Jan. 2007, *Trichies 07024\** (GT, H). **Germany**, Niedersachsen, Rotenburg, Freetz, *F. sylvatica*, 11 Nov. 1989, *Hechler 89.130* (HBG). **Russia**, Nizhny Novgorod Reg., Lukoyanov Dist., Razino, *T. cordata*, 23 Jul 2018, *Spirin 12005* (H); Primorie Reg., Ussuriisk Dist., Ussuri Nat. Res., hardwood, 15 Aug. 2011, *Malysheva* (LE 262888, 262946). **Ukraine**, Ivano-Frankivsk Reg., Nadrivna Dist., Gorgany, *Acer platanoides*, 18 Jul. 2012, *Savchenko* (CWU 6331\*). **USA**, Ohio, Huron Co., Wakeman, *Quercus* sp., Sept. 1933, *Rogers* (FH 00486503); South Carolina, Pickens Co., Eastatoee River, very rotten wood, 16 Jul. 1951, *Olive* (TENN 43192), 25 Jul. 1951, *Olive* (TENN 43191); Tennessee, Sevier Co., Gatlinburg, on remnants of old resupinate fungus, 29 Jul. 1953, *Olive* (TENN 43224).
- H. septifera*. **Norway**, Oppland, Nord-Fron, Liadalane Nat. Res., *S. aucuparia*, 12 Sep. 2016, *Spirin 11035* (O), *Ulmus glabra*, 12 Sep. 2016, *Spirin 11036* (O) (infected by *A. chlamydospora*), *P. tremula*, 12 Sep. 2016, *Spirin 11043\** (O, H, LE) (infected by *Tulasnella pallida*), 29 Sep. 2017, *Spirin 11654* (O) (infected by *A. chlamydospora*); Sogn og Fjordane, Luster, Loi, *Ulmus glabra*, 8 Sep. 2000, *Roberts* (O F300013, infected by *A. chlamydospora* – **isotype** of the latter species); Møre og Romsdal, Nesset, Eikesdalen, *A. incana*, 27 Sep. 2017, *Spirin 11593, 11605* (O); Nord-Trøndelag, Grong, Sanddøla, *Ulmus* sp., 13 Jul. 1977, *Holten & Siversten\** (H, **holotype**, TRH, **isotype and paratypes**); Troms, Storfjord, Skibotndalen, hardwood, 19 Aug. 1992, *Torkelsen* (O F295518). **Russia**, Karachay-Cherkessia, Karachaeusk Dist., Teberda Nat. Res., hardwood, 10 Aug. 2009, *Malysheva* (LE 253866\*); Leningrad Reg., Boksitogorsk Dist., Efimovskoe, *B. pubescens*, 18.VIII.2018 *Spirin 12172* (H), Tosno Dist., Lisino, *Betula* sp., 3 Sep. 1960, *Bondartseva* (LE 260\*). **USA**, Iowa, Johnson Co., North Liberty, 11 Jun. 1934, *Martin 1381* (FH 00486500).
- H. sputum*. **Norway**, Vestfold, Larvik, Jordstøyp i Kvelde, *P. tremula*, 19 Oct. 1995, *Andersen\** (O, **holotype**).
- H. subardosiaca*. **Finland**, Uusimaa, Inkoo, Prästholmen, *P. sylvestris*, 20 Nov. 2017, *Pennanen 3668\** (H). **France**, Aveyron, Causse Noir, *P. sylvestris*, 9 Dec. 1910, *Galzin 7868* (PC, **lectotype**), *Galzin 7896* (PC); Meuse, Vacherauville, *P. sylvestris*, 22 Apr. 2002, *Trichies 02038* (GT, H); Moselle, Neufchef, *P. abies* / *P. sylvestris*, 4 Dec. 2002, *Trichies 02234, 02235* (GT, H), 24 Nov. 2006, *Trichies 06239* (GT, H), *P. sylvestris*, 30 Jan. 2002, *Trichies 02005* (GT, H), Ottange, *P. sylvestris*, 14 Jan. 2004, *Trichies 04013* (GT, H), Roussy-le-Village, *P. sylvestris*, 8 Dec. 2004, *Trichies 04276* (GT, H).
- H. terminalis*. **USA**, North Carolina, Macon Co., Highlands, *Betula* sp., 14 Aug. 1952, *Olive* (NY, **holotype**).
- Helicogloea* sp. 1. **Canada**, British Columbia, Squamish, hardwood, 1 Jul. 1983, *Wells 3141\** (BPI 883188), *Wells 3142, 3143* (BPI 883189, 883187). **USA**, California, Solano Co., Green Valley, hardwood, 7 Jan. 1961, *Wells 720-2* (BPI 719890).
- Helicogloea* sp. 2. **Brazil**, Rio Grande do Sul, Saõ Leopoldo, *Rick* (FH 00304771), 1931, *Rick* (FH 00304772).
- Saccosoma contortum*. **USA**, Florida, Alachua Co., Devil's Millhopper, *Liquidambar styraciflua*, 13 Jul. 1972, *Burdsall 6540* (CFMR), Highlands Co., Highlands Hammock State Park, *Sabal palmetto*, 29 Jul. 1970, *Burdsall 4815* (CFMR).
- S. farineum*. **Canada**, Ontario, Temagami, *Corylus rostrata*, 31 Aug. 1936, *Biggs* (BPI 719908). **Denmark**, Midtjylland, Skive, Tastum Plantage, *Pinus sylvestris* (bark), 29 Dec. 2012, *Boertmann 2012-493835\** (C). **Estonia**, Valgamaa, Otepää, Trommi, *P. tremula* (fallen log), 12 Sep. 2012, *Pecoraro\** (TU 115541, H). **Finland**, Varsinais-suomi, Karjalohja, Tammisto,

- Acer pseudoplatanus*, 8 Oct. 1985, *Alanko 54286c* (H). **France**, Aveyron, Millau, Causse Noir, *P. sylvestris* (fallen branches), 10 Nov. 1908, *Galzin* (S, **lectotype** of *Saccoblastia pinicola*). **Germany**, Bayern, Passau, *Pinus* sp. (manufactured wood), Sep. 1919, *Killermann* (BPI, **lectotype** of *Stypinella killermannii*). **Norway**, Vestfold, Tønsberg, Gullkronene, *F. excelsior*, 15 Sep. 2016, *Spirin 11092\** (O); Hordaland, Granvin, *F. excelsior* (fallen branches), 11 Sep. 1951, *Stordal & Eriksson 6036* (O); Oppland, Gausdal, Benndalen, *P. tremula*, 2 Sep. 2007, *Klepsland JK07-S181* (O, H), Lunner, Flåtaseter, *S. caprea*, 23 Sep. 1982, *Ryvarden 20391* (O, H). **Russia**, Moscow, Losinyi Ostrov Nat. Res., *P. sylvestris* (fallen log), 13 Oct. 2016, *Viner 2655\** (IV, dupl. H); Nizhny Novgorod Reg., Lukoyanov Dist., Sanki, *Corylus avellana* (dry branch), 4 Aug. 2017, *Spirin 11365\**, *11370* (H), *U. glabra*, 20 Aug. 2015, *Spirin 9730\** (H), Lyskovo Dist., Makarievo, *Salix* sp. (dry branch), 11 Aug. 2015, *Spirin 9099\** (H, **neotype**), Valki, *Quercus robur*, 11 Aug. 2015, *Spirin 9103* (H). **Sweden**, Skåne, Dalby Söderskog, *F. excelsior*, 7 Oct. 1951, *Eriksson 6532* (FH 00304777); Småland, Vimmerby, *P. abies*, 27 Oct. 2010, *J. Nordén 7859\** (O, H). **Ukraine**, Donetsk Reg., Slovyansk Dist., Svyati Hory Nat. Park, *F. excelsior* (fallen branch), 18 Oct. 2009, *Ordynets* (CWU 4009\*). **UK**, Surrey, Godalming, Witley Common, *P. sylvestris*, 8 Feb. 1997, *Legon* (K(M) 49091\*). **USA**, Connecticut, Union, *Prunus virginiana*, 4 Aug. 1937, *Hansbrough* (BPI 719911); Massachusetts, Worcester Co., Worcester, *Quercus* sp., 10 Nov. 2013, *Miettinen 17547\** (H); Washington, Pend Oreille Co., Muskegon Lake, *Abies grandis* (dry branch) and living *Aleurodiscus grantii*, 16 Oct. 2014, *Spirin 8601a\** (TU 119510).
- S. farinaceum* f. *alniviridis*. **Italy**, South Tyrol, Bolzano, Vipiteno, *Alnus viridis*, 10 Sep. 1997, *Kotiranta 13179\** (H). **Russia**, Chukotka, Anadyr, *Alnus fruticosa*, 27 Aug. 2009, *Kotiranta 27168* (H); Magadan Reg., Severo-Evensky Dist., *A. fruticosa*, 21 Aug. 1973, *Järva* (TAAM 49708), Tenkinsky Dist., Madaun, *Salix arbutifolia*, 14 Aug. 1995, *Corfixen* (C, **holotype** of *Achroomyces sibiricus*). **Switzerland**, Bern, Axalp, Hinterburgseeli, *A. viridis*, 16 Sep. 1997, *Küffer* (N.K.); Uri, Schächental, Sittisalp, *A. viridis*, 24 Jun. 1998 *Senn-Irlet* (N.K.). **USA**, Washington, Pend Oreille Co., Gypsy Meadows, *A. fruticosa* (dry branch), 17 Oct. 2014, *Spirin 8721\** (H).
- S. floccosum*. **Russia**, Lipetsk Reg., Krasnoe Dist., Olenii Nat. Park, *Quercus robur* (fallen branches), 30 Sep. 2016, *Volobuev* (LE 313308\*, **holotype**); Nizhny Novgorod Reg., Lukoyanov Dist., Panzelka, *P. abies* (fallen branches), 9 Aug. 2016, *Spirin 10595* (H).
- S. medium*. **St. Helena**, Scotland Research Station, hardwood, 3 Feb. 2014, *Ryvarden 49436* (K, **holotype**).
- S. sphaerosporum*. **Mexico**, Vera Cruz, Los Tuxtlas, corticated wood, 10 Jul. 1978, *Welden 4462* (BPI 883935), Barranca de Pescado, hardwood, 26 Sep. 1985, *Ryvarden 23431\**, *23458* (O). **USA**, Florida, Dade Co., Pine Island Research Area, strangle fig, 11 Aug. 1972, *Burdsall 7082* (CFMR).

### DNA extraction, amplification (PCR) and phylogeny

Extraction of genomic DNA was carried out using the NucleoSpin Plant II Kit (Macherey-Nagel GmbH & Co. KG), according to the manufacturer's instructions. ITS regions were amplified and sequenced with primers ITS1F-ITS4 (Gardes & Bruns 1993, White *et al.* 1990) and the nrLSU with primers JS1and LR5 (Landvik 1996; <http://www.biology.duke.edu/fungi/mycolab/>

primers.htm). PCR products were purified applying the GeneJET Gel Extraction Kit (Thermo Scientific, Thermo Fisher Scientific Inc., MA, USA). Sequencing was performed with an ABI model 3130 Genetic Analyzer (Applied Biosystems, CA, USA). Raw data were edited and assembled in MEGA v. 6 (Tamura *et al.* 2013). All steps of molecular studies were carried out at the Center for collective use of scientific equipment "Cellular and molecular technology of studying plants and fungi" (Komarov Botanical Institute, Russian Academy of Sciences, St. Petersburg). In case of specimens processed at the molecular lab of the mycology chair in the University of Tartu, the protocols described in Pärtel *et al.* (2016), were followed.

### Phylogenetic analyses:

For this study, 51 nrITS and 34 nrLSU sequences were generated (Table 1). The new sequences were aligned with additional related sequences downloaded from GenBank (Table 1) using MAFFT v. 7 web tool (<http://mafft.cbrc.jp/alignment/server/>) under the Q-INS-i option for both markers; the alignments were manually adjusted in MEGA v. 6.

Phylogenetic reconstructions were performed with Maximum likelihood (ML) and Bayesian (BA) analyses for two datasets (nrITS+nrLSU and nrITS). Before the analyses, the best-fit substitution model for the alignment was estimated based on the Akaike Information Criterion (AIC) using FindModel web server (<http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html>). GTR model was chosen for all datasets.

Maximum likelihood analysis (ML) was run on PhyML server (<http://www.atgc-montpellier.fr/phyml/>), under one hundred rapid bootstrap replicates. Bayesian analysis (BA) was performed with MrBayes v. 3.1 software (Ronquist & Huelsenbeck 2003), for two independent runs, each with 3 million generations with sampling every 100 generations, under described model and four chains. To quickly diagnose convergence of MCMC analyses and to get estimates of the posterior distribution of parameter values Tracer v. 1.6 was used (Rambaut *et al.* 2014).

Newly generated sequences have been deposited in GenBank with accession numbers listed in Table 1. The alignments have been deposited in TreeBASE (S22969 – nrITS + nrLSU and S22760 – nrITS dataset dataset).

## RESULTS

### Phylogeny

The phylogenetic analyses resulted in two trees for nrITS+nrLSU and nrITS datasets (Figs 1, 2). The phylogeny derived from the nrITS+nrLSU dataset (1 675 characters, including gaps) (Fig. 1) shows that members of *Helicogloea s. lato* (as advocated by Baker 1936) are spread among three lineages within the class. In general, these phylogenetic reconstructions follow the results of earlier studies (in particular, Aime *et al.* 2006, 2018, Bauer *et al.* 2006) demonstrating that *Helicogloea* is polyphyletic and *Platygloea vestita* (= *Helicogloea vestita*) belongs to the *Atractiellomycetes*. Most species of *Helicogloea s. lat.* included in the analyses form a strongly supported clade with a reference specimen of *H. lagerheimii*, the generic type (Fig. 1, pp = 0.99, bs = 75 %), thus constituting *Helicogloea s. str.* The single representatives of *Leucogloea* (*L. compressa*) and *Neogloea* (*N. variabilis*) belong to *Helicogloea*, too, and therefore we consider these generic names taxonomic synonyms. The second

Table 1. Sequences used in the present study.

Species	Specimen / fungarium	Geographic origin (ISO code)	Host	nrLSU GenBank number	ITS GenBank / Unite number
<i>Atractidochium hillariae</i>	cas001(65b)	-	<i>Pinus taeda</i>	MF461291	KM519195
	cas012(72a)	-	<i>Pinus taeda</i>	MF461292	KM519202
	caw001(1.1.6b)	-	<i>Pinus taeda</i>	MF461293	MF461287
<i>Atractiella rhizophila</i>	CBS 137288	USA	<i>Populus deltoides</i>	JX243797	JX243797
<i>A. solani</i>	Strain TUB F107	-	-	AY512831	DQ198781
<i>Atractiella</i> sp.	P30	-	-	KX812533	-
<i>Basidiopycnis hyalina</i>	TUB FO44664	-	-	DQ363322	DQ198779
<i>Bourdotigloea cerea</i>	VS 11057 (O)	NO	<i>Picea abies</i>	MH304455	MH304504
<i>B. concisa</i>	GT 11015 (H)	FR	<i>Alnus glutinosa</i>	MH304456	MH304505
<i>B. dura</i>	VS 11054 (O)	NO	<i>Betula pubescens</i>	MH304457	MH304506
	VS 11645 (O)	NO	<i>Alnus incana</i>	MH304458	MH304507
<i>B. grisea</i>	VS 11624 (O)	NO	<i>A. incana</i>	MH304459	MH304508
	VS 11629 (O)	NO	<i>A. incana</i>	MH304460	MH304509
<i>B. lanea</i>	JN 9962 (O)	NO	<i>P. abies</i>	MH304461	MH304510
<i>B. multifurcata</i>	VS 11785 (O)	NO	<i>Quercus robur</i>	-	MH304511
<i>B. vestita</i>	GT 09017 (H)	FR	conifer?	-	MH304512
<i>Helicogloea aquilonia</i>	Söderholm 4241 (H)	FI	<i>Sorbus aucuparia</i>	-	MH304476
	Høgholen 56/97 (O)	NO	hardwood	-	MH304477
	Degelius w/n (O)	NO	<i>Ulotia phyllantha</i> , wood	MH304439	MH304478
	VS 11163 (H)	RU-LEN	<i>Populus tremula</i>	MH304440	MH304479
<i>H. burdsallii</i>	CFMR HHB-6017	US-AZ	<i>Fraxinus velutina</i>	-	MH304484
<i>H. compressa</i>	LE 313253	RU-SPE	<i>P. tremula?</i>	MH304442	MH304482
	TU119718	US-NC	decayed wood	MH304441	MH304481
	OM 19493 (H)	US-NC	hardwood	-	MH304480
<i>H. crassitexta</i>	LE 312773	RU-KYA	<i>Pinus sibirica</i>	MH304443	MH304483
<i>H. dryina</i>	JN 7745 (O)	SE	<i>P. abies</i>	MH304444	MH304486
	SS 786 (O)	NO	<i>P. abies</i>	-	MH304485
<i>H. eburnea</i>	AS 171127/1127A (H)	KE	hardwood	MH304445	MH304487
<i>H. exigua</i>	CFMR HHB-8162	US-MI	<i>Acer saccharum</i>	MH304446	MH304488
<i>H. lagerheimii</i>	KW 1711-2 (BPI)	US-CA	hardwood	-	MH304489
<i>H. 'lagerheimii'</i>	TUB FO36341	DE	-	AY512849	-
<i>H. lunula</i>	PDD 88360	NZ	hardwood	-	MH304490
<i>H. microsaccata</i>	LE 262936	RU-PRI	hardwood	-	MH304491
<i>H. pellucida</i>	VS 10610 (H)	RU-NIZ	<i>A. glutinosa</i>	MH304448	MH304493
	CWU 4000	UA	<i>P. tremula</i>	MH304447	MH304492
<i>H. sebacea</i>	JHC 11-066 (C)	DK	<i>Betula</i> sp.	-	MH304495
	GT 07024 (H)	FR	hardwood	-	MH304494
	CWU 6331	UA	<i>Acer platanoides</i>	-	MH304502
<i>H. septifera</i>	VS 11043 (O)	NO	<i>P. tremula</i>	MH304452	MH304499
	Holten w/n (H)	NO	<i>Ulmus</i> sp.	MH304451	MH304498
	LE 260	RU-LEN	<i>Betula</i> sp.	MH304450	MH304497
	LE 253866	RU-KC	hardwood	MH304449	MH304496
<i>H. sputum</i>	Andersen (O F90728)	NO	<i>P. tremula</i>	MH304453	MH304500

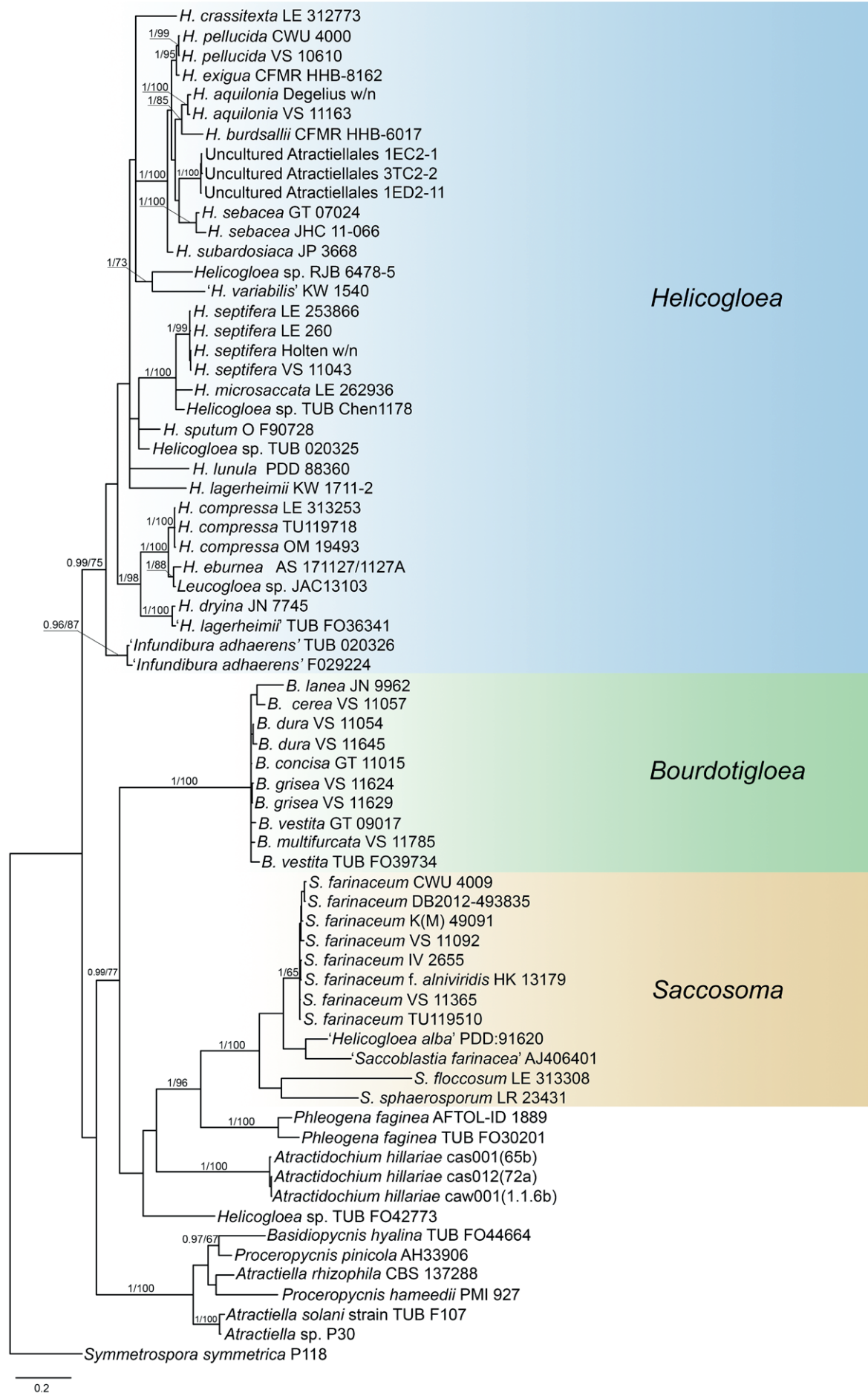
Table 1. (Continued).

