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presented by James Kameron Mitchell

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Date: May 10, 2021

Investigations into Resinicolous Fungi

A dissertation presented

by

James Kameron Mitchell

to

The Department of Physics

in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

in the subject of

Physics

Harvard University

Cambridge, Massachusetts

May 2021

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Dissertation Advisor: Donald H. Pfister James Kameron Mitchell

Investigations into Resinicolous Fungi

Abstract

Fungi growing on resin have been known since the description of *Helotium aureum* by Christiaan Hendrik Persoon in 1801. The majority of the fungi described since then are known from extant conifer resins, though a handful are known from angiosperm resins and various fossilized resins. For the most part, these species are not well understood, and have been treated piecemeal in the literature. To promote better understanding of this group of fungi, records and descriptions are gathered and presented in an organized format. In addition, more in-depth examinations are given of fungi historically treated in the genus *Sarea* and of the species known as *Eustilbum aureum*/*Bisporella resinicola*. Taxonomic and nomenclatural issues are discussed, as are some related but non-resinicolous species.

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Finally, I would like to thank my partner, Daniel Adamec, for his love and support for the past year and a half. Without you, I would not have been able to do this.

Chapter 1

Resinicolous fungi on conifers: a review

This chapter has been edited by Dr. Joey Tanney and Prof. Donald H. Pfister.

Section 1.1

Introduction

Conifers produce resins as a defensive mechanism against attack by herbivores (Smith 1961; Rudinsky 1966; van Buijtenen and Santamour 1972), fungi (Whitney and Denyer 1969; Gibbs 1972; Hart et al. 1975; Yamada 2001), protists (Krupa and Nylund 1972; Bunny and Tippett 1988), and bacteria (Hemingway and Greaves 1973; Hartmann et al. 1981). In addition to simply acting as a mechanical barrier to invasion by fungi (Verrall 1938; Shain 1971; Rishbeth 1972; Prior 1976), resin components have been shown to act as chemical barriers to fungal growth (Shrimpton and Whitney 1968; Cobb et al. 1968; Hintikka 1970; De Groot 1972; Väisälä 1974; Flodin and Fries 1978; Bridges 1987). Despite the apparent hostility of this substrate, some pathogenic fungi are apparently immune to the effects of the resin (Flodin and Fries 1978). Perhaps more surprising still, some saprobic fungi have evolved to preferentially utilize this substrate (Cappelletti 1924, 1926; Hawksworth and Sherwood 1981; Selva and Tuovila 2016).

There are perhaps fifty-one published "resinicolous" fungi occurring on conifers, all of which are regarded as members of phylum *Ascomycota*. With the exception of a handful of publications (Cappelletti 1924; McCune 2017a), these fungi have not been treated comprehensively; they have instead been described and researched piecemeal, and are scattered

through the literature. The goal of this review is to provide a synthesis of available information, allowing authors to access this body of literature more easily. To this end, we provide copious citations and discussions of current taxonomic views. Because these fungi are typically sparsely collected, herbarium specimens accessed at https://gbif.org, https://www.mycoportal.org, https://lichenportal.org, or other herbarium databases may be mentioned if they supplement the host or geographical range; these have been largely not seen, however. Where appropriate, ecology of species is discussed; at present however, the precise biochemical mechanisms of the resinicolous lifestyles are a mystery. Discussions of species are arranged alphabetically by classification from phylum to species.

This review explicitly references fossil resinicolous taxa identified to genus or species. Many fossil fungal taxa in amber have recently been proposed to have been resinicolous, and these may be of interest to the reader (Breton et al. 2014; Speranza et al. 2015; Peñalver et al. 2017; Schmidt et al. 2018; Grimaldi et al. 2018; Lozano et al. 2020).

Parasitic species associated with resin will not be treated here, because the association with resin is causal; the tree produces resin in response to the invasion by the fungus, rather than the fungus being present due to the prior presence of the resin.

Section 1.2

Body

Ascomycota*: *Pezizomycotina

Coniocybomycetes*: *Coniocybales*: *Coniocybaceae

Chaenotheca (Th. Fr.) Th. Fr., *Lich. arct.*: 250 (1860).

≡ *Calicium* b. *Chaenotheca* Th. Fr., *Öfvers. Kongl. Vetensk.-Akad. Förh.* **13**(5): 128 (1856).

Strictly speaking, this genus does not have any known resinicolous species. However, several species have been reported as sometimes growing over resin. These may be confused with resinicolous calicioids in *Mycocaliciales* and *Bruceomycetaceae*, warranting their inclusion here. *Chaenotheca phaeocephala* was reported once growing over the resin of *Abies grandis* in Washington (Hardman et al. 2017). *Chaenotheca trichialis* has similarly been reported several times growing on the resin of various conifers: on *Pseudotsuga menziesii* in Washington (Hardman et al. 2017), on *Sequoia sempervirens* in California and *Picea abies* in Finland (Rikkinen and Schmidt 2018), and on *Picea* in Quebec (Paquette et al. 2019; Bell-Doyon et al. 2021).

Dothideomycetes

The number of known resinicolous species in *Dothideomycetes*, both published and unpublished, is moderate; with one exception, though, molecular data are not available for published species. Taxonomic placements, thus, are somewhat uncertain.

Capnodiales

Cladosporiaceae

Cladosporium Link, *Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin* **7**(1): 37 (1816).

***Cladosporium* sp.**

Several publications have reported fossils of fungi they likened to species of *Cladosporium* in resinite, or amber which occurs in coal seams (Hower et al. 2009, 2010; O'Keefe and Hower 2011). These may be some of the oldest known fossils of resinicolous fungi. Some micrographs are provided; it is unclear what the true affinities of these fungi are from the details available. The cladosporioid fungus reported in non-coal associated amber is possibly similar (Saint Martin et al. 2012).

Euantennariaceae

Strigopodia Bat., in Batista, Maia & Vital, *Anais Soc. Biol. Pernambuco* **15**(2): 440 (1957).

This genus at present contains three species, of which two are definitely resinicolous. Placements have been based on morphological similarities, as molecular data are not available for any species. *Strigopodia spongiosa*, which dwells on conifer bark in western North America, is perhaps resinicolous and should be subjected to closer examination and molecular analyses to determine if it is truly congeneric with the type species of the genus (Barr 1955, 1972). The genus has also been suggested to be very close to *Euantennaria* (= *Aithalomyces*) (Hughes 1968; Chomnunti et al. 2014), so this relationship should also be tested, as should the placement in *Euantennariaceae* (Mibey 1997; Barr 2009; Wijayawardene et al. 2020b). Previous placements include *Parodiopsidaceae* (Batista et al. 1957), *Naetrocymbaceae* (Barr 1979; Sivanesan 1984), *Coccodiniaceae* (Barr 1987), and *Pleosporales* (Hughes 1972).

Strigopodia pini (Berk. & M.A. Curtis) J.K. Mitch., *comb. nov.* (MB XXXXXXXX)

≡ *Capnodium pini* Berk. & M.A. Curtis, *Grevillea* **4**(32): 157 (1876).

Holotype: K(M), USA: Maine, on pine bark, no. 5689, examined by Hughes, *Mycologia* **68**(4): 801 (1976).

≡ *Polychaeton pini* (Berk. & M.A. Curtis) Kuntze, *Revis. gen. pl.* **1**: 13 (1891).

≡ *Polychaetella pini* (Berk. & M.A. Curtis) Speg., *Physis* (Buenos Aires) **4**(17): 295 (1918).

= *Racodium resinae* var. *piceum* Pers., *Mycol. eur.* **1**: 68 (1822) (*fide* Hughes, *Canad. J. Bot.* **36**(6): 781 (1958)).

= *Helminthosporium resinaceum* Cooke, *Grevillea* **17**(83): 68 (1889).