Species	Specimen / fungarium	Geographic origin (ISO code)	Host	nrLSU GenBank number	ITS GenBank / Unite number
<i>H. subardosiaca</i>	JP 3668 (H)	FI	<i>Pinus sylvestris</i>	MH304454	MH304501
<i>H. variabilis</i>	KW 1540	BR	hardwood	L20282	-
<i>Helicogloea</i> sp.	KW 3141 (BPI)	CA-BC	hardwood	-	MH304503
	TUB FO42773	DE	-	AY512847	-
	TUB Chen1178	TW	-	AY512848	-
	TUB 020325	USA	roots of <i>Baccharis</i> sp.	KF061297	-
	RJB 6478-5	-	-	KX812536	MF476085
<i>Infundibura adhaerens</i>	TUB 020326	EC	stems of <i>Bambus</i> sp.	KF061296	-
<i>I. adhaerens</i>	F029224	-	-	AJ406404	-
<i>Leucogloea</i> sp.	JAC13103	NZ	-	KP191766	KP191965
' <i>Platygloea vestita</i> '	TUB FO39734	DE	-	AY512872	-
<i>Phleogena faginea</i>	TUB FO30201	-	-	AY512869	-
<i>P. faginea</i>	AFTOL-ID 1889	GB	-	DQ831021	-
<i>Proceropycnis hameedii</i>	PMI 927	USA	<i>Populus trichocarpa</i>	-	KF428609
<i>P. pinicola</i>	AH33906	-	-	DQ363323	DQ198780
' <i>Saccoblastia farinacea</i> '	GEL 4771	-	-	AJ406401	-
<i>Saccosoma album</i>	PDD 91620	NZ	-	-	GQ411522
<i>S. farinaceum</i>	DB 2012-493835 (C)	DK	<i>P. sylvestris</i>	MH304435	MH304469
	TU115541	EE	<i>P. tremula</i>	-	UDB016397
	K(M) 49091	GB	<i>P. sylvestris</i>	MH304430	MH304465
	VS 11092 (O)	NO	<i>Fraxinus excelsior</i>	MH304432	MH304471
	IV 2655 (H)	RU-MOW	<i>P. sylvestris</i>	MH304431	MH304470
	VS 9099 (H)	RU-NIZ	<i>Salix</i> sp.	-	MH304467
	VS 11365 (H)	RU-NIZ	<i>Corylus avellana</i>	MH304433	MH304472
	VS 9730 (H)	RU-NIZ	<i>Ulmus glabra</i>	-	MH304464
	JN 7859 (O)	SE	<i>P. abies</i>	-	MH304463
	CWU 4009	UA	<i>F. excelsior</i>	MH304434	MH304468
	OM 17547 (H)	US-MA	<i>Quercus</i> sp.	MH304462	MH304462
	TU119510	US-WA	<i>Abies grandis</i>	MH304429	MH304466
	<i>S. farinaceum</i> f. <i>alniviridis</i>	HK 13179 (H)	IT	<i>Alnus viridis</i>	MH304436
VS 8721 (H)		US-WA	<i>Alnus fruticosa</i>	-	MH304473
<i>S. floccosum</i>	LE 313308	RU-LIP	<i>Q. robur</i>	MH304437	MH304475
<i>S. sphaerosporum</i>	LR 23431 (O)	MX-VC	hardwood	MH304438	-
<i>Symmetrospora symmetrica</i>	P118	USA	<i>Pinus nigra</i>	KJ701211	KJ701210
Uncultured <i>Atractiellales</i>	Clone 1EC2-1	EC	<i>Epidendroideae</i>	GU079580	GU079580
	Clone 1ED2-11	EC	<i>Epidendroideae</i>	GU079581	GU079581
	Clone 3TC2-2	EC	<i>Maxillaria</i>	GU079597	GU079597

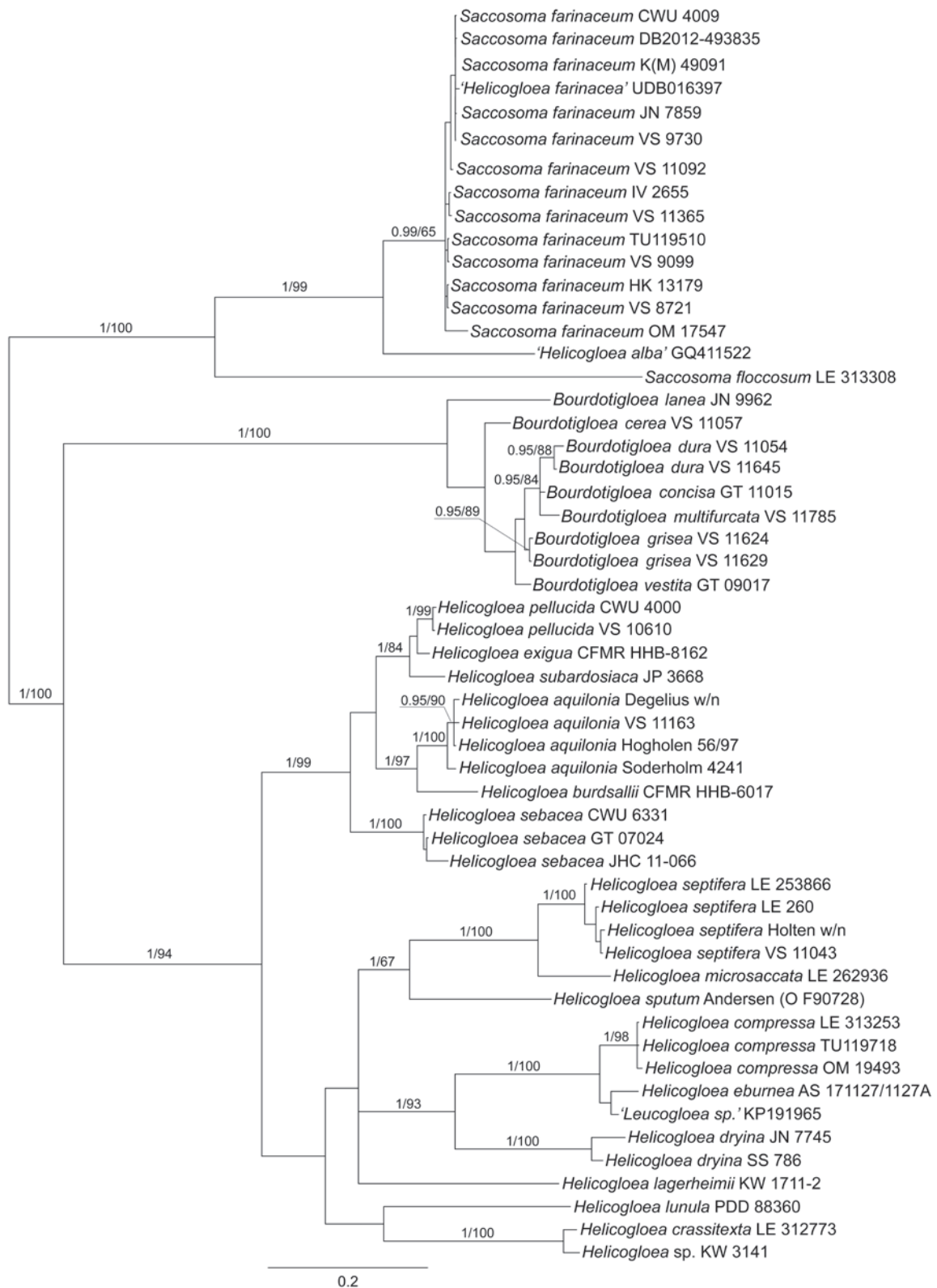
clade is represented by *Helicogloea farinacea* and its closest relatives (Fig. 1, pp = 1, bs = 100 %). Traditionally, this group was associated with the generic name *Saccoblastia*. However, we argue below that the latter generic epithet is not applicable to the *H. farinacea* complex, and a new genus *Saccosoma* is described to encompass it. *Helicogloea vestita* and its siblings form a third lineage in the phylogeny (Fig. 1, pp = 1, bs = 100 %)

only distantly related to both *Helicogloea s. str.* and *Saccosoma*. As a consequence, they are separated into the recently described genus, *Bourdotigloea*.

ITS dataset for the corticioid *Atractiellomycetes* (972 characters, including gaps) included sequences from 54 fungal samples (Fig. 2). The three major clades (*Saccosoma*, *Bourdotigloea*, *Helicogloea*) are highly supported and the



**Fig. 1.** Combined nrITS + nrLSU topology from Bayesian analysis showing major lineages of the *Atractiellomyces*. Collection numbers are given for all specimens. Support values (Bayesian posterior probability / Maximum likelihood Bootstrap values) are given above the branches. Scale bar shows expected changes per site.



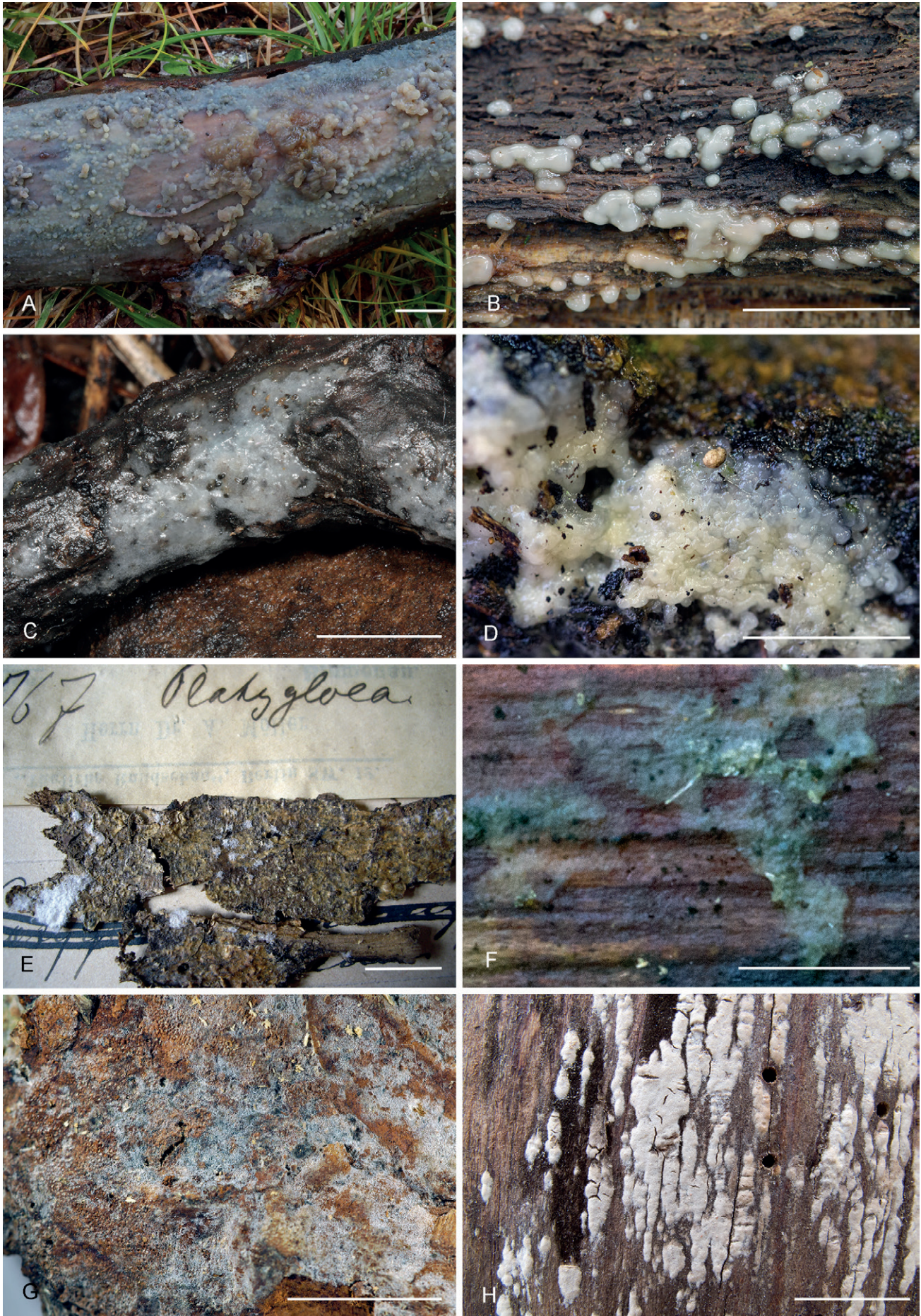
**Fig. 2.** Bayesian phylogram for the nrITS dataset. Collection numbers are given for newly sequenced specimens and accession numbers for additional sequences retrieved from GenBank. Support values (Bayesian posterior probability / Maximum likelihood Bootstrap values) are given above the branches. Scale bar shows expected changes per site.

internal topology of these clades is well resolved and support the distinction of 26 accepted species.

DNA data obtained in the present study correspond well to the morphological evidence. All species of *Helicogloea* s. str. and all but one of *Bourdotigloea* spp. possess gelatinous, semitranslucent basidiocarps that turn to a vernicose crust after

drying, while *Saccosoma* spp. have sturdier, arid fructifications, unchanged in dry condition (Fig. 3). In microscopic terms, presence of clamps and shape of basidia are of crucial value for recognizing crust-like genera of the *Atractiellomyces*. Both *Helicogloea* and *Bourdotigloea* spp. are totally devoid of clamps; basidia are variably curved, with a terminal cell bearing





**Fig. 3.** Fructifications of the *Atractiellomycetes*. **A.** *Helicogloea crassitexta* (holotype). **B.** *H. eburnea* (holotype). **C.** *H. microsaccata* (holotype). **D.** *H. septifera* (Spirin 11043). **E.** *H. ovispora* (lectotype). **F.** *Bourdotigloea cerea* (holotype). **G.** *B. multifurcata* (holotype). **H.** *Saccosoma farinaceum* (Miettinen 17547). Scale bar = 10 mm.

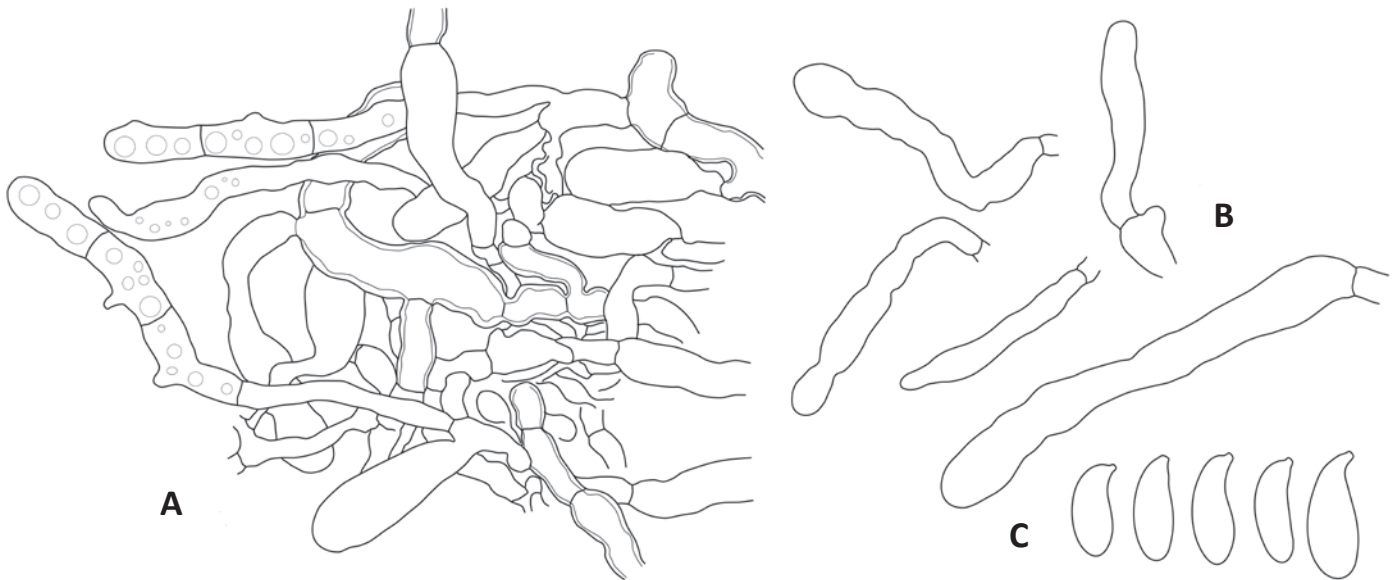


Fig. 4. *Bourdotigloea lanea* (holotype). A. Basidia, subicular and subhymenial hyphae, hymenial cells. B. Cystidia. C. Basidiospores. Scale bar = 10  $\mu$ m.

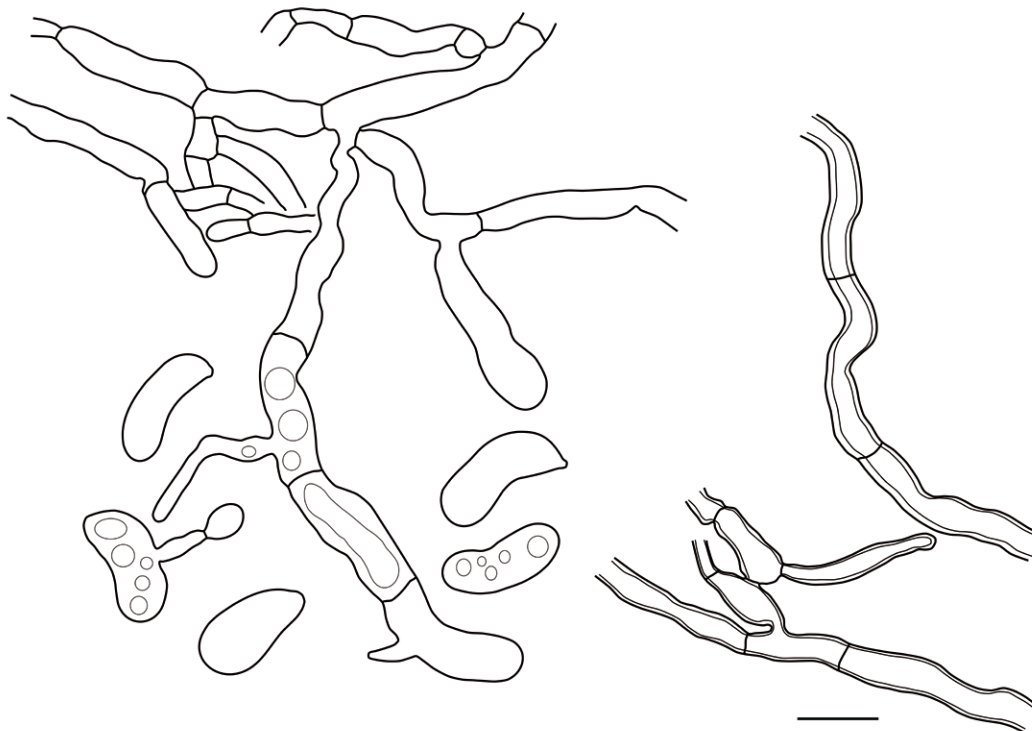


Fig. 5. *Helicogloea subardosiaca* (Pennanen 3668). Subicular hyphae, hymenium, basidiospores. Scale bar = 10  $\mu$ m.

a laterally arranged sterigma (Figs 4, 5). However, almost all *Bourdotigloea* species treated below have differentiated cystidia and distinctly coloured (brownish), very thick-walled subicular hyphae, whereas *Helicogloea* lacks cystidia and hyphal colouration (subicular hyphae are in general less differentiated from subhymenial ones). In contrast, all hyphae in *Saccosoma* spp. are clamped, basidia are straight (not curved) and their terminal cell bears an apical sterigma (Fig. 6). Sporodochial asexual morphs (*Leucogloea*, *Infundibura*) have been so far detected in *Helicogloea* s. str. only (see Kirschner 2004 for a detailed discussion).

Even when *Bourdotigloea* and *Saccosoma* are separated from *Helicogloea*, the latter genus shows rather high morphological diversity and divergency of nrITS and LSU sequences. Therefore,

we do not exclude that further splitting may become necessary. Fulfilling this task, however, implies much wider sampling of the *Atractiellomyces*, especially of asexual taxa, and use of additional genetic markers.

## TAXONOMY

***Bourdotigloea*** Aime, *Mycologia* **110**: 144. 2018.

*Basidiocarps* resupinate, very thin, at first pruinose, then waxy to ceraceous. *Hyphae* clampless, in many cases rather short-celled and variably inflated. *Basal hyphae* coloured (brownish), in a few species hyaline, slightly to very thick-walled, 7–19  $\mu$ m

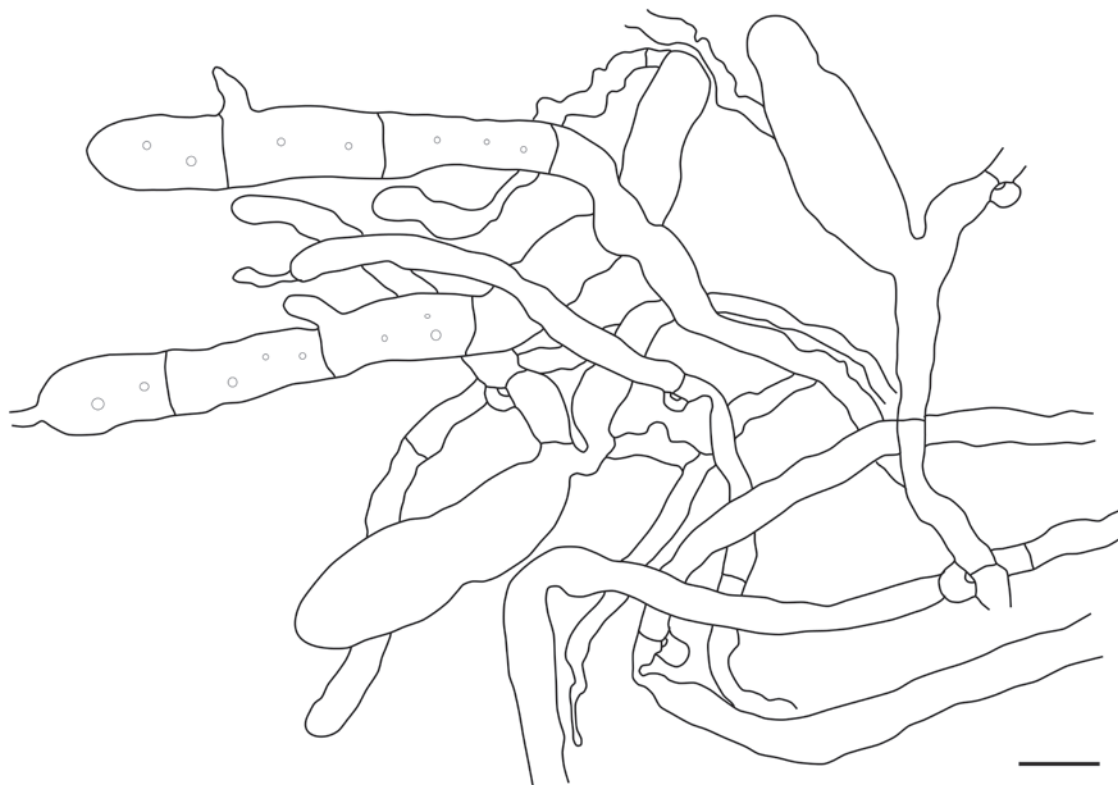


Fig. 6. *Saccosoma farinaceum* (neotype). Hyphae and basidia. Scale bar = 10  $\mu\text{m}$ .

diam, strongly cyanophilous. *Subhymenial hyphae* hyaline, thin- to slightly thick-walled, often easily collapsing, 3.5–8  $\mu\text{m}$  diam, slightly to moderately cyanophilous. *Basidia* four-celled, tubular-clavate, straight or somewhat curved, with sharp-pointed, thick sterigmata; probasidia saccate. *Cystidia* as a rule present, tubular, more or less straight to somewhat sinuous or moniliform, decumbent but often with ascending apical part. *Basidiospores* cylindrical, fusiform or sigmoid, 12–36  $\times$  4–10  $\mu\text{m}$ , germinating by repetition.

On decayed wood, dead fructifications of other basidiomycetes and plant debris.

*Type species: Bourdotigloea vestita* (Bourdot & Galzin) Aime.

*Notes:* This genus is re-introduced here to embrace *P. vestita* and its closest relatives. The species of *Bourdotigloea* are morphologically most similar to *Helicogloea* spp. The latter ones differ in having narrower and not inflated, colourless hyphae, and their basidia bear more slender sterigmata. No differentiated cystidia are detected among *Helicogloea* species. Moreover, basidiospores of all known *Helicogloea* spp. (except *H. angustispora*) are ellipsoid/subglobose or broadly cylindrical, not fusiform.

Nine species are accepted below as belonging to *Bourdotigloea*. However, actual species diversity in this genus seems to be much higher. According to the protologue (Olive 1953) and later redescription by Bandoni (1956), *Platygloea subvestita* may also belong to *Bourdotigloea*, although a presence of gloeocystidia looks confusing. Olive's description of *P. vestita* specimens from the southern Appalachians (Olive 1953) does not fit to any species we currently accept. Moreover, two collections from Iowa labelled by G.W. Martin as *H. lagerheimii*, certainly represent one more species in this complex (treated

as *Bourdotigloea* sp. under Specimens examined). However, we decided to limit our study to existing species names or newly collected and sequenced material. Therefore, we leave these problems until we find new collections of the aforementioned problematic taxa.

***Bourdotigloea cerea*** Spirin & V. Malysheva, *sp. nov.* MycoBank MB825588. Figs 3, 7.

*Etymology:* Cereus (Lat., adj.) – waxy.

*Holotype:* Norway, Oppland, Sel, Sagåa Nat. Res., *Picea abies*, 13 Sep. 2016, Spirin 11057 (O).

*Basidiocarps* resupinate, 0.03–0.05 mm thick, first pruinose, then semitranslucent, greyish, waxy. *Basal hyphae* hyaline, slightly to distinctly thick-walled, easily collapsing, (7.2–)8.0–11.0(–11.2)  $\mu\text{m}$  diam ( $n = 20/1$ ). *Subhymenial hyphae* thin-walled, easily collapsing, (3.3–)3.7–7.0(–7.8)  $\mu\text{m}$  diam ( $n = 20/1$ ). *Basidia* tubular-clavate, straight or somewhat curved, 53–63  $\times$  (5.4–)5.6–7.0(–8.1)  $\mu\text{m}$  ( $n = 20/1$ ), with sharp-pointed sterigmata up to 8  $\times$  4  $\mu\text{m}$ ; probasidia saccate, 26–33  $\times$  10–12.5  $\mu\text{m}$ . *Cystidia* rare, tubular, more or less straight to somewhat sinuous, 44–121  $\times$  5–6  $\mu\text{m}$ . *Basidiospores* narrowly fusiform, some more or less sigmoid, (18.0–)18.6–32.8(–36.2)  $\times$  (4.0–)4.2–7.0(–7.2)  $\mu\text{m}$  ( $n = 32/1$ ),  $L = 23.53$ ,  $W = 5.39$ ,  $Q' = (3.1–)3.4–5.7(–6.1)$ ,  $Q = 4.41$ .

*Distribution and ecology:* Europe (Norway); fallen, decorticated but hard branch of *Picea abies*.

*Notes:* *Bourdotigloea cerea* differs from other species of the genus in having narrow basidiospores and non-constricted cystidia.

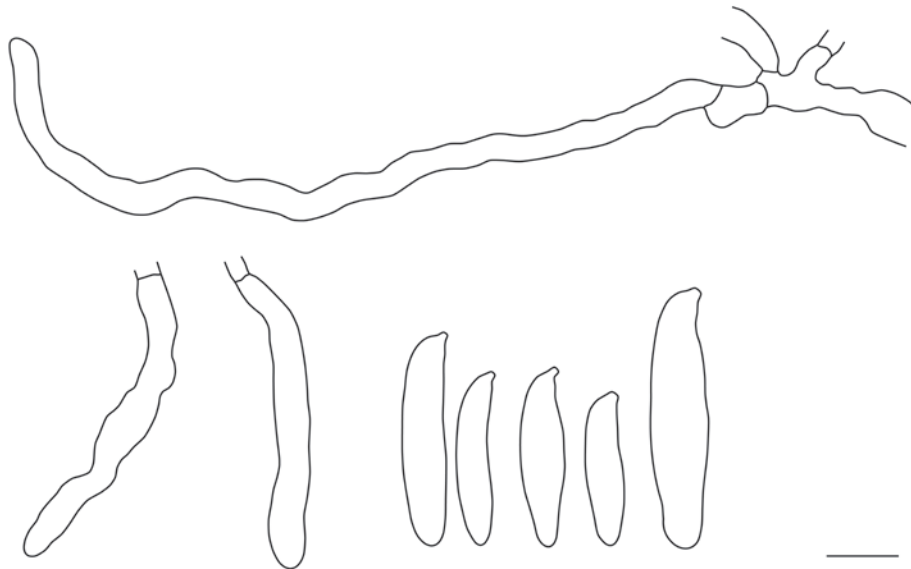


Fig. 7. *Bourdotigloea cerea* (holotype). Cystidia and basidiospores. Scale bar = 10  $\mu$ m.

***Bourdotigloea concisa*** Spirin & Trichies, *sp. nov.* MycoBank MB825589. Fig. 8.

*Etymology:* Concisus (Lat., adj.) – concise, brief.

*Holotype:* France, Moselle, Fontoy, dead *Stereum rugosum* on *Alnus glutinosa*, 27 Feb. 2011, Trichies 11015 (H, **isotype** – GT).

*Basidiocarps* resupinate, 0.03–0.05 mm thick, first pruinose, greyish, then pale ochraceous, semitranslucent to opaque, rather tough. *Basal hyphae* hyaline to brownish, slightly to distinctly thick-walled, sturdy, (6.7–)7.7–11.9(–12.0)  $\mu$ m diam (n = 30/2). *Subhymenial hyphae* thin- to slightly thick-walled, easily collapsing, some irregularly inflated, (4.1–)4.3–7.3(–7.0)  $\mu$ m diam (n = 40/2). *Basidia* tubular-clavate, straight or somewhat curved, 61–87  $\times$  (6.2–)6.4–8.2(–8.8)  $\mu$ m (n = 20/2), with sharp-pointed sterigmata up to 11  $\times$  7  $\mu$ m; probasidia saccate, 25–66

$\times$  11–13  $\mu$ m. *Cystidia* abundant, distinctly moniliform, 80–121  $\times$  7.5–12.5  $\mu$ m. *Basidiospores* mostly fusiform, (14.1–)15.2–27.2(–27.8)  $\times$  (5.0–)5.7–8.2(–9.2)  $\mu$ m (n = 90/3), L = 18.67–20.42, W = 6.39–6.86, Q' = (2.1–)2.2–4.2(–4.6), Q = 2.74–3.15.

*Distribution and ecology:* Europe (France, UK); fallen branches and logs of deciduous trees (*Alnus*, *Fagus*, *Salix*), occasionally also dead basidiocarps of corticioid fungi (*Hymenochaete*, *Stereum*).

*Notes:* *Bourdotigloea concisa* is most similar to *B. grisea*, *B. dura* and *B. vestita*. It differs from the two latter species in having distinctly moniliform (bearing multiple, rather regular and pronounced constrictions) cystidia. Moreover, basidiospores of *B. vestita* are wider. Differences between *B. concisa* and *B. grisea* are more subtle: the species can mainly be distinguished due to differently looking subicular hyphae, as well as maximal length of basidia and basidiospores.

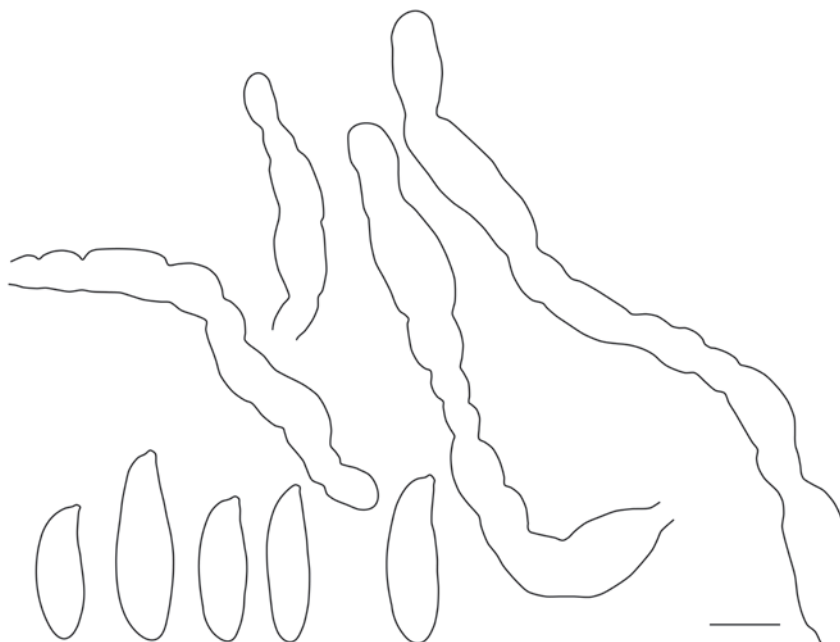
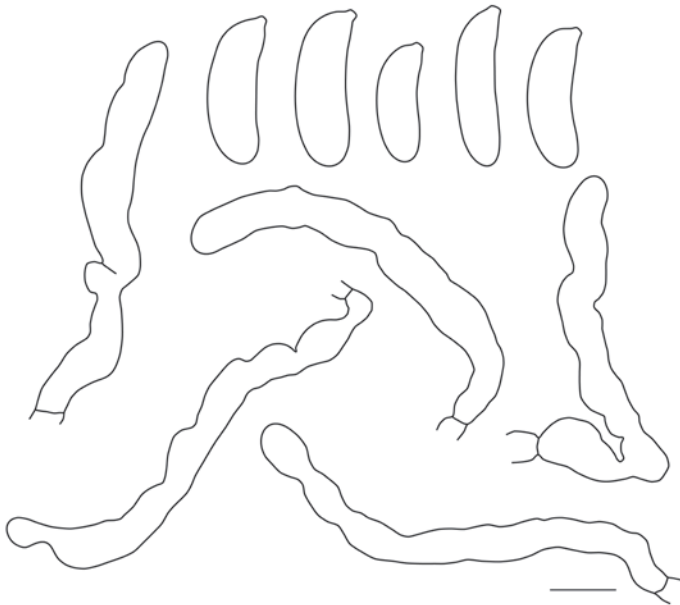


Fig. 8. *Bourdotigloea concisa* (holotype): cystidia and basidiospores. Scale bar = 10  $\mu$ m.



**Fig. 9.** *Bourdotigloea dura* (holotype). Cystidia and basidiospores. Scale bar = 10  $\mu$ m.

***Bourdotigloea dura*** Spirin & V. Malysheva, *sp. nov.* MycoBank MB825590. Fig. 9.

**Etymology:** Durus (Lat., adj.) – hard, tough.

**Holotype:** Norway, Oppland: Nord-Fron, Liadalane Nat. Res., *Betula pubescens*, 12 Sep. 2016, Spirin 11054 (O).

**Basidiocarps** resupinate, 0.03–0.05 mm thick, first pruinose, greyish, then strongly gelatinized, tough, almost invisible in dry condition. **Basal hyphae** hyaline to brownish, slightly to distinctly thick-walled, sturdy, (7.6–)7.8–13.8(–17.0)  $\mu$ m diam (n = 30/2). **Subhymenial hyphae** thin- to slightly thick-walled, some irregularly inflated, (4.0–)4.2–8.0(–8.2)  $\mu$ m diam (n = 30/2). **Basidia** tubular-clavate, straight or somewhat curved, 52.5–80  $\times$  (6.1–)6.2–7.6(–7.7)  $\mu$ m (n = 25/2), with sharp-pointed sterigmata up to 6  $\times$  5  $\mu$ m; probasidia saccate, 23.5–39  $\times$  7–12  $\mu$ m. **Cystidia** abundant, tubular-clavate, often sinuose and with several slight constrictions, 80–121  $\times$  7.5–12.5  $\mu$ m. **Basidiospores** cylindrical to fusiform, (15.1–)16.7–27.7(–32.3)  $\times$  (5.6–)5.7–7.4(–10.4)  $\mu$ m (n = 60/2), L = 20.90–21.69, W = 6.16–6.55, Q' = (2.3–)2.8–4.4(–4.9), Q = 3.34–3.39.

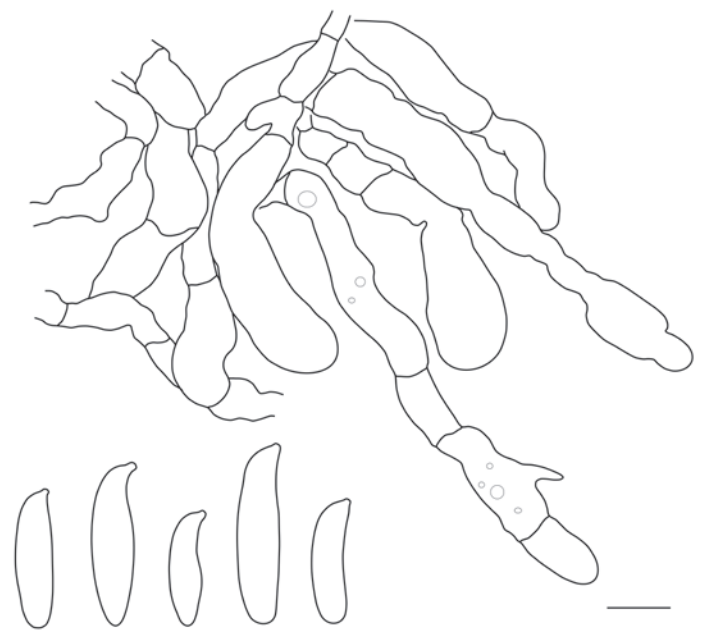
**Distribution and ecology:** Europe (Norway); rather rotten decorticated logs of deciduous trees (*Alnus*, *Betula*).

**Notes:** Morphologically, *Bourdotigloea dura* is most similar to *B. concisa* but it differs in having only slightly constricted cystidia. *Bourdotigloea vestita* with similarly looking cystidia possesses wider basidiospores.

***Bourdotigloea grisea*** Spirin & V. Malysheva, *sp. nov.* MycoBank MB825591. Fig. 10.

**Etymology:** Griseus (Lat., adj.) – grey.

**Holotype:** Norway, Møre og Romsdal, Nesset, Eikesdalen, *Alnus incana*, 28 Sep. 2017, Spirin 11629 (O).



**Fig. 10.** *Bourdotigloea grisea* (holotype). Hyphae, hymenial structures and basidiospores. Scale bar = 10  $\mu$ m.

**Basidiocarps** resupinate, 0.03–0.05 mm thick, pruinose, greyish. **Basal hyphae** hyaline to brownish, slightly thick-walled, sparse, (6.2–)6.3–10.7(–10.8)  $\mu$ m diam (n = 20/2). **Subhymenial hyphae** thin- or only slightly thick-walled, easily collapsing, some irregularly inflated, (3.8–)4.2–7.7(–7.8)  $\mu$ m diam (n = 20/2). **Basidia** tubular-clavate, straight or somewhat curved, 61.5–108  $\times$  (5.8–)6.0–8.1(–8.2)  $\mu$ m (n = 48/2), with sharp-pointed sterigmata up to 11  $\times$  3.5  $\mu$ m; probasidia saccate, 28–48  $\times$  10–14  $\mu$ m. **Cystidia** abundant, distinctly moniliform, 80–163  $\times$  8–10.5  $\mu$ m. **Basidiospores** fusiform, the longest ones sigmoid, (17.2–)17.8–34.8(–36.6)  $\times$  (4.7–)5.0–8.2  $\mu$ m (n = 60/2), L = 21.73–23.93, W = 5.98–6.99, Q' = (2.2–)2.4–4.8(–5.7), Q = 3.13–3.98.

**Distribution and ecology:** Europe (Norway); fallen branches and logs of deciduous trees (*Alnus incana*).

**Notes:** *Bourdotigloea grisea* differs from other European species of the genus in having rather poorly differentiated subicular hyphae which are only slightly wider than subhymenial ones. The species is detected twice in an isolated mountain valley in Norway, occurring on alder wood remnants in inundated habitats.

***Bourdotigloea lanea*** Spirin & V. Malysheva, *sp. nov.* MycoBank MB825592. Fig. 4.

**Etymology:** Laneus (Lat., adj.) – soft.

**Holotype:** Norway, Østfold, Aremark, *Picea abies*, 25 Oct. 2011, J. Nordén 9962 (O).

**Basidiocarps** resupinate, 0.03–0.06 mm thick, first pruinose, then compact floccose, greyish. **Basal hyphae** hyaline to brownish, slightly to distinctly thick-walled, easily collapsing, (7.0–)7.4–14.0(–14.2)  $\mu$ m diam (n = 20/1). **Subhymenial hyphae** thin- to slightly thick-walled, easily collapsing, (4.0–)4.1–6.0(–6.2)  $\mu$ m diam (n = 20/1). **Basidia** tubular-clavate, straight or somewhat curved, 69–88.5  $\times$  (6.0–)6.2–8.2(–8.3)  $\mu$ m (n = 20/1),

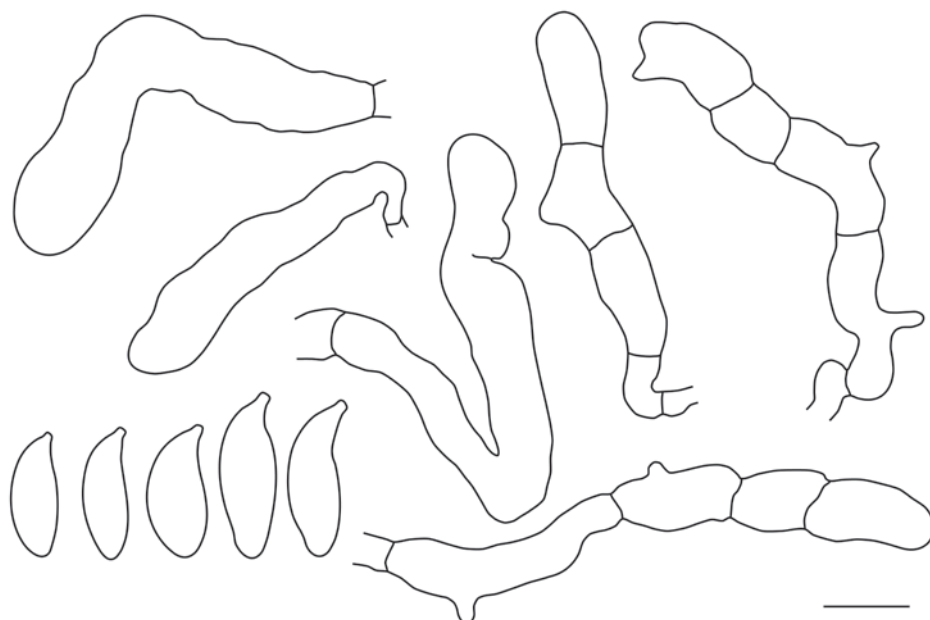


Fig. 11. *Bourdotigloea longispora* (lectotype). Cystidia, basidia and basidiospores. Scale bar = 10  $\mu$ m.

with sharp-pointed sterigmata up to  $11 \times 4.5 \mu\text{m}$ ; probasidia saccate,  $24\text{--}37 \times 8\text{--}11.5 \mu\text{m}$ . *Cystidia* rare, tubular, more or less straight to somewhat sinuous, rarely with several inconspicuous constrictions,  $34\text{--}86 \times 6.5\text{--}10 \mu\text{m}$ . *Basidiospores* fusiform, some cylindrical, very rarely narrowly ellipsoid,  $(11.3\text{--})12.4\text{--}19.2\text{--}(19.4) \times (5.0\text{--})5.1\text{--}9.1\text{--}(10.2) \mu\text{m}$  ( $n = 30/1$ ),  $L = 15.98$ ,  $W = 7.22$ ,  $Q' = (1.6\text{--})1.8\text{--}3.1\text{--}(3.5)$ ,  $Q = 2.26$ .

*Distribution and ecology*: Europe (Norway); fallen, decorticated log of *Picea abies*.

*Notes*: Basidiocarps of *Bourdotigloea lanæa* are floccose, while they are gelatinized and of more compact structure in other species of the genus. However, anatomical features and DNA data indicate it is a member of *Bourdotigloea*. Microscopically, *B. lanæa* is most similar to the North American *B. longispora*. The latter species has shorter cystidia, smaller basidia and narrower basidiospores.

***Bourdotigloea longispora*** (G.E. Baker) Spirin, *comb. nov.* MycoBank MB825593. Fig. 11.

*Basionym*: *Helicogloea longispora* G.E. Baker, Mycologia 38: 634. 1946. Lectotype. **USA**, Oregon, Lane Co., Lorane, *Pseudotsuga menziesii*, 22 Oct. 1938 Doty 522 (NY00834142, selected here) (MycoBank MBT 383604).