Holotype: K(M), [UK: England: Surrey]: Shere, on pine resin, Apr. 1870; Isotype: NY, [UK: England: Surrey]: Shere, on fir-tree resin, examined by Hughes, *Canad. J. Bot.* **46**(9): 1103 (1968).

≡ *Hyphosoma resinaceum* (Cooke) S. Hughes, *Canad. J. Bot.* **36**(6): 781 (1958).

= *Helminthosporium resinae* Bres., *Malpighia* **11**(6-8): 322 (1897).

Syntypes: S & PAD, [Italy: Vercelli]: Riva-Valsesia, sulle cicatrices della corticcia des *Larix* ed *Abies*, 29 May 1891, leg. A. Carestia, no. 788, examined by Hughes, *Canad. J. Bot.* **46**(9): 1103 (1968).

≡ *Sporhelminthium resinae* (Bres.) Speg., *Physis* (Buenos Aires) **4**(17): 292 (1918).

= *Capnodium resinae* Sacc. & Bres., in Bresadola & Saccardo, *Malpighia* **11**(6-8): 322 (1897).

Holotype: PAD, [Italy]: Rabbi nel Trentino, in resina in *Laricis*, leg. G. Bresadola, examined by Hughes, *Canad. J. Bot.* **46**(9): 1102 (1968).

≡ *Limacinia resinae* (Sacc. & Bres.) Sacc. & P. Syd., *Syll. fung.* **14**: 475 (1899).

≡ *Phragmocapnias resinae* (Sacc. & Bres.) Bat. & Cif., *Saccardoa* **2**: 182 (1963).

≡ *Strigopodia resinae* (Sacc. & Bres.) S. Hughes, *Canad. J. Bot.* **46**(9): 1100 (1968).

= *Clasterosporium resinae* Rilstone, *J. Bot.* **79**: 188 (1941).

Holotype: K(M), [UK: England: Somerset: Huish Champflower, near Wiveliscombe], on resin on larch, leg. W. Watson, examined by Hughes, *Canad. J. Bot.* **46**(9): 1103 (1968).

= *Strigopodia piceae* Bat., in Batista, Maia & Vital, *Anais Soc. Biol. Pernambuco* **15**(2): 440 (1957).

Holotype: BPI 618549, USA: Maine: Mt. Desert Island, on *Picea rubra*, 30 Jun. 1929, leg. D.S. Johnson, examined by Hughes, *Canad. J. Bot.* **46**(9): 1103 (1968).

Description: (Rilstone 1941; Batista et al. 1957; Hughes 1968; Sivanesan 1984).

Illustrations: (Rilstone 1941; Batista et al. 1957; Hughes 1968; Ellis 1971; Kendrick 1971; Barr 1972; Corlett et al. 1973; Sivanesan 1984; Chomnunti et al. 2014).

Hosts: *Abies*, *Cedrus*, *Larix*, *Picea*, *Pinus*.

Distribution: Asia (Pakistan), Europe (Austria, France, Germany, Hungary, Italy, UK), North America (New England).

Molecular data: None available.

Additional notes: Despite its epithet, there is little evidence that this fungus frequently occurs on members of the genus *Pinus*; nineteenth-century authors often included members of several genera in *Pinaceae* in the genus *Pinus*. A recent collection from Scotland on *Pinus* held at E suggests it does occur on this host, however.

A specimen collected in Pakistan and identified as this species is deposited in IMI (http://www.herbimi.info/herbimi/specimen.htm?imi=142001); this report was apparently not published.

Additional references: (Traverso 1912; Cappelletti 1924; Batista and Ciferri 1963; Dennis 1975, 1986; Henderson and Watling 1978; Minter 1983; Krieglsteiner 1991; Müller et al. 2011; Glatz-Jorde et al. 2019).

Strigopodia pseudotsugae (W.B. Cooke) J.K. Mitch., *comb. nov.* (MB XXXXXXXX)

≡ *Helminthosporium pseudotsugae* W.B. Cooke, *Mycologia* **44**(2): 251 (1952).

Holotype: WIS-f-0019364, [USA]: Idaho: Nez Perce County, on *Pseudotsuga taxifolia* var. *glauca*, 14 May 1949, leg. W.B. & V.G. Cooke, no. 25161, examined by Hughes, *Canad. J. Bot.* **46**(9): 1106 (1968).

= *Strigopodia batistae* S. Hughes, *Canad. J. Bot.* **46**(9): 1104 (1968).

Holotype: DAOM 56129, Canada: British Columbia: Vancouver Island, on *Pseudotsuga taxifolia var. taxifolia*, 21 Aug. 1957, leg. S.J. Hughes.

Description: (Cooke 1952; Hughes 1968; Sivanesan 1984).

Illustrations: (Cooke 1952; Hughes 1968; Cole and Kendrick 1969).

Hosts: *Larix*, *Pinus*, *Pseudotsuga*.

Distribution: North America (Pacific Northwest, Rocky Mountains).

Molecular data: None available.

Additional notes: A specimen from Oregon on *Pinus* at NY identified by M.E. Barr confirms this host.

Additional references: (Sherwood and Carroll 1974; Cooke 1979).

Strigopodia spongiosa (M.E. Barr) M.E. Barr, *Contr. Univ. Michigan Herb.* **9**(8): 622 (1972).

≡ *Capnodium spongiosum* M.E. Barr, *Canad. J. Bot.* **33**(5): 511 (1955).

Holotype: UC 681382, USA: California: Del Norte County, on *Libocedrus decurrens*, Apr. 1937 or Nov. 1938, leg. H.E. Parks, California Fungi 418; Isotype?: NY 03633613.

≡ *Capnophaeum spongiosum* (M.E. Barr) Bat. & Cif., *Saccardoa* **2**: 108 (1963).

Description: (Barr 1955, 1972; Sivanesan 1984).

Illustrations: (Barr 1955).

Hosts: *Calocedrus, Chamaecyparis, Cupressus*/*Hesperocyparis, Pseudotsuga, Tsuga*.

Distribution: North America (Pacific Northwest, Rocky Mountains).

Molecular data: None available.

Additional notes:

Additional references: (Baranyay 1966; Reynolds 1989; Barr 2009).

Metacapnodiaceae

Metacapnodium Speg., *Physis (Buenos Aires)* **4**(17): 288 (1918).

McCune notes that Jouko Rikkinen told him (pers. comm.) that in the Pacific Northwest, apparently unidentified species of *Metacapnodium* are extremely common on resin (McCune 2017b). One of the fungi in question is illustrated there. It is unclear whether these species display any host specificity, are confined to the Pacific Northwest, or have been sequenced.

Similarly, Tanney reported without illustrating it an extremely common unidentified species of *Metacapnodium* on resin of spruce in New Brunswick (Tanney 2020). The same qualifiers as above apply.

Mycosphaerellaceae

***Mycosphaerellaceae* sp.**

An apparently undescribed dematiaceous hyphomycete was recently reported growing on resin of *Araucaria humboldtensis* in New Caledonia, France (Beimforde et al. 2017a). It was described as extremely frequent on Mont Humboldt, appearing on almost all resin surfaces examined. Photographs and a basic description are provided. The authors also conducted culture studies on this fungus and demonstrating that it required its host resin to grow; cultures with standard media and even attempts to culture with another conifer resin (Canada balsam) failed. The authors also suggested that this fungus may be dispersed by beetles. Beimforde et al. (2017a) state that at least an ITS sequence for this fungus was obtained, but it is not clear whether the sequence has been made public.

Mytilinidiales*: *Mytilinidiaceae

Several strictly resinicolous species occur in this family. The first author has also noted that the not-strictly-resinicolous fungus *Lophium mytilinum* may also be found growing on resin (pers. obs.).

Mytilinidion Duby, *Mém. Soc. Phys. Genève* **16**(1): 34 (1861).

= *Camaroglobulus* Speer, *Bull. Trimestriel Soc. Mycol. France* **102**(1): 100 (1986).