*Basidiocarps* resupinate, 0.02–0.04 mm thick, semitranslucent or not macroscopically visible, developing as hyphae with basidia inside or under basidiocarps of corticioid fungi. *Basal hyphae* hyaline to pale brownish, slightly to distinctly thick-walled, sturdy,  $6\text{--}12 \mu\text{m}$  diam. *Subhymenial hyphae* thin- to slightly thick-walled,  $(3.0\text{--})3.7\text{--}7.3\text{--}(8.3) \mu\text{m}$  diam ( $n = 20/1$ ). *Basidia* tubular-clavate, straight or somewhat curved,  $41\text{--}63 \times (5.2\text{--})5.8\text{--}7.0\text{--}(7.6) \mu\text{m}$  ( $n = 20/1$ ), with sharp-pointed sterigmata up to  $6 \times 3 \mu\text{m}$ ; probasidia saccate,  $35\text{--}50 \times 8\text{--}11 \mu\text{m}$ . *Cystidia* infrequent, tubular, more or less straight to somewhat sinuous,  $34\text{--}52 \times 6\text{--}8 \mu\text{m}$ . *Basidiospores* cylindrical-fusiform, some more or less sigmoid,  $(12.0\text{--})12.8\text{--}18.3\text{--}(19.1) \times (4.9\text{--})5.1\text{--}7.3\text{--}(7.6) \mu\text{m}$  ( $n = 30/1$ ),  $L = 15.00$ ,  $W = 5.73$ ,  $Q' = (1.7\text{--})2.1\text{--}3.1\text{--}(3.2)$ ,  $Q = 2.64$ .

*Distribution and ecology*: Europe (Russia), North America (USA – North Carolina, Oregon); rotten logs of *Pseudotsuga menziesii* and *Pinus* spp.

*Notes*: Rather wide and clearly thick-walled, occasionally coloured basal hyphae, inflated subhymenial hyphae, cystidia and fusiform basidiospores of *H. longispora* support its transfer to *Bourdotigloea*. Evidently, the species has been overlooked due to tiny basidiocarps often hidden among or under fructifications of other fungi. One recent collection from North-West Russia (Spirin 12192) agrees with the North American material, except slightly shorter basidiospores,  $(10.7\text{--})10.8\text{--}15.6\text{--}(17.7) \times (5.0\text{--})5.3\text{--}7.4\text{--}(7.6) \mu\text{m}$  ( $n = 30/1$ ),  $L = 13.42$ ,  $W = 6.22$ ,  $Q' = (1.7\text{--})1.8\text{--}2.6\text{--}(3.1)$ ,  $Q = 2.17$ . For now, we treat it as *B. longispora*.

***Bourdotigloea multifurcata*** Spirin & V. Malysheva, *sp. nov.* MycoBank MB825594. Figs 3, 12.

*Etymology*: Multifurcatus (Lat., adj.) – intensively branched in a fork-like manner.

*Holotype*: **Norway**, Aust-Agder, Grimstad, Sæveli Nat. Res., *Quercus robur* (fallen branch) and dead *Fuscoporia ferrea*, 2 Nov. 2017, Spirin 11785 (O).

*Basidiocarps* resupinate, 0.03–0.05 mm thick, pruinose, greyish. *Basal hyphae* hyaline to brownish, slightly to distinctly thick-walled,  $(9.1\text{--})9.2\text{--}18.8\text{--}(19.3) \mu\text{m}$  diam ( $n = 20/1$ ). *Subhymenial hyphae* thin- to slightly thick-walled, often distinctly inflated,  $(4.2\text{--})4.3\text{--}7.9\text{--}(8.1) \mu\text{m}$  diam ( $n = 20/1$ ). *Basidia* tubular-clavate, straight to clearly twisted,  $61.5\text{--}85 \times (6.2\text{--})6.3\text{--}8.3\text{--}(9.0) \mu\text{m}$  ( $n = 20/1$ ), with sharp-pointed, often bi- or trifurcate and randomly arranged sterigmata up to  $15 \times 5 \mu\text{m}$ ; probasidia saccate, often twisted,  $28\text{--}48 \times 10.5\text{--}16 \mu\text{m}$ . *Cystidia* abundant, distinctly moniliform,  $60\text{--}153 \times 6\text{--}12.5 \mu\text{m}$ . *Basidiospores* cylindrical to broadly fusiform,  $(15.3\text{--})16.2\text{--}32.2\text{--}(35.6) \times (5.1\text{--})5.2\text{--}9.6\text{--}(9.7) \mu\text{m}$  ( $n = 30/1$ ),  $L = 22.64$ ,  $W = 6.51$ ,  $Q' = (2.6\text{--})2.7\text{--}4.5\text{--}(4.7)$ ,  $Q = 3.50$ , often germinating by bi-trifurcate sterigmata.

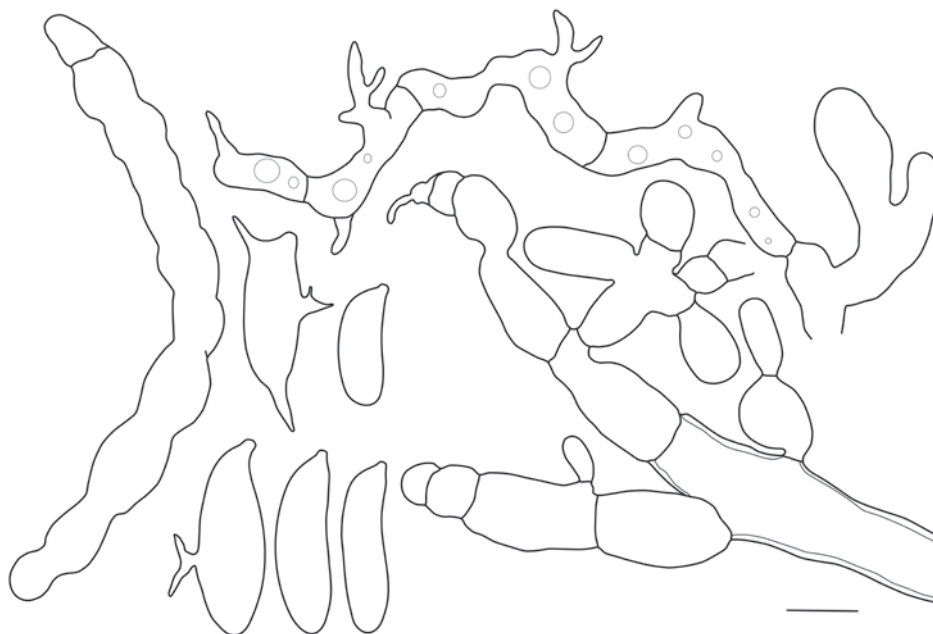


Fig. 12. *Bourdotigloea multifurcata* (holotype). Hyphae, hymenial structures and basidiospores. Scale bar = 10  $\mu$ m.

**Distribution and ecology:** Europe (Norway); fallen branches of deciduous trees (*Quercus*) and dead basidiocarps of polypores (*Phellinus* s.l.).

**Notes:** Moniliform cystidia and rather wide basidiospores place *B. multifurcata* in the difficult *B. vestita* complex, alongside *B. concisa*, *B. dura*, *B. grisea* and *B. vestita* s. str. The most striking feature of *B. multifurcata* is the highly irregular shape and number of sterigmata: they are usually furcate, and up to three separate sterigmata may occur at one basidial cell. This might explain a high variability of basidiospores, also showing multiple germination by fork-like sterigmata.

***Bourdotigloea sebacinoidea*** (L.S. Olive) Spirin, **comb. nov.** MycoBank MB825595. Fig. 13.

**Basionym:** *Helicogloea sebacinoidea* L.S. Olive, *Mycologia* **40**: 588. 1948. **Lectotype:** USA, Louisiana, Caddo Parish, Shreveport, dead *Exidia glandulosa* on branch of *Quercus* sp., 4 Jul. 1947, Olive (NY00834143, selected here) (MycoBank MBT383605).

**Synonym:** *Helicogloea parasitica* L.S. Olive, *Mycologia* **43**: 677. 1951 (nomen superfluum).

**Basidiocarps** resupinate, hypochnoid, almost invisible by a naked eye. **Basal hyphae** hyaline to pale brownish, slightly to distinctly thick-walled, easily collapsing, (6.2–)7.0–12.3(–12.7)  $\mu$ m diam (n = 20/1). **Subhymenial hyphae** thin- to slightly thick-walled, (4.0–)4.2–6.9(–7.2)  $\mu$ m diam (n = 20/1). **Basidia** tubular-clavate, straight or somewhat curved, ca. 94  $\times$  6–8  $\mu$ m, with sharp-pointed sterigmata up to 6  $\times$  2  $\mu$ m; probasidia saccate, 30–46  $\times$  9–11  $\mu$ m. **Cystidia** not detected. **Basidiospores** cylindrical-fusiform, some slightly or moderately curved, 13–23.2  $\times$  4.8–7.3  $\mu$ m (n = 14/1), L = 17.54, W = 5.86, Q' = (2.0–)2.1–3.9(–4.3), Q = 3.03.

**Distribution and ecology:** North America (USA – Louisiana); corticated oak branch and dead *Exidia glandulosa*.

**Notes:** The original material of *H. sebacinoidea* is very scanty although hyphal shape and width, as well as basidia and

basidiospores agree with the current generic concept of *Bourdotigloea*. Hence a new combination. However, cystidia have not been detected in *B. sebacinoidea*, and it is still uncertain if they are absent or just not properly developed in the single existing specimen. The species deserves further study.

***Bourdotigloea vestita*** (Bourdot & Galzin) Aime, *Mycologia* **110**: 144. 2018. Fig. 14.

**Basionym:** *Platygloea vestita* Bourdot & Galzin, *Bull. Soc. Mycol. France* **39**: 261, 1924. **Lectotype:** France, Aveyron, Bouissou, *Genista tinctoria*, 24 Dec. 1916, Galzin 21380 (herb. Bourdot 19240) (PC 0706699, selected here) (MycoBank MBT383606).

**Basidiocarps** resupinate, 0.03–0.06 mm thick, first pruinose, greyish, then pale ochraceous, opaque, ceraceous. **Basal hyphae** hyaline to brownish, slightly to distinctly thick-walled, sturdy, (6.7–)7.1–11.8(–13.0)  $\mu$ m diam (n = 50/3). **Subhymenial hyphae** thin- to slightly thick-walled, (3.4–)3.7–7.7(–7.8)  $\mu$ m diam (n = 50/3). **Basidia** tubular-clavate, straight or somewhat curved, 61–81  $\times$  (6.8–)7.0–10.3(–11.6)  $\mu$ m (n = 20/1), with sharp-pointed sterigmata up to 21  $\times$  5.5  $\mu$ m; probasidia saccate, 25–48  $\times$  9–16  $\mu$ m. **Cystidia** rather numerous, tubular, irregularly constricted, 45–109  $\times$  6.5–12  $\mu$ m. **Basidiospores** fusiform, rarely long cylindrical and then moderately curved, (14.6–)15.2–30.4(–31.3)  $\times$  (6.0–)6.1–9.8(–10.3)  $\mu$ m (n = 85/3), L = 21.96–22.55, W = 7.29–7.89, Q' = (2.1–)2.2–3.9(–4.1), Q = 2.95–3.05.

**Distribution and ecology:** Europe (France); fallen branches and rotten wood of angiosperms (*Alnus*, *Erica*, *Genista*) and possibly also gymnosperms.

**Notes:** Bourdot & Galzin (1924) introduced *P. vestita* based on numerous collections from France and England. Our study shows that they belong to two different species. Therefore, a lectotype is designated here to settle the species identity of *P. vestita*. Another species present among the authentic material is described above as *B. concisa*. From other species of the genus, *B. vestita* differs by wider basidia and basidiospores. Cystidia

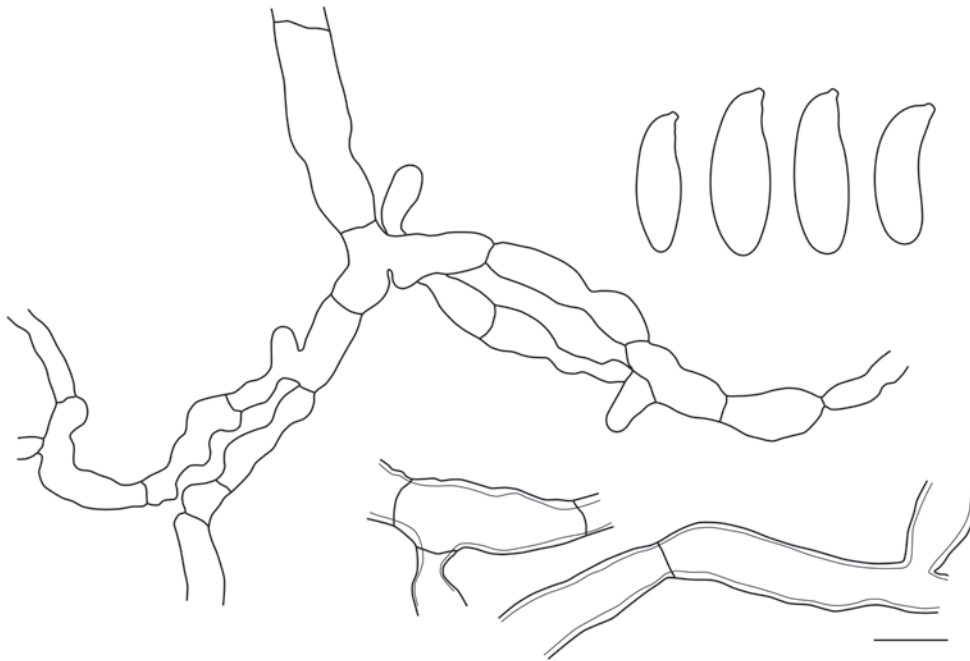


Fig. 13. *Bourdotigloea sebacinoidea* (lectotype). Hyphae and basidiospores. Scale bar = 10  $\mu$ m.

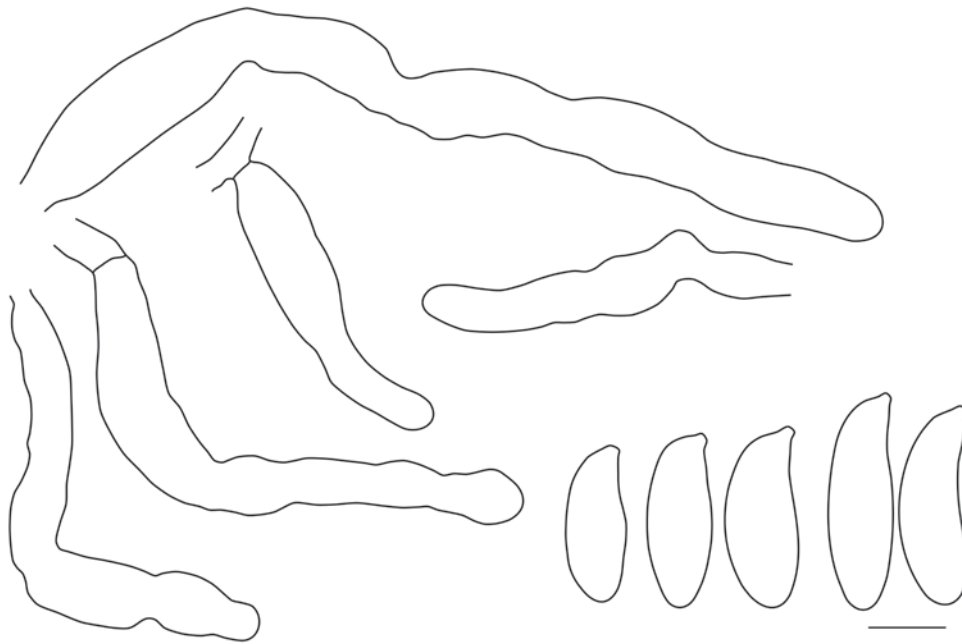


Fig. 14. *Bourdotigloea vestita* (Trichies 09017). Cystidia and basidiospores. Scale bar = 10  $\mu$ m.

of *B. vestita* possess occasional constrictions although they are much less regular and pronounced than in *B. concisa*, *B. grisea* and *B. multifurcata*.

***Helicogloea*** Pat., *Bull. Soc. Mycol. France* **8**: 121. 1892.

*Synonyms*: *Saccoblastia* Möller, *Botanische Mittheilungen aus den Tropen* **8**: 16. 1895. *Lectotype*: *Saccoblastia ovispora* Möller (selected by Clements & Shear 1931).

*Infundibura* Nag Raj & Kendrick, *Canad. J. Bot.* **59**: 544. 1981. *Type species*: *Infundibura adhaerens* Nag Raj & Kendrick (asexual).

*Leucogloea* R. Kirschner in Agerer et al., *Frontiers in Basidiomycete Mycology*: 177. 2004. *Type species*: *Dendrodochium compressum* Ellis & Everh. (asexual).

*Neogloea* Aime, *Mycologia* **110**: 143. 2018. *Type species*: *Helicogloea variabilis* K. Wells.

*Basidiocarps* resupinate, normally thin, rarely addressed-pulvinate, semitranslucent, waxy to gelatinous. *Hyphae* clampless, short- or long-celled, usually not inflated, slightly to moderately cyanophilous. *Basal hyphae* hyaline, slightly to distinctly thick-walled, 2–7  $\mu$ m diam. *Subhymenial hyphae* thin- to slightly thick-walled, 2–5  $\mu$ m diam, slightly cyanophilous. *Basidia* four-celled, tubular-clavate, straight or curved / twisted, with sharp-pointed, slender sterigmata; probasidia clavate or saccate. *Cystidia* absent. *Basidiospores* cylindrical to broadly ellipsoid / subglobose (except *H. angustispora* with narrowly fusiform basidiospores), 7–30  $\times$  4–15  $\mu$ m, germinating by repetition.



On decayed wood of deciduous trees and conifers, rarely on other plant remnants (fallen cones or dead palm stems), as well as in or under other corticioid fungi.

*Type species: Helicogloea lagerheimii* Pat. (selected by Clements & Shear 1931).

*Notes:* As defined here, *Helicogloea* embraces 25 species with waxy or gelatinous, semitranslucent basidiocarps and clampless hyphae. Basal hyphae of almost all *Helicogloea* species treated here are wider than subhymenial ones, and they possess thicker walls. They are, however, colourless, and this feature, as well as absence of differentiated cystidia, differentiates *Helicogloea* from *Bourdotigloea*. *Saccosoma* species have floccose or dense, arid (non-gelatinized) basidiocarps and clamped hyphae, as well as straight (not curved) basidia.

Four species earlier ascribed to *Helicogloea* have been excluded from the present treatment. According to Baker (1936), *H. graminicola* (Bres.) G.E. Baker is similar to other species of *Helicogloea s. str.* but it has clamped hyphae. Moreover, its occurrence on herbaceous stems is untypical for the genus because all species so far known inhabit wood remnants. *Helicogloea musaispora* Chee J. Chen & Oberw. (2000) from Taiwan have fusiform basidiospores and swollen, rather wide hyphae (7–12 µm diam), and thus it may belong to *Bourdotigloea*. No pigmentation of basal hyphae nor cystidia were mentioned in the protologue, however, and we feel this species deserves further study. The type material of *H. irregularis* by Olive (1958) from Tahiti consists of undifferentiated, irregularly thick-walled, partly swollen and somewhat winding but rather narrow hyphae. A hyphal structure of this kind looks different from other *Helicogloea* species although basidia and basidiospores of *H. irregularis* are more or less typical for this genus. For now, we exclude this species from *Helicogloea*. Finally, *Helicogloea indica* Boedijn (1937) was described as having lunate (strongly curved, tapering to both ends) basidiospores and exceptionally narrow hyphae. These features do not fit the generic concept of *Helicogloea* accepted here.

Bourdot & Galzin (1928) and Bresadola (in Coker 1928) believed that *S. ovispora*, the type of *Saccoblastia*, is a species with floccose fructifications, i.e. it belongs to the vicinities of *S. farinacea* and its relatives. Donk (1958, 1966) provided a detailed argumentation for this viewpoint. However, we cannot accept it for the following reasons. First, the protologue of *S. ovispora* (Möller 1895: 16) certainly refers to a species with hygroscopic, gelatinized basidiocarps almost disappearing in dry condition ("Bei sehr feuchtem Wetter sieht dieser Ueberzug fast schleimig, bei trockenem Wetter dagegen bemerkt man nur einen lockeren Hyphenfilz, der bei vollständigem Trocknen zur Unsichtbarkeit zusammenfällt"). This description is not applicable to *S. farinacea* and closely related species with arid basidiocarps almost unchanging in herbarium. Second, *S. ovispora* was described and illustrated as a clampless species ("keine Schnallen besitzen" – *ibid.*, p. 16) but all hitherto known species with floccose basidiocarps have clamped hyphae. Third, basidia of *S. ovispora* are characterized as irregularly curved ("unregelmässig hin und hergebogen" *ibid.*, p. 17). To summarize, gelatinous basidiocarps, clampless hyphae and curved basidia of *S. ovispora* indicate that it belongs to *Helicogloea s. str.* The species is typified below with the only authentic specimen so labelled and it is transferred to *Helicogloea*. Kizimova-Horovitz *et al.* (2000) proposed to select another of Möller's species, *S.*

*sphaerospora*, as a lectotype of the genus. This opportunity is precluded by Art. 10.5 of the Code because the lectotypification by Clements & Shear (1931) has priority. Moreover, as Donk (1958) correctly noted, *S. ovispora* was the main element of Möller's generic concept.

Diagnostic features of sexual *Helicogloea* spp. distributed in temperate Northern Hemisphere are summarized in Table 2.

*Helicogloea angustispora* L.S. Olive, *Bull. Torrey Bot. Club* **78**: 107. 1951.

*Lectotype:* USA, North Carolina, Macon Co., Highlands, on very rotten frondose stump in a rhododendron thicket, 29 Aug. 1950 Olive (TENN 43272, selected here) (MycoBank MBT383607).

*Synonym:* *Infundibura adhaerens* Nag Raj & Kendrick, *Canad. J. Bot.* **59**: 544. 1981 (fide Kirschner 2004).

*Notes:* *Helicogloea angustispora* is the only known representative of the genus with fusiform basidiospores strongly reminiscent of *Bourdotigloea*. However, all other structures (in particular, hyaline, only faintly cyanophilous basal hyphae and rather narrow, curved basidia with regularly arranged sterigmata) are typical for *Helicogloea s. str.* Kirschner (2004) proved that *Infundibura adhaerens* is an asexual morph of *H. angustispora*.

*Helicogloea aquilonia* Spirin & V. Malysheva, *sp. nov.* MycoBank MB825597. Fig. 15.

*Etymology:* Aquilonius (Lat., adj.) – northern.

*Holotype:* Russia, Leningrad Reg., Boksitogorsk Dist., Vozhani, *Populus tremula*, 1 Oct. 2016, Spirin 11163 (H, isotype LE).