The genus *Mytilinidion* as currently circumscribed contains three resinicolous species; one is undescribed. However, it is clear that as currently circumscribed the genus is highly polyphyletic, with the type species of many other genera internal to *Mytilinidion* (Boehm et al. 2009a, b; Mugambi and Huhndorf 2009; Delgado et al. 2019; Hongsanan et al. 2020). Which species is the type of *Mytilinidion* is apparently a topic of some contention, as an attempt to designate a "neotype" was made despite the undisputable type status of *Mytilinidion aggregatum* (DC.) Duby for the genus (Zogg 1962; Boehm et al. 2009b); this situation seems a good candidate for a conservation proposal. As things stand, there is little point in attempting to segregate genera, and we list all species under *Mytilinidion*, though *Camaroglobulus* is treated separately by some recent publications (Wijayawardene et al. 2014, 2020a; Ekanayaka et al. 2017).

Mytilinidion resinae Speer, *Bull. Trimestriel Soc. Mycol. France* **102**(1): 98 (1986).

Syntypes: PC & hb. Speer, Brazil: Rio Grande do Sul: prope Cambará do Sul, on *Araucaria angustifolia*, 13 Mar. 1976, leg. E.O. Speer.

= *Camaroglobulus resinae* Speer, *Bull. Trimestriel Soc. Mycol. France* **102**(1): 98 (1986).

Syntypes: PC & hb. Speer, Brazil: Rio Grande do Sul: prope Cambará do Sul, on *Araucaria angustifolia*, 13 Mar. 1976, leg. E.O. Speer.

Description: (Speer 1986).

Illustrations: (Speer 1986).

Hosts: *Araucaria*.

Distribution: South America (Brazil).

Molecular data: None available.

Additional notes: This fungus is one of only three described resinicolous fungi growing on exudates of species in *Araucariaceae*, and the only known resinicolous fungus on a conifer from South America. As was typical at the time, the sexual and asexual stages of this fungus were described separately and simultaneously.

Additional references:

Mytilinidion resinicola M.L. Lohman, *Pap. Michigan Acad. Sci.* **17**: 256 (1933) [1932]

Holotype: MICH 14656, [USA]: Michigan: [Washtenaw County]: north of Pinckney, on *Larix laricina*, 6 Aug. 1930, leg. M.L. Lohman, no. 260; Isotypes: BPI 648707, FH 00995501, MU-F-037137; Ex-type culture: CBS 304.34.

Description: (Lohman 1933).

Illustrations: (Lohman 1933).

Hosts: *Abies*, *Larix*, *Pinus*.

Distribution: North America (Canadian Maritimes, Midwestern US, New England), Europe (Germany).

Molecular data: FJ161145 (SSU), FJ161185 (LSU), FJ161101 (*TEF1*), FJ161120 (*RPB2*), from ex-type culture. The genome is also sequenced: https://gold.jgi.doe.gov/organism?id=Go0111702.

Additional notes: The first author has collected this in Vermont on *Abies* and *Pinus*. A specimen was collected in New Brunswick and is held at NBM.

Additional references: (Krieglsteiner 1991; Wai et al. 2019).

"***Mytilinidion* n. sp. *A*** M.L. Lohman"

This species is apparently undescribed and was designated as above by Lohman on a specimen in FH; when attempting to key it out in a recent treatment of *Mytilinidiaceae* (Boehm et al. 2009a), this species comes out between *M. tortile* and *M. resinicola*. It differs from *M. resinicola* by having slightly shorter, unconstricted spores, and from *M. tortile* by its longer, uncurved spores. The first author has collected specimens from New England and the Pacific Northwest on *Larix, Picea*, and *Pinus*; two specimens from Wisconsin at MU on *Thuja* and *Tsuga* identified as "*Mytilinidion resinicola* (near)" may be this species, as may be a specimen from Oregon at WSP on *Thuja* given the provisional name "*Mytilinidion resinicola* var. *oregonicum.*" This taxon and these specimens require additional attention.

Pleosporales

Testudinaceae

Testudina Bizz., *Atti Reale Ist. Veneto Sci. Lett. Arti* ser. 6 **3**(3): 303 (1885).

= *Marchaliella* G. Winter ex E. Bommer & M. Rousseau, *Bull. Soc. Roy. Bot. Belgique* **29**(1): 243 (1890).

This genus is monotypic; all further notes will be offered under the species.

Testudina terrestris Bizz., *Atti Reale Ist. Veneto Sci. Lett. Arti* ser. 6 **3**(3): 303 (1885).

Neotype: BR, Belgium: Bruxelles: Jardin Botanique de Bruxelles, sur une planche de sapin imprégnée de fumier depuis deux ans, 15 Dec. 1885, leg. É. Marchal, designated by Hawksworth and Booth, *Mycol. Pap. Commonw. Mycol. Inst.* **135**: 31 (1974).

≡ *Zopfia terrestris* (Bizz.) D. Hawksw. & C. Booth, *Mycol. Pap. Commonw. Mycol. Inst.* **135**: 31 (1974).

= *Marchaliella zopfielloides* E. Bommer & M. Rousseau, *Bull. Soc. Roy. Bot. Belgique* **29**(1): 243 (1890).

Holotype: BR, Belgium: Bruxelles: Jardin Botanique de Bruxelles, sur une planche de sapin imprégnée de fumier depuis deux ans, 15 Dec. 1885, leg. É. Marchal, examined by Hawksworth and Booth, *Mycol. Pap. Commonw. Mycol. Inst.* **135**: 31 (1974).

Description: (Bizzozero 1885; von Arx 1971; Hawksworth and Booth 1974).

Illustrations: (Bizzozero 1885; von Arx 1971; Hawksworth and Booth 1974; Hawksworth et al. 2016).

Hosts: conifer wood and needles, soil, animal fur, *Cedrus* resin.

Distribution: Australasia (Australia), Europe (Austria, Belgium, Denmark, Germany, Italy, Luxembourg, UK).

Molecular data: None available.

Additional notes: Cappelletti (1924) apparently examined the type, which has now been lost according to Hawksworth and Booth (1974). Cappelletti's observations indicate that rather than solely being on soil or needles of *Taxus*, as assumed by most other authors, this specimen grew additionally on resin fallen on the ground. He apparently examined another specimen collected in Florence with a similar habit. This association was only recorded by him, however, with the balance of specimens being on various other substrates; this species can thus hardly be called strictly resinicolous. A specimen collected in Australia associated with angiosperms and identified as this is held at IMI.

This species typifies a family but lacks molecular data. Other genera have been assigned to this family based on morphological grounds. These relationships should be verified.

Additional references: (Cappelletti 1924; Koch 1974; Hawksworth 1979; Eriksson 2014; Hawksworth and Wiltshire 2015).

Torulaceae

Torula Pers., in Usteri, *Ann. Bot.* **15**: 25 (1795).

Two resinicolous species have been placed in *Torula*; one was moved to *Helicoma* in the era prior to the applications of molecular methods. The true affinities of these dematiaceous hyphomycetes are unclear; they should be recollected to determine their true systematic placements.

Torula resinicola Peyronel, *Mem. Reale Accad. Sci. Torino, ser. 2* **66**(10): 42 (1915).

Syntypes: ROPV?, Italy, [Torino]: Riclaretto: La Tirièro & La Figliolo, in plagis resina obductis ramorum *Laricis deciduae* dejectorum, Jan.-Feb. 1918, leg. B. Peyronel.

Description: (Peyronel 1915).

Illustrations: (Peyronel 1915).

Hosts: *Cedrus*, *Larix*, *Picea*, *Pinus*.

Distribution: Africa (Morocco), Europe (France, Italy).

Molecular data: None available.

Additional notes: This species appears to have been almost completely forgotten within a few decades of its original description. Original material is probably at ROPV, but this remains to be verified. The most recent collection is apparently that held at MPU, collected in Morocco on *Cedrus* in 1941.

Additional references: (Dufrenoy 1919; Cappelletti 1924).