*Basidiocarps* resupinate, 0.05–0.1 mm thick, in fresh condition semitranslucent, waxy, in herbarium specimens covered by greyish pruina or almost invisible. *Basal hyphae* slightly to distinctly thick-walled, (3.2–)3.6–6.0(–6.2) µm in diam (n = 30/2). *Subhymenial hyphae* thin-walled, rarely slightly thick-walled, easily collapsing, (1.8–)2.2–3.3(–3.5) µm in diam (n = 30/2). *Basidia* tubular-clavate, straight or curved, 43–74 × (5.1–)5.2–7.6(–8.1) µm (n = 30/3), with sharp-pointed sterigmata up to 4 × 1.5 µm; probasidia saccate or clavate, 16–37 × 6.5–11.5 µm. *Basidiospores* broadly cylindrical to broadly ellipsoid, rarely subglobose, ventral side as a rule flat or convex, (8.2–)8.3–12.8(–13.4) × (5.2–)5.5–9.3(–10.3) µm (n = 160/5), L = 9.91–10.93, W = 6.50–8.03, Q' = (1.1–)1.2–1.9(–2.0), Q = 1.34–1.63.

*Distribution and ecology:* Europe (Finland, Germany, Norway, North-West Russia); fallen logs and branches of deciduous trees (*Fagus*, *Populus*, *Quercus*, *Salix*, *Sorbus*, *Tilia*).

*Notes:* *Helicogloea aquilonia* is morphologically most similar to *H. dryina* and *H. sebacea*, and it differs from those species in having wider basidia and basidiospores. Moreover, *H. dryina* is so far detected exclusively on *Picea abies*, while *H. sebacea* certainly has a more southern distribution.

*Helicogloea aurea* G.E. Baker, *Mycologia* **38**: 635. 1946.

This species was described from Panama (Baker 1946) and recently reported from Costa Rica (Kizimova-Horovitz *et al.* 2000). According to descriptions, it is a typical *Helicogloea*

**Table 2.** Sexual members of *Helicogloea* distributed in temperate Northern Hemisphere.

Species	Distribution / hosts	Subicular / tramal hyphae	Basidia ( $\mu\text{m}$ )	Basidiospores ( $\mu\text{m}$ )	Other characters
<i>angustispora</i>	North America, Europe / various plant remnants	thin to slightly thick-walled, 3–4.5 $\mu\text{m}$ diam / distinctly thick-walled, 4.5–7.5 $\mu\text{m}$ diam	30–40 $\times$ 3.5–5	subfusiform, straight or slightly curved, L = 16.52, W = 3.70, Q = 4.46	
<i>caroliniana</i>	North America / <i>Quercus</i>	slightly to distinctly thick-walled, 3–5 $\mu\text{m}$ diam / thin- to distinctly thick-walled, sturdy, 2–4 $\mu\text{m}$ diam	80 $\times$ 6.5–9	cylindrical to broadly cylindrical, L = 14.81, W = 6.51, Q = 2.30	exidioid basidiocarps consisting of extensive gelatinose matrix and embedded, scattered hyphae and basidia
<i>crassitexta</i>	Asia / conifers	slightly to very thick-walled, 4.5–7 $\mu\text{m}$ diam / thin- to slightly thick-walled, 3–4.5 $\mu\text{m}$ diam	70–87 $\times$ 5.5–7	broadly cylindrical to narrowly ovoid, L = 13.75, W = 7.37, Q = 1.88	
<i>lagerheimii</i>	North America, South America / deciduous trees	slightly to distinctly thick-walled, 4–6 $\mu\text{m}$ diam / thin- to slightly thick-walled, 3–4 $\mu\text{m}$ diam	75–114 $\times$ 7.5–8	narrowly ellipsoid to broadly cylindrical, L = 15.33, W = 8.23, Q = 1.88	basidiocarps up to 1 mm thick, basidiospores occasionally 1-septate
<i>microsaccata</i>	East Asia / deciduous trees	thin- to slightly thick-walled, 3–5.5 $\mu\text{m}$ diam / thin- or slightly thick-walled, 2.5–4 $\mu\text{m}$ diam	53–73 $\times$ 6–8	cylindrical to broadly cylindrical, L = 13.08, W = 7.42, Q = 1.77	
<i>septifera</i>	Europe, North America / deciduous trees	slightly to moderately thick-walled, 4–6 $\mu\text{m}$ diam / thin- to slightly thick-walled, 2.5–4.5 $\mu\text{m}$ diam	56–101 $\times$ 7–9	broadly cylindrical to narrowly ellipsoid, L = 13.09–14.67, W = 7.14–7.92, Q = 1.84–1.94	basidiospores occasionally 1–2-septate
<i>sputum</i>	Europe / deciduous trees	thin- to slightly thick-walled, 3.5–6 $\mu\text{m}$ diam / thin-walled, 2.5–4 $\mu\text{m}$ diam	52.5–71 $\times$ 6–9	broadly cylindrical to ellipsoid, more rarely ovoid, L = 13.82, W = 7.17, Q = 1.94	basidia occasionally bearing bifurcate sterigmata
<i>subardosiaca</i>	Europe / conifers	slightly thick-walled, 4–5 $\mu\text{m}$ diam / thin- to slightly thick-walled, 2.5–4.5 $\mu\text{m}$ diam	60–110 $\times$ 5.5–7.5	cylindrical to narrowly ellipsoid, L = 12.22–14.71, W = 6.50–7.11, Q = 1.76–2.19	basidiocarps appearing very late in the season
<i>terminalis</i>	North America / deciduous trees	3–4 $\mu\text{m}$ diam	40 $\times$ 5–7	broadly cylindrical, L = 13.82, W = 6.06, Q = 2.30	

Long-spored species (mean spore length exceeding 12  $\mu\text{m}$ )

Table 2. (Continued).

Species	Distribution / hosts	Subicular / tramal hyphae	Basidia ( $\mu\text{m}$ )	Basidiospores ( $\mu\text{m}$ )	Other characters
<i>aquilonia</i>	Europe / deciduous trees	slightly to distinctly thick-walled, 3.5–6 $\mu\text{m}$ diam / thin-walled, rarely slightly thick-walled, easily collapsing, 2–3.5 $\mu\text{m}$ diam	43–74 $\times$ 5–7.5	broadly cylindrical to broadly ellipsoid, L = 9.91–10.93, W = 6.50–8.03, Q = 1.34–1.63	
<i>burdsallii</i>	North America / deciduous trees	slightly to distinctly thick-walled, 3–5 $\mu\text{m}$ diam / thin-walled, 2.5–3.5 $\mu\text{m}$ diam	32–50 $\times$ 5–6	ellipsoid to broadly ellipsoid, L = 9.00–10.02, W = 6.75–6.78, Q = 1.33–1.49	
<i>dryina</i>	Europe / conifers	thin- or slightly thick-walled, 2–3.5 $\mu\text{m}$ diam	25–68 $\times$ 4–5.5	broadly ellipsoid to subglobose, L = 8.38–9.19, W = 6.60–7.11, Q = 1.18–1.30	basidia clearly curved, often found inside or under basidiocarps of some corticioid fungi, mostly <i>Botryobasidium</i> spp.
<i>exigua</i>	Europe, North America / deciduous trees	slightly to distinctly thick-walled, 3–5.5 $\mu\text{m}$ diam / thin- to slightly thick-walled, 2–3.5 $\mu\text{m}$ diam	29–38 $\times$ 3.5–5	cylindrical, often slightly curved, L = 7.94–8.99, W = 4.23–4.76, Q = 1.73–2.02	
<i>pellucida</i>	Europe, North America / deciduous trees	thin-walled, 3.5–4.5 $\mu\text{m}$ diam / thin-walled, 2–3.5 $\mu\text{m}$ diam	31–40 $\times$ 4–5.5	broadly cylindrical to narrowly ellipsoid, sometimes lacrymoid, L = 8.58–9.24, W = 5.19–5.51, Q = 1.56–1.75	probasidia occasionally 1–2-septate
<i>sebacea</i>	Europe, Asia, North America / deciduous trees	slightly to distinctly thick-walled, 4.0–5.5 $\mu\text{m}$ diam / thin- or slightly thick-walled, 2–4.5 $\mu\text{m}$ diam	27–48 $\times$ 5–7	broadly cylindrical to narrowly ellipsoid, L = 8.95–11.39, W = 5.78–6.26, Q = 1.54–1.83	

species having gelatinous basidiocarps, clampless, narrow hyphae, and rather large, ovoid basidiospores. However, it is the only species in the genus producing conidia directly in basidiocarps (Kisimova-Horovitz *et al.* 2000) seemingly causing a golden-yellow colouration of its dry fructifications.

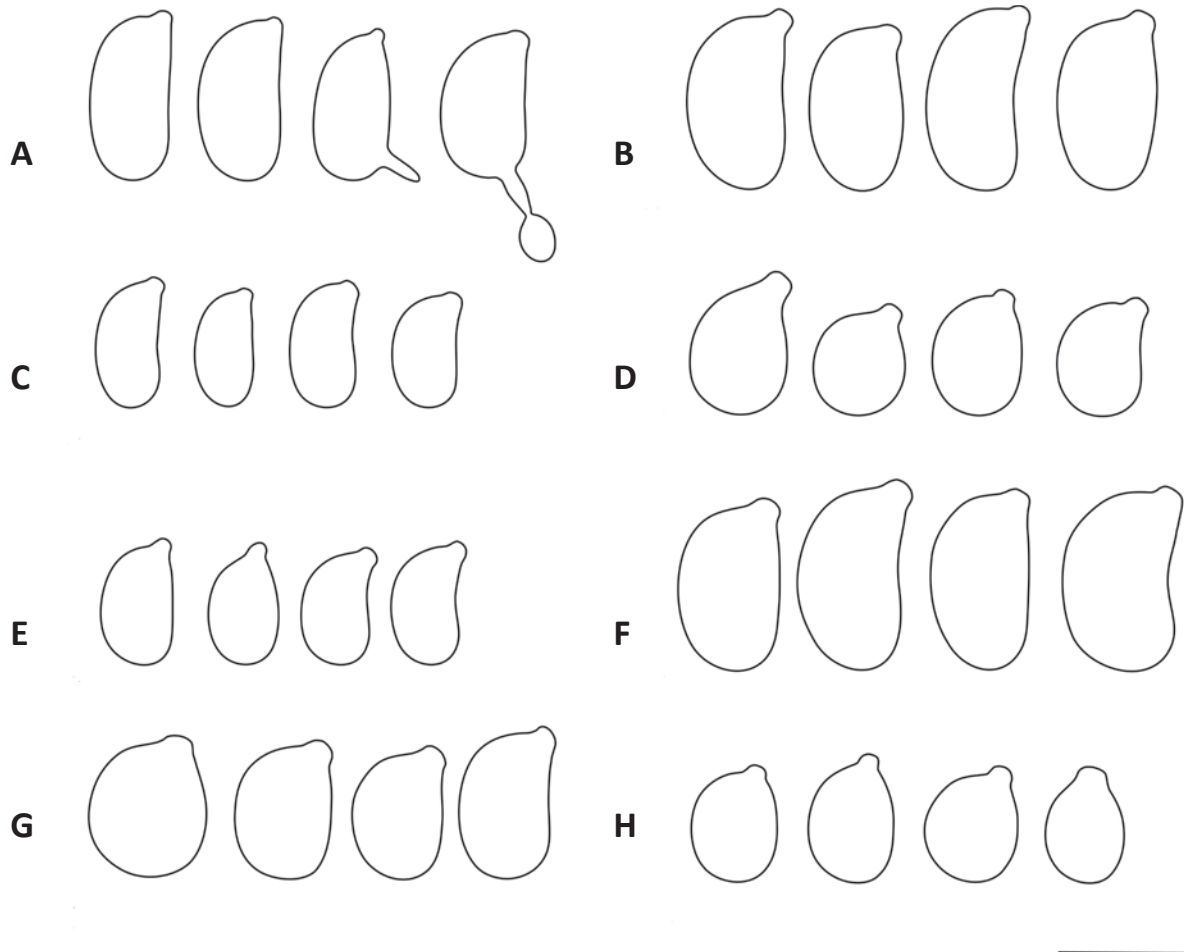
*Helicogloea burdsallii* Spirin & V. Malysheva, *sp. nov.* MycoBank MB825598. Fig. 15.

*Etymology:* After H.H. Burdsall, the eminent North American mycologist.

*Holotype:* USA, Arizona, Santa Cruz Co., Coronado Nat. Forest, *Fraxinus velutina*, 12 Aug. 1971, Burdsall 6017 (CFMR, isotype H).

*Basidiocarps* resupinate, 0.03–0.1 mm thick, in fresh condition semitranslucent, waxy, in herbarium turning to hardly visible greyish bloom. *Basal hyphae* slightly to distinctly thick-walled, (3.1–)3.2–4.8(–4.9)  $\mu\text{m}$  diam (n = 20/1). *Subhymenial hyphae* thin-walled, (2.2–)2.3–3.3(–3.4)  $\mu\text{m}$  diam (n = 20/1). *Basidia* tubular-clavate, straight or curved, 32–50  $\times$  (4.8–)5.0–6.0(–6.1)  $\mu\text{m}$  (n = 20/1), with sharp-pointed sterigmata up to 8  $\times$  2  $\mu\text{m}$ ; probasidia saccate, 21–26  $\times$  7–8  $\mu\text{m}$ . *Basidiospores* ellipsoid to broadly ellipsoid, ventral side as a rule flat or convex, rarely slightly concave, (7.3–)8.2–11.6(–12.1)  $\times$  (5.8–)5.9–7.8(–8.2)  $\mu\text{m}$  (n = 60/2), L = 9.00–10.02, W = 6.75–6.78, Q' = (1.1–)1.2–1.9(–2.0), Q = 1.33–1.49.

*Distribution and ecology:* North America (USA – Arizona, California); fallen logs of deciduous trees (*Fraxinus*, possibly *Umbellularia*).



**Fig. 15.** Basidiospores of *Helicogloea* spp. **A.** *H. sebacea* (lectotype). **B.** *H. crassitexta* (holotype). **C.** *H. exigua* (holotype). **D.** *H. dryina* (holotype). **E.** *H. pellucida* (holotype). **F.** *H. subardosiaca* (lectotype). **G.** *H. aquilonia* (holotype). **H.** *H. burdsallii* (holotype). Scale bar = 10  $\mu$ m.

**Notes:** *Helicogloea burdsallii* is morphologically most similar to *H. aquilonia*, and differs mainly by its shorter basidia. According to DNA data, these species are closely related (Figs 1, 2). However, ITS sequences of *H. aquilonia* are different in about 40 bp from that one of *H. burdsallii*. According to our current knowledge, distribution areas of these species do not overlap.

***Helicogloea caroliniana*** (Coker) G.E. Baker, *Ann. Missouri Bot. Gdn.* **23**: 92. 1936. Fig. 16.

**Basionym:** *Saccoblastia ovispora* var. *caroliniana* Coker, *J. Elisa Mitchell Sci. Soc.* **35**: 121. 1920. **Lectotype:** USA, North Carolina, Orange Co., Chapel Hill, *Quercus* sp. (in the hollow of a living tree), 4 Feb. 1920, *Couch 4078* (BPI 726596, selected here) (MycoBank MBT383609).

**Basidiocarps** adpressed-pulvinate, easily detaching from the substrate, up to 2 mm thick in dry condition, amber-coloured, semitranslucent, tuberculate. **Basal hyphae** slightly to distinctly thick-walled, 3–5  $\mu$ m diam, strongly swelling in KOH. **Subhymenial hyphae** scattered in extensive gelatinous matter, thin- to distinctly thick-walled, sturdy, (2.0–)2.2–3.8(–4.1)  $\mu$ m diam (n = 20/1). **Basidia** tubular-clavate, straight or curved, ca. 80  $\times$  6.6–8.8  $\mu$ m, with sharp-pointed sterigmata up to 6  $\times$  2  $\mu$ m; probasidia saccate or clavate, 31–50  $\times$  10–14  $\mu$ m. **Basidiospores** cylindrical to broadly cylindrical, often slightly curved, (13.0–)13.2–16.7(–17.7)  $\times$  (5.2–)5.7–7.5(–8.7)  $\mu$ m (n = 30/1), L = 14.81, W = 6.51, Q' = (1.8–)2.0–2.7(–2.8), Q = 2.30.

**Distribution and ecology:** North America (USA – North Carolina); on *Quercus* sp.

**Notes:** This remarkable species is so far known only from the type material. It produces large, hygroscopic, exidioid basidiocarps consisting of an extensive gelatinose matrix and embedded, scattered hyphae and basidia. *Helicogloea septifera* is most similar to *H. caroliniana* but it does not produce abundant gelatinous matter detectable in microscopic slides and its hyphae are glued together in a dense tissue. Moreover, basidiospores of *H. septifera* are wider and occasionally septate.

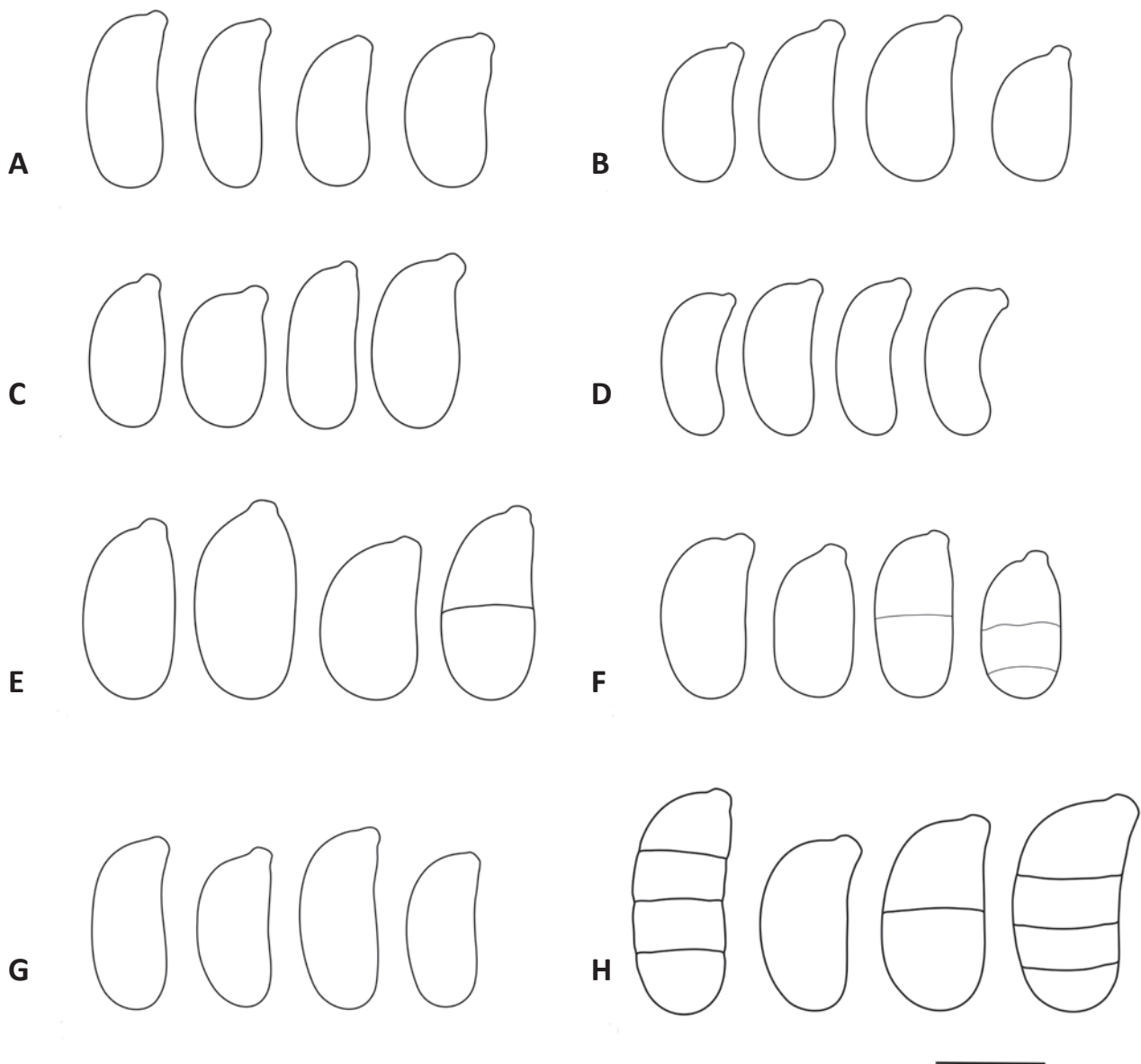
***Helicogloea compressa*** (Ellis & Everh.) V. Malysheva & K. Pöldmaa, **comb. nov.** MycoBank MB825599.

**Basionym:** *Dendrodochium compressum* Ellis & Everh., *Bull. Torrey Bot. Club* **24**: 475. 1897.

**Synonym:** *Helicogloea pauciseptata* R. Kirschner & Chee J. Chen, *Frontiers in Basidiomycote Mycology*: 175. 2004.

**Notes:** Kirschner (2004) proved a connection of this asexual fungus with a *Helicogloea* species described as *H. pauciseptata*. He also proposed a new generic name, *Leucogloea*, for its asexual morph. Our data confirm that *L. compressa* is a member of *Helicogloea* as outlined in this study.

***Helicogloea crassitexta*** V. Malysheva & Spirin, **sp. nov.** MycoBank MB825600. Figs 3, 15.



**Fig. 16.** Basidiospores of *Helicogloea* spp. **A.** *H. terminalis* (holotype). **B.** *H. microsaccata* (holotype). **C.** *H. sputum* (holotype). **D.** *H. lunula* (holotype). **E.** *H. lagerheimii* (lectotype). **F.** *H. septifera* (holotype). **G.** *H. caroliniana* (lectotype). **H.** *H. ovispora* (lectotype). Scale bar = 10  $\mu\text{m}$ .

**Etymology:** *Crassitextus* (Lat., adj.) – possessing distinct tissue.

**Holotype:** **Russia**, Krasnoyarsk Reg., Ermakovskoe Dist., Sayano-Shushensky Nat. Res., *Pinus sibirica*, 17 Aug. 2015 *Malysheva* (LE 312773, isotype H).

**Basidiocarps** resupinate, 0.3–0.5 mm thick, in fresh condition semitranslucent, gelatinous, tuberculate, in herbarium specimens turning to a smooth vernicose crust. **Basal hyphae** slightly to very thick-walled, (4.2–)4.4–7.1(–7.2)  $\mu\text{m}$  diam ( $n = 20/1$ ). **Subhymenial hyphae** thin- to slightly thick-walled, (2.7–)3.0–4.6(–4.8)  $\mu\text{m}$  diam ( $n = 20/1$ ). **Basidia** tubular-clavate, often slightly curved, 70–87  $\times$  (5.4–)5.8–7.2(–7.3)  $\mu\text{m}$  ( $n = 20/1$ ), with sharp-pointed sterigmata up to 5  $\times$  2.5  $\mu\text{m}$ ; probasidia clavate, 17–26  $\times$  6–8  $\mu\text{m}$ . **Basidiospores** broadly cylindrical to narrowly ovoid, ventral side slightly concave or convex, (12.2–)12.3–15.2(–16.2)  $\times$  (6.1–)6.3–9.3(–9.5)  $\mu\text{m}$  ( $n = 30/1$ ),  $L = 13.75$ ,  $W = 7.37$ ,  $Q' = (1.5\text{--})1.6\text{--}2.2(2.3)$ ,  $Q = 1.88$ .

**Distribution and ecology:** Asia (Russia – Siberia); fallen decorticated log of *Pinus sibirica*.

**Notes:** *Helicogloea crassitexta* is morphologically similar to three other long-spored *Helicogloea* species, distributed in temperate-boreal Eurasia – *H. microsaccata*, *H. subardosiaca* and *H. septifera*. First two species possess thinner basidiocarps, almost invisible in dry condition, and distinctly narrower, thin- or only slightly thick-walled basal hyphae. *Helicogloea septifera* is seemingly restricted to angiosperm trees in Europe, and its basidiospores are occasionally septate. One specimen from British Columbia (*Wells 3141*) sequenced during our study shows a 7 bp difference from *H. crassitexta*. Morphologically, this collection is identical to three other specimens from British Columbia and California (listed as *Helicogloea* sp. 1 under Specimens examined). These North-American specimens have much thinner basidiocarps than *H. crassitexta*, and their basidiospores are clearly narrower than in the latter species, (9.7–)10.0–14.3(–14.8)  $\times$  (5.1–)5.2–7.3(–7.9)  $\mu\text{m}$  ( $n = 120/4$ ),  $L =$

11.03–12.22,  $W = 5.78\text{--}6.14$ ,  $Q' = (1.6\text{--})1.7\text{--}2.6(-2.7)$ ,  $Q = 1.80\text{--}2.12$ . Therefore, we refrain from considering them conspecific. This problem should be solved based on other DNA markers.

***Helicogloea dryina*** Spirin & Miettinen, *sp. nov.* MycoBank MB825601. Fig. 15.

*Etymology*: Dryinus (Lat., adj.) – wood-inhabiting.

*Holotype*: Norway, Akershus, Nannestad, *Picea abies*, 8 Oct. 2011, Svantesson 786 (O, isotype H).

*Basidiocarps* resupinate, 0.02–0.1 mm thick, whitish or greyish, waxy, sometimes not macroscopically visible, developing as hyphae with basidia inside or under basidiocarps of corticioid fungi. *Hyphae* thin- or slightly thick-walled,  $(2.2\text{--})2.3\text{--}3.4(-3.8)$   $\mu\text{m}$  diam ( $n = 20/1$ ), not differentiated. *Basidia* tubular-clavate, often clearly curved,  $25\text{--}68 \times (3.1\text{--})4.2\text{--}5.5(-5.6)$   $\mu\text{m}$  ( $n = 32/3$ ), with sharp-pointed sterigmata up to  $5 \times 2.5$   $\mu\text{m}$ ; probasidia clavate, occasionally constricted at the middle part,  $23\text{--}37 \times 5\text{--}9$   $\mu\text{m}$  ( $n = 20/2$ ), sometimes strongly reduced and thus difficult to observe. *Basidiospores* broadly ellipsoid to subglobose, occasionally lacrymoid, some spores distinctly arcuate near apiculus,  $(7.2\text{--})7.3\text{--}10.2(-10.7) \times (6.0\text{--})6.1\text{--}7.9(-8.2)$   $\mu\text{m}$  ( $n = 120/4$ ),  $L = 8.38\text{--}9.19$ ,  $W = 6.60\text{--}7.11$ ,  $Q' = 1.1\text{--}1.4(-1.5)$ ,  $Q = 1.18\text{--}1.30$ .

*Distribution and ecology*: Europe (Finland, Germany, Norway, Sweden); fallen logs of *Picea abies*.

*Notes*: *Helicogloea dryina* is a distinct species due to clearly curved basidia and relatively large, broadly ellipsoid spores. It has often been found inside or under basidiocarps of corticioid fungi, mostly *Botryobasidium* spp., but no haustorial cells connected with hyphae of the host species were detected. Moreover, *H. dryina* is able to produce its own, sometimes rather extensive and well-visible basidiocarps. It seems that it is a saprotrophic species using the host tree and that it is facilitated by *Botryobasidium* and some other corticioid fungi. No parasites are so far recognised among the corticioid members of the *Atractiellales*. All our records of *H. dryina* come from coarse spruce logs at an advanced decay stage, and from old natural-like spruce forests. The specimens were collected from September to November.

***Helicogloea eburnea*** A. Savchenko & V. Malysheva, *sp. nov.* MycoBank MB825602. Figs 3, 17.

*Etymology*: Eburneus (Lat., adj.) – ivory.

*Holotype*: Kenya, Taita-Taveta, Taita Hills, Chawia, decayed hardwood log, 17 Nov. 2017, Savchenko 171127/1127A (H7008830, isotypes LE and EA).

*Sporodochia* pustulate, gelatinous and soft, white semitranslucent; separate pustules up to 1 mm diam and 400  $\mu\text{m}$  thick, partly coalescing, in herbarium shrinking to a thin, waxy, yellowish film. *Internal hyphae* with thickened (up to 0.3–0.5  $\mu\text{m}$ ) walls,  $1.5\text{--}2.5(-3)$   $\mu\text{m}$  diam. *Surface hyphae* thin- to slightly thick-walled (wall 0.1–0.3  $\mu\text{m}$  thick), 1.5–2  $\mu\text{m}$  diam. *Conidiophores* irregularly branched, branches generally parallel to the main axis. *Conidiogenous cells* cylindrical to slightly obclavate, straight or curved, tapering to the apex, with multiple

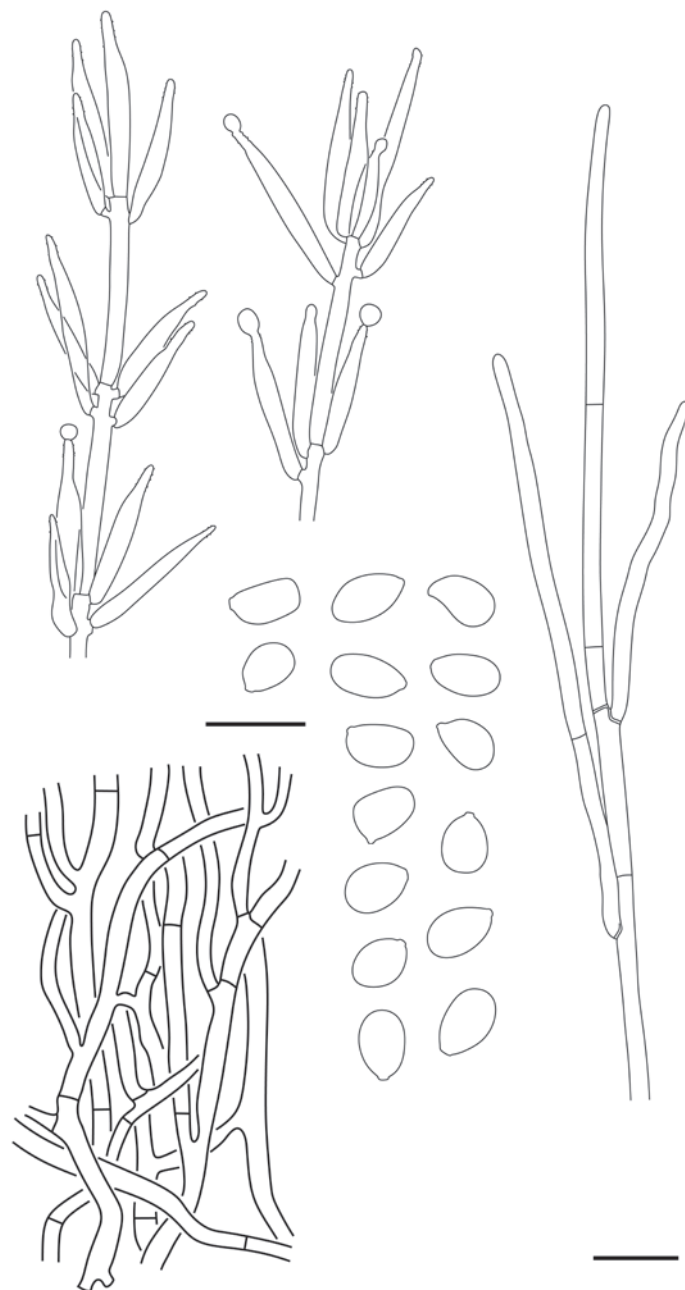


Fig. 17. *Helicogloea eburnea* (holotype). Hyphae, conidiophores (scale bar = 10  $\mu\text{m}$ ) and conidia (scale bar = 5  $\mu\text{m}$ ).

indistinct annellation scars at the top,  $12\text{--}34 \times 1.5\text{--}2.6$   $\mu\text{m}$ . *Conidia* subglobose to ellipsoid, smooth, hyaline, slightly thick-walled,  $(2.8\text{--})2.9\text{--}3.7(-4) \times (2\text{--})2\text{--}2.6(-2.7)$   $\mu\text{m}$  ( $n = 30/1$ ).

*Distribution and ecology*: Africa (Kenya); well-decayed decorticated angiosperm log.

*Notes*: *Helicogloea eburnea* is closely related to another asexual species of the genus, *H. compressa* (see above). Morphologically, they are evidently indistinguishable but differ in their DNA sequences and geographic distribution.

***Helicogloea exigua*** Spirin & V. Malysheva, *sp. nov.* MycoBank MB825603. Fig. 15.

*Etymology*: Exiguus (Lat., adj.) – thin.

**Holotype:** USA, Michigan, Marquette Co., Big Bay, *Acer saccharum*, 6 Aug. 1974, Burdsall 8162 (CFMR FP-8162, isotype H).

*Basidiocarps* resupinate, 0.02–0.04 mm thick, in fresh condition semitranslucent, waxy, in herbarium specimens covered by greyish pruina, almost invisible. *Basal hyphae* slightly to distinctly thick-walled (walls unevenly thickened, up to 1  $\mu\text{m}$  thick), (3.0–)3.2–5.3(–5.6)  $\mu\text{m}$  diam ( $n = 40/2$ ), occasionally inflated up to 6–6.5  $\mu\text{m}$  diam, sturdy. *Subhymenial hyphae* thin- to slightly thick-walled, (2.0–)2.2–3.3(–3.7)  $\mu\text{m}$  diam ( $n = 20/1$ ). *Basidia* tubular-clavate, often curved, 29–38  $\times$  (3.4–)3.9–5.0(–5.2)  $\mu\text{m}$  ( $n = 22/2$ ), with sharp-pointed sterigmata up to 5  $\times$  1.5  $\mu\text{m}$ ; probasidia clavate, 12–33  $\times$  4–5  $\mu\text{m}$ . *Basidiospores* cylindrical, often slightly curved, occasionally ovoid to narrowly ellipsoid, (6.8–)7.0–10.6(–10.8)  $\times$  (3.8–)3.9–5.6(–5.8)  $\mu\text{m}$  ( $n = 90/3$ ),  $L = 7.94\text{--}8.99$ ,  $W = 4.23\text{--}4.76$ ,  $Q' = (1.4\text{--})1.5\text{--}2.4(2.5)$ ,  $Q = 1.73\text{--}2.02$ .

**Distribution and ecology:** Europe (France), North America (Canada – Ontario, USA – Michigan); fallen logs of deciduous trees (*Acer*, *Betula*, *Populus*).

**Notes:** *Helicogloea exigua* is most similar to *H. pellucida* and *H. sebacea* but it possesses distinctly narrower basidiospores and basidia. It seemingly prefers well-decayed wood of deciduous trees although data on its ecology and distribution are still insufficient.

***Helicogloea globosa*** Chee J. Chen & Oberw., *Mycotaxon* **76**: 280. 2000.

**Notes:** This species was described based on one specimen collected on an unidentified deciduous host in Taiwan (Chen & Oberwinkler 2000). The protologue of *H. globosa* points towards *H. aquilonia*. However, the basidiospores of *H. globosa* were described and illustrated as globose to subglobose, 8–10  $\times$  7–9  $\mu\text{m}$  while they are predominantly broadly cylindrical to broadly ellipsoid in all collections of *H. aquilonia* studied by us. Moreover, there are no records of the latter species outside of North Europe. Another similar species from Europe, *H. dryina*, has on average narrower basidiospores and strongly curved basidia, and it occurs exclusively on fallen spruce logs.

***Helicogloea inconspicua*** G.E. Baker, *Mycologia* **38**: 635. 1946.

**Notes:** This species was described based on a single collection from Columbia (Baker 1946). It was differentiated from *H. intermedia* due to regularly 1–2-septate basidiospores. However, the reliability of this feature is vague because all other characters fit well to *H. intermedia*. Further studies are needed to re-confirm the status of *H. inconspicua*.

***Helicogloea incrustans*** Kobayasi, *Misc. Rep. Res. Institute Nat. Resources* **17–18**: 45. 1950.

**Notes:** So far, this species is known only from the type locality in Japan (Kobayashi 1950). Rather thick, extensive, gelatinous fructifications, as well as large, 1–3-septate basidiospores point towards possible affinities to *H. septifera* from Europe. However, basidiospores of *H. incrustans* are certainly longer and wider than in the latter species. The identity of *H. incrustans* deserves further study.

***Helicogloea intermedia*** (Linder) G.E. Baker, *Ann. Missouri Bot. Gdn.* **23**: 91. 1936.

**Basionym:** *Saccoblastia intermedia* Linder, *Ann. Missouri Bot. Gdn.* **16**: 487. 1929. **Lectotype:** Cuba, Pinar del Río, Soledad, on moist decaying stump, Sep. 1924, Linder (MO, not studied) (selected by Baker 1936: 92).

**Notes:** We studied one collection from Panama (FH 00304773) which agrees in all essential aspects with the protologue of *H. intermedia* (Linder 1929). It has thin, gelatinous basidiocarps, four-celled, slightly curved basidia 60–70  $\times$  8–10  $\mu\text{m}$ , and narrowly ellipsoid or broadly cylindrical, occasionally one-septate basidiospores, (15.0–)15.1–19.8(–21.6)  $\times$  (7.4–)7.7–9.2(–9.3)  $\mu\text{m}$  ( $n = 30/1$ ),  $L = 17.54$ ,  $W = 8.39$ ,  $Q' = (1.7\text{--})1.8\text{--}2.4(2.6)$ ,  $Q = 2.09$ . If our identification is correct, *H. intermedia* belongs in the vicinity of *H. lagerheimii*. The latter species, however, produces more extensive fructifications and shorter basidiospores but longer basidia. Identity of *H. intermedia* versus *H. inconspicua* must be re-checked based on newly collected and sequenced material.

***Helicogloea lagerheimii*** Pat., *Bull. Soc. Mycol. France* **8**: 121. 1892. Fig. 16.

**Lectotype:** Ecuador, Baños, Chorrera de Agoyan, rotten branch, Jan. 1892, Lagerheim (FH 00304791, selected by Baker 1936: 93).

*Basidiocarps* resupinate, up to 1 mm thick, in fresh condition semitranslucent, waxy, greyish, tuberculate, in herbarium specimens turning to brownish vernicose crust. *Basal hyphae* slightly to distinctly thick-walled, (3.6–)3.9–6.2(–6.7)  $\mu\text{m}$  diam ( $n = 20/1$ ). *Subhymenial hyphae* thin- to slightly thick-walled, easily collapsing, (2.7–)2.8–4.1(–4.2)  $\mu\text{m}$  diam ( $n = 20/1$ ). *Basidia* tubular-clavate, straight or curved, 75–114  $\times$  7.5–8  $\mu\text{m}$ , with sharp-pointed sterigmata up to 5  $\times$  2  $\mu\text{m}$ ; probasidia saccate or clavate, 29–43  $\times$  8.5–11.5  $\mu\text{m}$ . *Basidiospores* narrowly ellipsoid to broadly cylindrical, ventral side flat or slightly concave, rarely slightly convex, occasionally 1-septate, (13.1–)13.3–18.2(–19.0)  $\times$  (6.3–)6.4–9.3(–9.4)  $\mu\text{m}$  ( $n = 32/1$ ),  $L = 15.33$ ,  $W = 8.23$ ,  $Q' = (1.5\text{--})1.6\text{--}2.2(2.3)$ ,  $Q = 1.88$ .

**Distribution and ecology:** North America (USA – California), South America (Ecuador); rotten wood of deciduous trees.

**Notes:** The description above is based on the type specimen only. *Helicogloea lagerheimii* is undoubtedly congeneric with other species treated here under *Helicogloea s. str.* A specimen from California (BPI 719891) used in DNA studies is morphologically almost identical to the type material, having basidiospores (13.1–)13.7–16.9(–17.2)  $\times$  (7.2–)7.6–9.1(–9.2)  $\mu\text{m}$  ( $n = 30/1$ ),  $L = 15.49$ ,  $W = 8.33$ ,  $Q' = (1.6\text{--})1.7\text{--}2.0(2.1)$ ,  $Q = 1.86$ , although it possesses shorter basidia, up to 80  $\mu\text{m}$  long. Newly collected and sequenced specimens from Ecuador are needed to designate an epitype for *H. lagerheimii*.

***Helicogloea lunula*** Spirin & V. Malysheva, *sp. nov.* MB825604. Fig. 16.

**Etymology:** Lunulus (Lat., adj.) – lunate.

**Holotype:** New Zealand, Wairarapa, Pigeon Bush Res., decorticated branch, 1 Jan. 2006, Paulus & Steer (PDD 88360).

*Basidiocarps* resupinate, extensive (covering several cm), 0.1–0.2 mm thick, waxy-gelatinous, whitish-greyish, opaque. *Basal hyphae* slightly to distinctly thick-walled, (4.8–)5.1–9.2(–9.7)  $\mu\text{m}$  diam ( $n = 20/1$ ), often rather short-celled and sometimes constricted at septa. *Subhymenial hyphae* thin- to slightly thick-walled, (3.2–)3.4–5.3(–5.4)  $\mu\text{m}$  diam ( $n = 20/1$ ), mostly rather short-celled, some bearing several constrictions at the terminal part (moniliform). Oil droplets abundant in slides made in CB. *Basidia* tubular-clavate, often curved, 39–62  $\times$  (5.0–)5.1–6.7(–7.2)  $\mu\text{m}$  ( $n = 22/2$ ), with sharp-pointed sterigmata up to 6  $\times$  3  $\mu\text{m}$ ; probasidia saccate or clavate, 16–21  $\times$  6.5–9  $\mu\text{m}$ . *Basidiospores* cylindrical, often distinctly curved, (12.0–)12.6–15.7(–16.0)  $\times$  (4.8–)4.9–6.1(–6.2)  $\mu\text{m}$  ( $n = 30/1$ ),  $L = 13.95$ ,  $W = 5.32$ ,  $Q' = (2.2–)2.3–2.9(–3.0)$ ,  $Q = 2.63$ .

*Distribution and ecology*: New Zealand; fallen decorticated branch.

*Notes*: *Helicogloea lunula* produces rather extensive basidiocarps with opaque (not semitranslucent) hymenial surface. They are gelatinized, however, as in other species of *Helicogloea s. str.* Distinctly curved basidiospores and a presence of moniliform hyphal ends in hymenium are good diagnostic features of this species.

*Helicogloea microsaccata* V. Malysheva & Spirin, *sp. nov.* MycoBank MB825605. Figs 3, 16.

*Etymology*: *Microsaccatus* (Lat., adj.) – bearing small-sized probasidial sacs.

*Holotype*: **Russia**, Primorie, Ussuriisk Dist., Ussuri Nat. Res., deciduous tree (fallen branch), 15 Aug. 2011, *Malysheva* (LE 262936, isotype H).

*Basidiocarps* resupinate, 0.03–0.06 mm thick, in fresh condition semitranslucent, waxy, in herbarium specimens almost invisible. *Basal hyphae* thin- to slightly thick-walled, (3.1–)3.3–5.2(–6.2)  $\mu\text{m}$  diam ( $n = 20/1$ ), easily collapsing. *Subhymenial hyphae* thin- or slightly thick-walled, (2.3–)2.4–3.9(–4.0)  $\mu\text{m}$  diam ( $n = 20/1$ ). *Basidia* tubular-clavate, often curved, 53–73  $\times$  (6.1–)6.2–8.2(–8.3)  $\mu\text{m}$  ( $n = 21/1$ ), with sharp-pointed sterigmata up to 6.5  $\times$  2.5  $\mu\text{m}$ ; probasidia saccate or clavate, 15–27  $\times$  7–11  $\mu\text{m}$ . *Basidiospores* cylindrical to broadly cylindrical, often slightly curved, more rarely ovoid, (10.4–)10.8–15.2  $\times$  (6.1–)6.2–9.3(–9.5)  $\mu\text{m}$  ( $n = 30/1$ ),  $L = 13.08$ ,  $W = 7.42$ ,  $Q' = (1.5–)1.6–2.0(–2.2)$ ,  $Q = 1.77$ .

*Distribution and ecology*: East Asia (Russia – Primorie); fallen hardwood branch.

*Notes*: *Helicogloea microsaccata* is morphologically most similar to *H. subardosiaca*, and it differs from the latter primarily by its shorter basidia and smaller probasidial sacs. Moreover, *H. subardosiaca* is a European species known exclusively from coniferous hosts while *H. microsaccata* has been detected in East Asia on hardwood. DNA data show that these species are not closely related.

*Helicogloea ovispora* (A. Möller) Spirin, *comb. nov.* MycoBank MB825606. Figs 3, 16.

*Basionym*: *Saccoblastia ovispora* A. Möller, *Botanische Mittheilungen aus den Tropen* 8: 16. 1895.

*Lectotype*: **Brazil**, Santa Catharina, Blumenau, rotten wood, Möller 767 (HBG, selected here) (MycoBank MBT 383610).

*Basidiocarps* resupinate, up to 1 mm thick, semitranslucent, waxy, well visible in dry condition. *Basal hyphae* slightly to distinctly thick-walled, (5.0–)5.1–7.2(–8.2)  $\mu\text{m}$  diam ( $n = 20/1$ ). *Subhymenial hyphae* thin- to slightly thick-walled, (2.8–)2.9–4.1(–4.2)  $\mu\text{m}$  diam ( $n = 20/1$ ). *Basidia* tubular-clavate, straight or curved, 79–100  $\times$  8–10.5  $\mu\text{m}$ , with sharp-pointed sterigmata up to 5  $\times$  2  $\mu\text{m}$ ; probasidia saccate or clavate, 23–56  $\times$  10–12  $\mu\text{m}$ . *Basidiospores* cylindrical to broadly cylindrical, often slightly curved, occasionally 1–3-septate, (14.8–)15.0–20.2(–23.8)  $\times$  (7.9–)8.0–11.1(–11.8)  $\mu\text{m}$  ( $n = 30/1$ ),  $L = 17.29$ ,  $W = 9.30$ ,  $Q' = (1.5–)1.6–2.1(–2.2)$ ,  $Q = 1.87$ .

*Distribution and ecology*: South America (Brazil – Santa Catarina); still corticated logs and branches.

*Notes*: The only authentic specimen of *Saccoblastia ovispora* collected and labelled by Möller survived in herbarium HBG (Friedrichsen 1977). It was studied by us and served as a source of the description above. Möller (1895) presented the basidiospore dimensions of *S. ovispora* in a somewhat confusing manner, and this probably was a reason for Baker (1936) and Lowy (1971) to consider it conspecific with *H. lagerheimii*. In the protologue, Möller (1895: 18) stated that basidiospores of *S. ovispora* still attached to sterigmata have dimensions 13  $\times$  7–8  $\mu\text{m}$ , while mature, detached spores reach up to 26  $\times$  10  $\mu\text{m}$ . The concise diagnosis provided in the end of his book (*ibid.*, p. 162) refers to juvenile basidiospores only. Our measurements given above are based exclusively on mature basidiospores.

Later records of *S. ovispora* were published by Rick (1933, 1958). We studied duplicates of his collections kept in FH (treated as *Helicogloea* sp. 2 in Specimens examined). They are thinner than the lectotype, 0.02–0.05 mm thick, almost invisible in dry condition, and they possess distinctly narrower basal hyphae, (3.6–)3.8–5.2(–5.7)  $\mu\text{m}$  diam ( $n = 20/1$ ). Basidiospores in Rick's collections are not septate, (14.7–)15.3–22.2(–22.6)  $\times$  (6.3–)7.0–10.0(–10.1)  $\mu\text{m}$  ( $n = 40/2$ ),  $L = 19.78–20.01$ ,  $W = 7.77–8.49$ ,  $Q' = (1.8–)1.9–3.1(–3.5)$ ,  $Q = 2.39–2.56$ , i.e. they are somewhat narrower than in *H. ovispora sensu typi*. This indicates that Rick's material belongs to yet another, seemingly unnamed *Helicogloea* species. We leave this problem for later study.

*Helicogloea pellucida* Spirin & V. Malysheva, *sp. nov.* MycoBank MB825607. Fig. 15.

*Etymology*: *Pellucidus* (Lat., adj.) – semitranslucent.

*Holotype*: **Russia**, Nizhny Novgorod Reg., Lukoyanov Dist., Razino, *Alnus glutinosa* (fallen log), 10 Aug. 2016, *Spirin 10610* (H, isotype LE).

*Basidiocarps* resupinate, 0.05–0.1 mm thick, in fresh condition semitranslucent, waxy, in herbarium specimens covered by greyish pruina, almost invisible. *Basal hyphae* thin-walled, (3.2–)3.8–4.6(–4.9)  $\mu\text{m}$  diam ( $n = 20/1$ ), easily collapsing. *Subhymenial hyphae* similar, (2.0–)2.2–3.7(–3.8)  $\mu\text{m}$  diam ( $n = 20/1$ ). *Basidia* tubular-clavate, slightly curved or twisted, 31–40  $\times$  (3.8–)4.2–5.4(–5.8)  $\mu\text{m}$  ( $n = 20/3$ ), with sharp-pointed sterigmata up to 4  $\times$  1.5  $\mu\text{m}$ ; probasidia clavate, 15–20  $\times$  5–7  $\mu\text{m}$ , occasionally 1–2-septate. *Basidiospores* broadly cylindrical to narrowly ellipsoid, sometimes



lacrymoid, ventral side as a rule flat or slightly concave, (7.2–)7.3–10.8(–12.0) × (4.1–)4.6–6.4(–6.6) μm (n = 140/5), L = 8.58–9.24, W = 5.19–5.51, Q' = (1.3–)1.4–2.0(–2.1), Q = 1.56–1.75.

**Distribution and ecology:** Europe (Norway, Russia, Ukraine), North America (Canada – Ontario, USA – Massachusetts, North Carolina); fallen logs of deciduous trees (*Alnus*, *Fraxinus*, *Malus*, *Populus*).

**Notes:** Thin-walled hyphae throughout the basidiocarp and rather narrow basidiospores make *H. pellucida* differ from the similarly looking *H. sebacea* and *H. aquilonia*. Basidiospores of *H. exigua* are cylindrical, often more distinctly curved, and they are even narrower than in *H. pellucida*. Basidial width can also help in identification of these four species although its value is limited to fresh or recent material.

***Helicogloea sebacea*** (Bourdot & Galzin) Spirin & Trichies, **comb. nov.** MycoBank MB825608. Fig. 15.

**Basionym:** *Saccoblastia sebacea* Bourdot & Galzin, *Bull. Soc. Mycol. France* **25**: 15. 1909.

**Lectotype:** France, Allier, St. Priest, *Cerasus* (?) (very rotten wood), 26 Nov. 1908, Bourdot 5882 (PC 0706732, isolectotype S F21004, selected here) (MycoBank MBT383611).

**Basidiocarps** resupinate, 0.05–0.1 mm thick, whitish or greyish, waxy. **Basal hyphae** slightly to distinctly thick-walled, (4.1–)4.2–5.4(–6.1) μm diam (n = 20/2). **Subhymenial hyphae** thin- or slightly thick-walled, (2.1–)2.2–4.3(–4.7) μm diam (n = 22/2). **Basidia** tubular-clavate, often moderately curved or twisted, 27–48 × (5.1–)5.2–6.8(–7.3) μm (n = 33/3), with sharp-pointed sterigmata up to 9 × 2.5 μm; probasidia clavate to saccate, 19–30 × 6–9 μm. **Basidiospores** broadly cylindrical to narrowly ellipsoid, ventral side as a rule concave or flat, (7.3–)7.6–12.8(–13.2) × (5.0–)5.1–7.3(–7.5) μm (n = 210/7), L = 8.95–11.39, W = 5.78–6.26, Q' = (1.3–)1.4–2.2(–2.3), Q = 1.54–1.83.

**Distribution and ecology:** Europe (Denmark, Estonia, France, Germany, Russia, Ukraine), Asia (Russian Far East), North America (USA – Ohio, South Carolina, Tennessee); fallen and rather rotten logs of deciduous trees (*Acer*, *Betula*, *Fagus*, *Fraxinus*, *Quercus* etc.).

**Notes:** *Helicogloea sebacea* was described from the southern part of France based on several collections (Bourdot & Galzin 1909). The best-preserved specimen is selected here as a lectotype. Later Bourdot & Galzin (1927) also introduced a subspecies *subardosiaca* which we consider a separate species (see below). The type material of *Helicobasidium inconspicuum* (described from Austria – Höhnle 1908) fits our concept of *H. sebacea* although it possesses distinctly thick-walled hyphae throughout. The identity of this taxon deserves further study; however, even if it proves to be a good species, *H. inconspicuum* cannot be combined to *Helicogloea*, due to the existence of another species with the same epithet (see above).

***Helicogloea septifera*** Spirin & V. Malysheva, **sp. nov.** MycoBank MB825609. Figs 3, 16.

**Etymology:** Septiferum (Lat., adj.) – bearing septa (referring to a presence of septate basidiospores).

**Holotype:** Norway, Nord-Trøndelag, Grong, Sanddøla, *Ulmus* sp., 13 Jul. 1977, Holten & Siversten (H, isotype TRH 22196, paratypes with the same collecting data – TRH 9167, TRH F16554).

**Basidiocarps** resupinate, 0.5–2 (3) mm thick, in fresh condition semitranslucent, whitish or greyish, gelatinous, in herbarium turning to perceptible, pale ochraceous or brownish vernicose film, hymenial surface often tuberculate. **Basal hyphae** slightly to moderately thick-walled, (3.4–)4.1–6.1(–6.4) μm diam (n = 30/2). **Subhymenial hyphae** thin- to slightly thick-walled, (2.6–)2.7–4.4(–5.0) μm diam (n = 40/2). **Basidia** tubular-clavate, slightly or distinctly curved, 56–101 × (6.7–)6.8–9.0(–9.2) μm (n = 40/2), with sharp-pointed sterigmata up to 10 × 5 μm; probasidia saccate or clavate, 18–52 × 6.5–10 μm. **Basidiospores** broadly cylindrical to narrowly ellipsoid, ventral side as a rule concave or flat, occasionally 1–2-septate, (10.8–)11.1–16.2 × (5.8–)6.2–9.1(–9.5) μm (n = 110/4), L = 13.09–14.67, W = 7.14–7.92, Q' = (1.4–)1.5–2.3(–2.6), Q = 1.84–1.94.

**Distribution and ecology:** Europe (Norway, Russia), North America (USA – Iowa); recently fallen logs and thick branches of deciduous trees (*Alnus*, *Betula*, *Populus*, *Sorbus*, *Ulmus*).

**Notes:** Roberts (2002) reported and described this species from Norway as *H. caroliniana*. We studied the type material of the latter species and found it distinctly different from our specimens from Europe (see remarks under *H. caroliniana*). Basidiocarps of *H. septifera* are normally rather thin (0.5–1 mm) and look the same as in many other species of the genus. Pulvinate and abnormally thick basidiocarps are infected by a pucciniomycete *Achroomyces chlamydospora* (Roberts 2002) whose presence most probably causes this unusual fructification growth. The same phenomenon occurs in some *Botryobasidium* species infected by *Spiculogloea* spp. (Spirin *et al.* 2016). So far, *A. chlamydospora* was known only from the type locality in Norway. Here it is reported from two new localities in the country; in one case, the host species was *H. aquilonia*.

***Helicogloea sputum*** Spirin & V. Malysheva, **sp. nov.** MycoBank MB825610. Fig. 16.

**Etymology:** Sputum (Lat., noun) – spittle; in metaphoric sense, “sputum” also refers to a thin layer of some substance.

**Holotype:** Norway, Vestfold, Larvik, Jordstøyp i Kvelde, *Populus tremula*, 19 Oct. 1995, Andersen (O F-90728).

**Basidiocarps** resupinate, 0.05–0.07 mm thick, in fresh condition semitranslucent, waxy, in herbarium specimens almost invisible. **Basal hyphae** thin- to slightly thick-walled, (3.4–)3.6–5.8(–6.0) μm diam (n = 20/1). **Subhymenial hyphae** thin-walled, (2.3–)2.4–4.2(–4.7) μm diam (n = 20/1). **Basidia** tubular-clavate, often curved, 52.5–71 × (5.6–)6.0–8.7(–9.2) μm (n = 20/1), with sharp-pointed, occasionally bi- or trifurcate sterigmata up to 12 × 3.5 μm; probasidia clavate, 34–47 × 7–10 μm. **Basidiospores** broadly cylindrical to ellipsoid, more rarely ovoid, (12.1–)12.2–15.6(–16.2) × (6.2–)6.3–8.3(–8.8) μm (n = 30/1), L = 13.82, W = 7.17, Q' = (1.5–)1.6–2.3(–2.6), Q = 1.94, occasionally germinating by bifurcate sterigmata.

**Distribution and ecology:** Europe (Norway); fallen decorticated log (*Populus*).

*Notes:* Very thin basidiocarps and rather short basidia occasionally bearing bi- to trifurcate sterigmata help to separate this species from other European long-spored species, i.e. *H. septifera* and *H. subardosiaca*.

***Helicogloea subardosiaca*** (Bourdot & Galzin) Donk, *Persoonia* **4**: 213. 1966. Figs 5, 15.

*Basionym:* *Saccoblastia sebacea* ssp. *subardosiaca* Bourdot & Galzin, *Hyménomycètes de France*: 5. 1927.

*Lectotype:* **France**, Aveyron, Causse Noir, *Pinus sylvestris*, 9 Dec. 1910, Galzin 7868 (PC 0706709, selected here) (MycoBank MBT383612).

*Basidiocarps* resupinate, 0.05–0.2 mm thick, in fresh condition semitranslucent, greyish, waxy, in herbarium turning to almost invisible vernicose film. *Basal hyphae* slightly thick-walled, (3.7–)3.8–5.2(–5.3)  $\mu\text{m}$  diam ( $n = 40/4$ ). *Subhymenial hyphae* thin- to slightly thick-walled, (2.3–)2.7–4.4(–4.7)  $\mu\text{m}$  diam ( $n = 80/4$ ). *Basidia* tubular-clavate, slightly twisted or curved, 60–110  $\times$  (5.2–)5.7–7.6(–7.9)  $\mu\text{m}$  ( $n = 30/3$ ), with sharp-pointed sterigmata up to 15  $\times$  3.5  $\mu\text{m}$ ; probasidia clavate, 20–43  $\times$  6–9.5  $\mu\text{m}$ . *Basidiospores* cylindrical to narrowly ellipsoid, ventral side as a rule concave (especially in longest spores), more rarely flat, (10.7–)10.8–18.0(–18.4)  $\times$  (5.2–)5.7–8.5(–9.0)  $\mu\text{m}$  ( $n = 140/5$ ),  $L = 12.22$ –14.71,  $W = 6.50$ –7.11,  $Q' = (1.5$ –)1.6–2.5(–2.6),  $Q = 1.76$ –2.19.

*Distribution and ecology:* Europe (Finland, France); fallen decorticated conifer logs (*Pinus sylvestris*, possibly also *Picea abies*).

*Notes:* *Helicogloea subardosiaca* is a long-spored, conifer-dwelling species distributed in Europe, appearing very late in the season. Morphological differences of *H. subardosiaca* from other similarly looking species are discussed under *H. crassitexta*. While restoring *H. subardosiaca* as a species, Donk (1966) claimed he studied collections of this species from Sweden although he did not specify in which herbarium they were being kept.

***Helicogloea terminalis*** L.S. Olive, *Bull. Torrey Bot. Club* **81**: 331. 1954. Fig. 16.

*Holotype:* **USA**, North Carolina, Macon Co., Highlands, *Betula* sp., 14 Aug. 1952, Olive (NY 00834144, studied).

*Notes:* The species is known so far from the type specimen collected in North Carolina (Olive 1954). Basidiocarps are very thin, inconspicuous, consisting of a few, parallel, terminally ascending hyphae (2.8–)3–4.0(–4.4)  $\mu\text{m}$  diam and bearing saccate probasidia 33–54  $\times$  6–9  $\mu\text{m}$ . Basidia four-celled, about 40  $\times$  5–7  $\mu\text{m}$ , arising both laterally or terminally from probasidia. Chen & Oberwinkler (2000) argued that terminal origin of basidia from probasidial cells precludes an affinity of *H. terminalis* to other *Helicogloea* species. After studying the type specimen, we conclude that this is an artefact most probably caused by extreme thinness of the basidiocarps. A presence of “normal” basidia developing from probasidia laterally in the type of *H. terminalis* supports our idea. Basidiospores of *H. terminalis* are broadly cylindrical, often slightly curved, (11.6–)12.0–15.3(–16.0)  $\times$  (5.0–)5.1–7.1(–7.2)  $\mu\text{m}$  ( $n = 30/1$ ),  $L = 13.82$ ,

$W = 6.06$ ,  $Q' = (1.9$ –)2.0–2.7(–2.8),  $Q = 2.30$ . Thin basidiocarps and basidiospore shape and dimensions place *H. terminalis* in a difficult species complex containing also *H. microsaccata* and *H. subardosiaca*. However, none of these species possess terminally arising basidia, and they all have well-differentiated subicular hyphae. New, sequenced specimens are needed to define a proper place for *H. terminalis* within the genus.

***Helicogloea variabilis*** K. Wells, *Mycol. Res.* **94**: 835. 1990.

*Notes:* This species was described from Brazil based on single collection (Wells 1990). Morphology as well as DNA data confirm that it belongs to the genus *Helicogloea* s. str.

***Saccosoma*** Spirin, *gen. nov.* MycoBank MB825611.

*Basidiocarps* resupinate, thin to rather thick, arid, floccose to dense, white to cream-coloured. *Hyphae* clamped, thin-walled to distinctly thick-walled, 3–8  $\mu\text{m}$  diam, slightly cyanophilous. Poorly differentiated cystidia present in one species. *Basidia* four-celled, tubular-clavate, straight; probasidia narrowly saccate to clavate, simple or bifurcate. *Basidiospores* narrowly ellipsoid to subglobose, 6–23  $\times$  5–15  $\mu\text{m}$ , with blunt, prominent apiculus.

*Type species:* *Saccosoma farinaceum* (Höhn.) Spirin & K. Pöldmaa.

*Notes:* The genus is introduced here to replace *Saccoblastia* sensu Donk (1966). Morphologically, it differs from both *Bourdotigloea* and *Helicogloea* s. str. in having non-gelatinised, arid, perceptible basidiocarps consisting of rather loosely interwoven, clamped hyphae. Hyphae are more or less uniform, not differentiated between subhymenium and subiculum as in *Bourdotigloea* and *Helicogloea*, except *S. contortum*. In contrast to *Helicogloea* spp., basidia in *Saccosoma* are straight, not curved, with a terminal cell bearing an apical (but occasionally somewhat asymmetric) sterigma.

***Saccosoma album*** (Burt) Spirin, *comb. nov.* MycoBank MB825612.

*Basionym:* *Septobasidium album* Burt, *Ann. Missouri Bot. Gdn.* **13**: 332. 1926.

*Notes:* Couch (1949) re-described and illustrated this species and moved it to *Helicogloea* s. lat. Morphological features and DNA data confirm that it is a member of *Saccosoma*. It is so far known only from New Zealand.

***Saccosoma contortum*** (G.E. Baker) Spirin, *comb. nov.* MycoBank MB825613.

*Basionym:* *Helicogloea contorta* G.E. Baker, *Mycologia* **38**: 634. 1946.

*Basidiocarps* resupinate, appearing as small, cream-coloured, soft, floccose patches, later fusing together and reaching up to 3 cm in diam, adnate, densely floccose, 0.07–0.1 mm thick; margin arachnoid. *Hyphae* thick-walled, 3–5  $\mu\text{m}$  in diam in basal part, strongly coiled and 1.5–2.5  $\mu\text{m}$  diam in subhymenium. *Basidia* 40–50  $\times$  7–9  $\mu\text{m}$ ; probasidia narrowly saccate to clavate, thin-walled, 30–40  $\times$  7–9  $\mu\text{m}$ . *Basidiospores* ovoid to broadly ellipsoid, (10.3–)10.9–14.0(–14.7)  $\times$  (8.1–)8.2–10.2(–11.0)  $\mu\text{m}$  ( $n = 30/1$ ),  $L = 12.35$ ,  $W = 8.90$ ,  $Q' = (1.2$ –)1.3–1.5(–1.6),  $Q = 1.39$ .

**Distribution and ecology:** North America (USA – Iowa, Florida); wood remnants of deciduous trees (*Liquidambar*, *Quercus*) and palms.

**Notes:** Coiled hyphae and rather short basidia differentiate *S. contortum* from other species in the genus. No DNA sequences have been available for this species so far.

***Saccosoma farinaceum*** (Höhn.) Spirin & K. Pöldmaa, **comb. nov.** MycoBank MB825614. Figs 3, 6, 18.

**Basionym:** *Helicobasidium farinaceum* Höhn., *Sitzungsber. Kaiserl. Akad. Wissenschaften Math.-Naturwiss. Klasse Abt. I* **116**: 84. 1907.

**Neotype:** **Russia**, Nizhny Novgorod Reg., Lyskovo Dist., Makarievo, dry branches of *Salix* sp., 11 Aug. 2015, Spirin 9099 (H, selected here) (MycoBank MBT383613).

**Synonyms:** *Saccoblastia pinicola* Bourdot & Galzin, Bourdot & Galzin, *Bull. Soc. Mycol. France* **25**: 15. 1909. **Lectotype:** **France**, Aveyron, Millau, Causse Noir, *Pinus sylvestris* (fallen branches), 10 Nov. 1908, Galzin (herb. Bourdot 6939) (S F-21016, selected here) (MycoBank MBT383614).

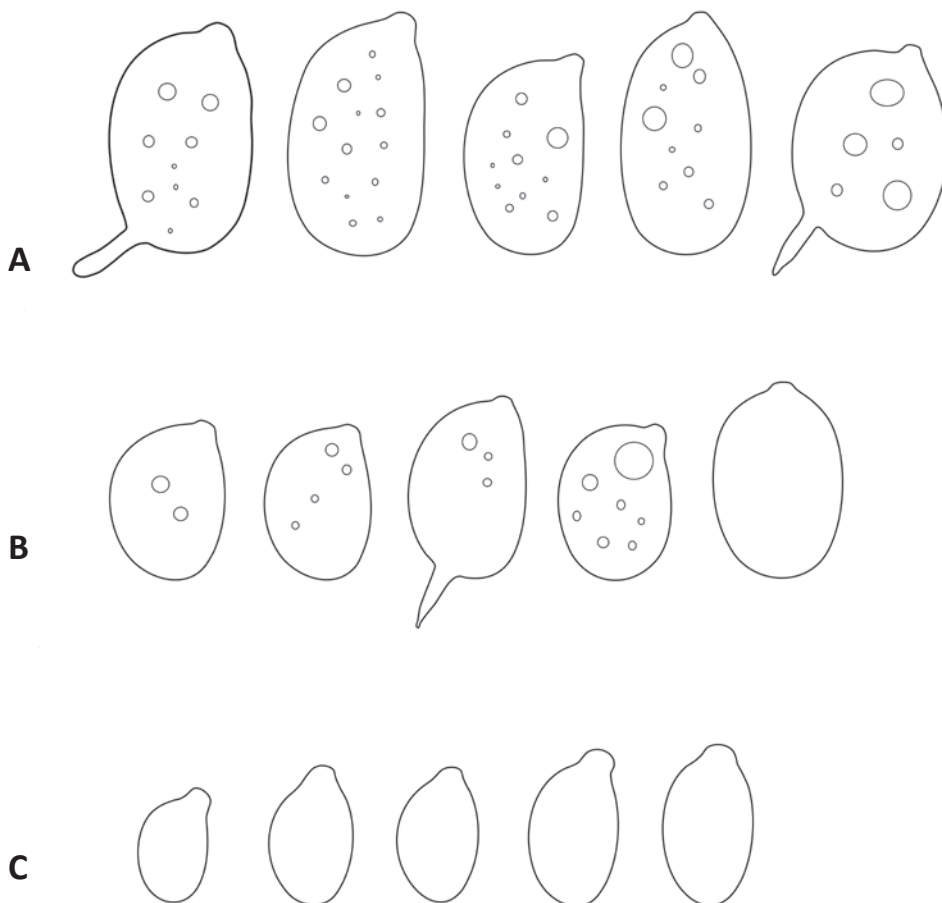
*Stypinella killermannii* Bres. in Killermann, *Denkschr. Baierischen Bot. Gesellsch. Regensburg* **15**: 34. 1922. **Lectotype:** **Germany**, Bayern, Passau, *Pinus* sp. (manufactured wood), Sep. 1919, Killermann (BPI 726593, selected here) (MycoBank MBT383615).

**Basidiocarps** orbicular, adnate, appearing as small, cream-colored, rather dense, farinaceous patches, a few mm diam, later fusing together and covering several cm, up to 0.5 mm

thick; margin floccose-pruinose, gradually thinning-out. **Hyphae** thin-walled or with distinct walls (wall up to 0.5 µm thick), (2.8–) 3.0–6.3(–7.2) µm diam (n = 200/10). **Basidia** 71–140 × (7.3–) 7.8–13.2(–13.8) µm (n = 190/11); probasidia narrowly saccate to clavate, occasionally furcate, thin- to slightly thick-walled, 28.5–81 × 10–17.5 µm, occasionally with 1–3 adventive septa. **Basidiospores** broadly to narrowly ellipsoid, rarely ovoid, (11.6–) 12.0–20.1(–20.6) × (8.1–) 8.2–14.5(–15.8) µm (n = 377/12), L = 14.46–17.92, W = 9.56–13.08, Q' = (1.1–) 1.2–1.7(–1.8), Q = 1.31–1.58.

**Distribution and ecology:** Europe (Austria, Denmark, Estonia, Finland, France, Germany, Norway, Russia, Sweden, Ukraine, United Kingdom), North America (Canada, USA); still attached thin branches, rarely recently fallen logs of deciduous trees (*Acer*, *Corylus*, *Fagus*, *Fraxinus*, *Populus*, *Quercus*, *Salix*, *Ulmus*) and more rarely conifers (*Abies*, *Picea*, *Pinus*).

**Notes:** Höhnel (1907) described this species as *Helicobasidium farinaceum* based on single collection from Austria. It was almost forgotten until D.P. Rogers (in Martin 1944) studied the type and concluded it is the same species as *Saccoblastia pinicola*. Rogers moved *H. farinaceum* to *Helicogloea*, in accordance with the genus concept introduced by Baker (1936). It seems that Höhnel's original specimen does not exist anymore: it could not be located in FH and our request to W remained unanswered. Therefore, the only source for judging *H. farinaceum* sensu orig. is its protologue. Höhnel's description referred to a pale-coloured, non-gelatinized, resupinate fungus of fine-granular, mealy consistence ("feinkörnig-mehlig") and possessing clamped hyphae. These statements preclude *Helicogloea* s.



**Fig. 18.** Basidiospores of *Saccosoma* spp. **A.** *S. farinaceum* f. *alniviridis* (Kotiranta 13179). **B.** *S. farinaceum* (neotype). **C.** *S. floccosum* (holotype). Scale bar = 10 µm.

*str.* Basidiocarps of *H. farinaceum* were described as initially patch-like, then fusing together and gradually thinning-out in marginal areas ("fleckenartig, dann zu ausgebreiten Überzügen zusammenfließend, dünn, gegen den Rand ganz allmählig verlaufend"). These features, together with microscopic characters (diameter of hyphae, width of basidia and dimensions of basidiospores) are crucial for our understanding of this species, and they correspond to recent collections used in the present phylogenetic studies. One of them is designated here as a neotype of *H. farinaceum*.

Morphological study reveals a considerable variation of *S. farinaceum*. In particular, specimens collected from coniferous hosts produce abundant bifurcate probasidia and on average larger basidiospores. However, ITS sequences show only negligible differences between collections from various host trees and geographic regions. Therefore, *S. farinaceum* is accepted here in a wide sense, i.e. including *S. pinicola*, although we cannot preclude that it contains several cryptic species.

The protologue of *Platyglœa laplata* (Lindsey 1986) and its redescription by Hauerslev (1999) suggest it may be a synonym of *S. farinaceum*. Lindsey described *P. laplata* as growing on living basidiocarps of *Peniophora nuda* and supposed it was parasitic. One of our collections of *S. farinaceum* came from living and sporulating fruitbodies of *Aleurodiscus grantii*. However, no specific cells (haustoria or appressoria), characteristic for parasitic heterobasidiomycetes, were detected in this collection, and they were not mentioned in descriptions of *P. laplata*. Therefore, we consider their growth on other fungi merely coincidental.

Specimens macroscopically identical to *S. farinaceum* but having wider hyphae and larger basidia and basidiospores than *S. pinicola* were collected in subalpine forests of Eurasia and North America. They all came from branches of shrub-like alders (*Alnus viridis* group). No certain differences were detected in ITS region between them and *S. farinaceum s. str.*, and therefore these specimens are redescribed here under an older name (forma *alniviridis*) introduced by Bourdot (1932).

***Saccosoma farinaceum* f. *alniviridis*** Bourdot, *Bull. Soc. Mycol. France* **48**: 204. 1932. Fig. 18.

*Synonym*: *Achroomyces sibiricus* Hauerslev, *Mycotaxon* **72**: 467. 1999. *Holotype*: **Russia**, Magadan Reg., Tenkinsky Dist., Madaun, *Salix arbutifolia*, 14 Aug. 1995, *Corfixen* (C 31369, studied).

*Basidiocarps* resupinate, appearing as small, cream-colored, soft, floccose patches, later fusing together and reaching up to 1 cm diam, adnate, densely floccose, 0.1–0.2 mm thick; margin arachnoid. *Hyphae* thin-walled, easily collapsing, some twisted, (3.5–)4.1–7.3(–7.8)  $\mu\text{m}$  diam ( $n = 60/3$ ). *Basidia* 100–150  $\times$  (9.4–)9.5–13.4(–15.3)  $\mu\text{m}$  ( $n = 40/2$ ); probasidia narrowly saccate to clavate, often tortuous or constricted, many bi- or trifurcate, thin- or slightly thick-walled, 42.5–76  $\times$  10.5–15.5  $\mu\text{m}$ . *Basidiospores* ovoid to broadly ellipsoid, (14.6–)15.4–23.6(–26.8)  $\times$  (10.2–)10.4–15.7(–17.0)  $\mu\text{m}$  ( $n = 110/4$ ),  $L = 17.15$ –19.66,  $W = 12.44$ –13.30,  $Q' = (1.1$ –)1.2–1.7(–1.8),  $Q = 1.36$ –1.53.

*Distribution and ecology*: Europe (Austria, France, Italy, Switzerland), Asia (Russian Far East), North America (US – Washington); still attached dry branches of shrub-like alders (*Alnus viridis* group, one record on *Salix arbutifolia*).

*Notes*: Further phylogenetic studies with other genes should clarify the taxonomic status of this 'form'. Morphologically, it is very distinctive if compared with *S. farinaceum*.

***Saccosoma floccosum*** V. Malysheva & Spirin, *sp. nov.* MycoBank MB825615. Fig. 18.

*Etymology*: Floccosus (Lat., adj.) – floccose.

*Holotype*: **Russia**, Lipetsk Reg., Krasnoe Dist., Olenii Nat. Park, *Quercus robur* (fallen branches), 30 Sep. 2016, *Volobuev* (LE 313308, isotype H).

*Basidiocarps* very soft, floccose, easily detaching from the substrate, cream-colored, covering a few cm, up to 0.2 mm thick; margin arachnoid. *Subicular* hyphae differentiated, sparse, slightly thick-walled, 5–7  $\mu\text{m}$  diam. *Subhymenial* hyphae thin-walled, easily collapsing, (3.0–)3.2–5.0(–5.1)  $\mu\text{m}$  diam ( $n = 40/2$ ). *Basidia* 54–79  $\times$  (6.0–)6.1–7.4(–7.8)  $\mu\text{m}$  ( $n = 26/2$ ); probasidia saccate to clavate, not furcate, thin-walled, 13–30  $\times$  7–10  $\mu\text{m}$ . *Basidiospores* narrowly lacrymoid to subfusiform, (8.8–)9.0–13.8(–14.2)  $\times$  (5.1–)5.2–8.0(–8.2)  $\mu\text{m}$  ( $n = 60/2$ ),  $L = 10.47$ –11.97,  $W = 6.64$ –6.71,  $Q' = (1.4$ –)1.5–2.0(–2.1),  $Q = 1.56$ –1.81.

*Distribution and ecology*: Europe (Russia); thin fallen branches of conifers (*Picea*) and deciduous trees (*Quercus*).

*Notes*: Soft, detaching basidiocarps, as well as narrow basidiospores help in identification of this species.

***Saccosoma globisporum*** (S.H. Wu & Z.C. Chen) Spirin, *comb. nov.* MycoBank MB825616.

*Basionym*: *Helicogloea globispora* S.H. Wu & Z.C. Chen, *Karstenia* **45**: 195. 2000.

*Notes*: *Saccosoma globisporum* was described from Taiwan (Wu & Chen 2000). According to the description, it is most similar to *S. sphaerosporum* and differs from the latter species in having larger basidiospores.

***Saccosoma medium*** (Spirin et al.) Spirin, *comb. nov.* MycoBank MB825617.

*Basionym*: *Saccoblastia media* Spirin et al., *Synopsis Fungorum* **33**: 28. 2015. *Holotype*: St. Helena, Scotland Research Station, on hardwood, 3 Feb. 2014 *Ryvarden 49436* (K, isotype – H).

*Notes*: This species was described in Spirin et al. (2015). *Saccosoma medium* is the only species of the genus having cystidia although they are infrequent and rather poorly differentiated.

***Saccosoma sphaerosporum*** (Möller) Spirin, *comb. nov.* MycoBank MB825618.

*Basionym*: *Saccoblastia sphaerospora* Möller, *Botanische Mitteilungen aus den Tropen* **8**: 20. 1895.

*Neotype*: **Costa Rica**, Puntarenas, Coto Brus, Las Alturas, 2 Dec. 1996, *Kisimova-Horovitz 222-vi* (USJ 55489, not studied) (selected and illustrated by Kisimova-Horovitz et al. 2000: 551).

*Basidiocarps* effused, corticioid, cream-colored, rather dense, covering a few cm, up to 0.3 mm thick; margin pruinose. *Hyphae*

slightly to distinctly thick-walled, 3–5 µm diam. *Basidia* 36–62 × 4.4–5.4 µm (n = 20/2); probasidia saccate, thin-walled, 13.5–20 × 6–8 µm. *Basidiospores* subglobose to globose, (5.3–)5.8–7.2(–7.7) × (5.0–)5.2–6.7(–7.4) µm (n = 60/3), L = 6.32–6.67, W = 5.85–6.27, Q = 1.07–1.08.

**Distribution and ecology:** South and North America (Brazil, Costa Rica, Mexico, USA – Florida); still attached or fallen, mostly corticated branches of deciduous trees.

**Notes:** This species is described, illustrated and discussed in detail as *Saccoblastia sphaerospora* by Kisimova-Horovitz *et al.* (2000). The latter authors reported basidiospores of the Costa Rican specimens as globose, 8–10 µm diam, whereas they are distinctly smaller in collections from Mexico and Florida studied by us. These differences may indicate that *S. sphaerosporum* is a species complex.

## ACKNOWLEDGEMENTS

The curators of herbaria TAAM, CWU, PC, HBG, K, C, S, NY, CFMR, BPI, FH, TENN, TRH, PDD are thanked for providing specimens for loan. Nicolas Küffer (Switzerland) and Ilya Viner (Russia) kindly shared with us collections from their personal herbaria. Jorma Pennanen (Finland) collected excellent material of *Helicogloea subardosiaca*. The research was supported by Norwegian Biodiversity Information Centre (the project “A survey of Norwegian jelly fungi”, grant number knr. 44-15, the authors KHL and VS, and the projects “Wood-inhabiting corticioid homo- and hetero-basidiomycetes in Norway”, knr. 59-12, and “International workshop on corticioid heterobasidiomycetes in Northern Europe”, knr 28-13, the authors JN, KHL, VS), by Finnish Academy of Sciences (project 315927, the authors OM and VS), by Komarov Botanical Institute (project “Biodiversity and spatial structure of fungi and myxomycetes communities in natural and anthropogenic ecosystems”, grant number AAAA-A18-118031290108-6, the author VM), by the Estonian Science Agency (project IUT20-30) and the European Union through the European Regional Development Fund (Centre of Excellence FIBIR) (the author KP).

## REFERENCES

Aime MC, Matheny PB, Henk DA, *et al.* (2006). An overview of the higher level classification of *Pucciniomycotina* based on combined analyses of nuclear large and small ribosomal subunit rDNA sequences. *Mycologia* **98**: 896–905.

Aime MC, Toome M, McLaughlin DJ (2014). *Pucciniomycotina*. In: *The Mycota VII. Systematics and evolution. Part A.* (McLaughlin DJ, Spatafora JW, eds.). Berlin: Springer: 271–294.

Aime MC, Urbina H, Liber JA, *et al.* (2018). Two new endophytic *Atractiellomycetes*, *Atractidochium hillariae* and *Proceropycnis hameedii*. *Mycologia* **110**: 136–146.

Baker GE (1936). A study of the genus *Helicogloea*. *Annals of the Missouri Botanical Garden* **23**: 69–128.

Baker GE (1946). Addenda to the genera *Helicogloea* and *Physalacia*. *Mycologia* **38**: 630–638.

Bandoni RJ (1956). A preliminary survey of the genus *Platyglöea*. *Mycologia* **48**: 821–840.

Bauer R, Begerow D, Sampaio JP, *et al.* (2006). The simple-septate basidiomycetes: a synopsis. *Mycological Progress* **5**: 41–66.

Boedijn KB (1937). The genus *Helicogloea* in the Netherlands Indies. *Bulletin du Jardin Botanique de Buitenzorg* **14**: 187–196.

Bonito G, Hameed K, Toome-Heller M, *et al.* (2017). *Atractiella rhizophila*, *sp. nov.*, an endorhizal fungus isolated from the *Populus* root microbiome. *Mycologia* **109**: 18–26.

Bourdot H (1932). Notes critiques sur quelques Hyménomycètes nouveaux ou peu connus. *Bulletin de la Société Mycologique de France* **48**: 204–232.

Bourdot H, Galzin A (1909). Hyménomycètes de France. I. Hétérobasiédiés. *Bulletin de la Société Mycologique de France* **25**: 15–36.

Bourdot H, Galzin A (1924). Heterobasidiales nondum descriptae. *Bulletin de la Société Mycologique de France* **39**: 261–266.

Bourdot H, Galzin A (1928). *Hyménomycètes de France. Hétérobasiédiés – Homobasiédiés gymnocarpes*. Sceaux.

Chen CJ, Oberwinkler F (2000). *Helicogloea* species collected in Taiwan. *Mycotaxon* **76**: 279–285.

Clements FE, Shear CL (1931). The genera of fungi. NY: H.W. Wilson.

Coker WC (1928). Notes on Basidiomycetes. *Journal of the Elisa Mitchell Scientific Society* **35**: 233–242.

Couch JN (1949). The taxonomy of *Septobasidium polypodii* and *S. album*. *Mycologia* **41**: 427–441.

Donk MA (1958). The generic names proposed for Hymenomycetes. VIII: *Auriculariaceae, Septobasidiaceae, Tremellaceae, Dacrymycetaceae*. *Taxon* **7**: 236–260.

Donk MA (1966). Check list of European hymenomycetous Heterobasidiales. *Persoonia* **4**: 145–335.

Friedrichsen I (1977). Das Schicksal der von A. Möller in Brasilien (1890–1895) gesammelten Pilze sowie eine Liste der noch vorhandenen Sammlungsstücke. *Mitteilungen aus dem Institut für allgemeine Botanik in Hamburg* **15**: 99–104.

Gardes M, Bruns TD (1993). ITS primers with enhanced specificity for basidiomycetes – applications to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**: 113–118.

Hauerslev K (1999). New and rare species of Heterobasidiomycetes. *Mycotaxon* **72**: 465–486.

Hönel F (1907). Fragmente zur Mykologie. III. Mitteilung, Nr. 92 bis 155. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch – Naturwissenschaftliche Klasse I* **116**: 83–162.

Hönel F (1908). Fragmente zur Mykologie. V. Mitteilung, Nr. 169 bis 181. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch – Naturwissenschaftliche Klasse I* **117**: 985–1032.

Jülich W (1976). Zur Morphologie von *Saccoblastia pinicola* and *S. sebacea*. *Persoonia* **9**: 39–48.

Kirschner R (2004). Sporodochial anamorphs of species of *Helicogloea*. In: *Frontiers in Basidiomycote Mycology* (Agerer R *et al.*, eds.). Eching: IHW-Verlag: 165–178.

Kisimova-Horovitz L, Oberwinkler F, Gómez LD (2000). Basidiomycetes resupinados de Costa Rica. Especies nuevas o raras de *Atractiellales* (*Auriculariales s.l.*), *Exidiaceae, Sirobasidiaceae* y *Tremellaceae*. *Revista de Biología Tropical* **48**: 539–554.

Kobayashi Y (1950). A new species of the genus *Helicogloea*, newly found in Isl. Hatijô. *Miscellaneous Reports of the Research Institute for Natural Resources* **17–18**: 43–47.

Kottke I, Suárez JP, Herrera P, *et al.* (2010). *Atractiellomycetes* belonging to the “rust” lineage (*Pucciniomycotina*) form micorrhizae with terrestrial and epiphytic neotropical orchids. *Proceedings of the Royal Society of London B: Biological Sciences* **277**: 1289–1298.

Linder DH (1929). The life history and cytology of *Saccoblastia intermedia*, *n.sp.* *Annals of the Missouri Botanical Garden* **16**: 487–498.

Lindsey JP (1986). Basidiomycetes that decay gamble oak in southwestern Colorado. III. *Mycotaxon* **27**: 325–345.

Martin GW (1944). The Tremellales of the north central United States and adjacent Canada. *University of Iowa Studies in Natural History* **18**: 1–88.

- Miettinen O, Vlasák J, Rivoire B, Spirin V (2018). *Pastia caesia* complex (*Polyporales*, *Basidiomycota*) in temperate Northern Hemisphere. *Fungal Systematics and Evolution* **1**: 101–129.
- Möller A (1895). Protobasidiomyceten. *Botanische Mittheilungen aus den Tropen* **8**: 1–180.
- Oberwinkler F, Kirschner R, Arenal F, *et al.* (2006). Two new pycnidial members of the *Atractiellales*: *Basidiopycnis hyalina* and *Proceropycnis pinicola*. *Mycologia* **98**: 637–649.
- Olive LS (1948). Taxonomic notes on Louisiana fungi. II. *Tremellales*. *Mycologia* **40**: 586–604.
- Olive LS (1953). New or noteworthy species of *Tremellales* from the southern Appalachians. II. *Bulletin of the Torrey Botanical Club* **80**: 33–42.
- Olive LS (1954). New or noteworthy species of *Tremellales* from the southern Appalachians. III. *Bulletin of the Torrey Botanical Club* **81**: 329–339.
- Olive LS (1958). The lower Basidiomycetes of Tahiti. I. *Bulletin of the Torrey Botanical Club* **85**: 5–27.
- Patouillard N, Lagerheim G (1892). Champignons de l'Equateur. *Bulletin de la Société Mycologique de France* **8**: 113–140.
- Pärtel K, Baral HO, Tamm H, Põldmaa K (2017). Evidence for the polyphyly of *Encoelia* and *Encoelioideae* with reconsideration of respective families in *Leotiomycetes*. *Fungal Diversity* **82**: 183–219.
- Rambaut A, Suchard MA., Xie D, Drummond AJ (2014). Tracer v1.6. <http://tree.bio.ed.ac.uk/software/tracer/> (accessed on 20.12.2017).
- Rick J (1933). Monografia dos protobasidiomicetos Rio-Grandenses. *Egatea* **18**: 209–215.
- Rick J (1958). Basidiomycetes eubasidii in Rio Grande do Sul – Brasilia. 1. *Auriculariaceae, Sirobasidiaceae, Tremellaceae, Dacryomycetaceae, Iheringia* (Ser. Bot.) **2**: 1–56.
- Roberts P (2002). Two unusual auricularioid fungi from Norway. *Polish Botanical Journal* **47**: 109–111.
- Ronquist F, Huelsenbeck JP (2003). MRBAYE S 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.
- Spirin V, Ryvarden L, Miettinen O (2015). Notes on heterobasidiomycetes from St. Helena. *Synopsis Fungorum* **32**: 25–31.
- Spirin V, Nordén J, Svantesson S, Larsson KH (2016). New records of intrahymenial heterobasidiomycetes (*Basidiomycota*) in north Europe. *Nordic Journal of Botany* **34**: 475–477.
- Tamura K, Stecher G, Peterson D, *et al.* (2013). MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution* **30**: 2725–2729.
- Thiers B (2017). Index Herbariorum: a global directory of public herbaria and associated stuff [continuously updated]. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih> (accessed on 5.5.2018)
- Toome-Heller M (2016). Latest developments in the research of rust fungi and their allies (*Pucciniomycotina*). In: *Biology of microfungi*. (Li DW, ed.). Basel: Springer: 147–168.
- Wells K (1990). An undescribed species of *Helicogloea* from Brazil. *Mycological Research* **94**: 835–839.
- Wojewoda W. 1981. Mała flora grzybów. Tom 2. Warsaw, Krakow, Państwowe Wydawnictwo Naukowe.
- White TJ, Burns T, Lee S, *et al.* (1990). Amplification and sequencing of fungal ribosomal RNA genes for phylogenetics. In: *PCR protocols. A guide to methods and applications* (Innis MA, Gelfand DH, Sninsky JJ, White TJ, eds.). San Diego (California): Academic Press: 315–322.
- Wu SH, Chen ZC (2000). *Helicogloea globispora* sp. nova from Taiwan. *Karstenia* **40**: 195–196.