Tubeufiales: Tubeufiaceae

Helicoma Corda, *Icon. fung.* **1**: 15 (1837).

See notes under *Torula*.

Helicoma resinae (Lindau) J.L. Crane & Schokn., *Mycologia* **67**(3): 669 (1975).

≡ *Torula resinae* Lindau, *Rabenh. Krypt.-Fl. ed. 2, Band 1, Abt. 8* **101**: 578 (1906).

Holotype: B, [France: Haute Savoie]: bei Chamonix, auf Fichtenharz, 22 Jul. 1905, leg. O. Jaap, Fl. v. Savoyn no. 21, examined by Crane and Schoknecht, *Mycologia* **67**(3): 671 (1975); Isotype: ILLS 35650.

Description: (Lindau 1906; Cappelletti 1924; Crane and Schoknecht 1975; Goos 1986).

Illustrations: (Cappelletti 1924; Crane and Schoknecht 1975; Goos 1986; Chuaseeharonnachai et al. 2013).

Hosts: *Abies*, *Larix*, *Picea*, *Pinus*.

Distribution: Asia (Thailand), Europe (France, Italy).

Molecular data: None available.

Additional notes: Cappelletti (1924) in his detailed cultural observations of this species reported a yeast-like state for this hyphomycetous fungus. He compared the life cycle most closely with that of *Dematium pullulans* (≡ *Aureobasidium pullulans*) but was able to demonstrate that in contrast with that fungus, he was able to grow *H. resinicola* directly on resin after culturing. In fact, his observations suggest that it preferentially grew where he added turpentine to his growth medium. However, he also showed that it was not required for development of the fungus and showed that the water-soluble components of the resin were the apparent source of sustenance.

This fungus was also able to grow on media without the addition of resin. In many ways, Cappelletti's observations make this one of the best characterized of all resinicolous fungi, despite having been collected by only a handful of people.

A recent paper reports this fungus from a stream in Thailand, and provides a photograph (Chuaseeharonnachai et al. 2013). This sample should be checked, since it is a somewhat unusual ecology and far outside of the previously reported range.

Additional references: (Traverso 1912).

Eurotiomycetes

Eurotiomycetes houses the largest concentration of resinicolous fungi, and in recent years has arguably seen the most work. Additionally, the majority of these species have some molecular data available, so placements are fairly stable. An exception to this will be addressed in the entry below under *Sphinctrinaceae*.

Chaetothyriales

Coccodiniaceae

Teichosporina (G. Arnaud) Cif. & Bat., in Batista & Ciferri, *Beih. Sydowia* **3**: 104 (1962).

≡ *Teichospora* subgen. *Teichosporina* G. Arnaud, *Ann. École Natl. Agric. Montpellier n.s.* **10**(4): 324 (1911).

This genus is not known to be resinicolous, but a *Teichosporina* sp. was reported as growing on resinous bud scales of *Pseudotsuga menziesii* (Sherwood and Carroll 1974). The identity of this species is unclear.

Cyphellophoraceae

Cyphellophora G.A. de Vries, *Mycopathol. Mycol. Appl.* **16**(1): 47 (1962).

This genus of black yeasts does not contain any species known specifically to be resinicolous, but the type strain of *Cyphellophora sessilis* (≡ *Phialophora sessilis*) was isolated from the resin of *Picea abies* in the Netherlands (de Hoog et al. 1999). This species has also been isolated from a biofilter, soil, a pustule on *Peltigera polydactylon*, marble powder, decaying plants, and is the causal agent of a flyspeck and sooty blotch disease, and so cannot be considered truly resinicolous (Réblová et al. 2013).

Herpotrichiellaceae

Sorocybe Fr., *Summa veg. Scand.* **2**: 468 (1849).

= *Pycnostysanus* Lindau, *Verh. Bot. Vereins Prov. Brandenburg* **45**(2): 160 (1904).

= *Hormoconis* Arx & G.A. de Vries, *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2* **61**(4): 62 (1973).

Four species have been placed in the genus *Sorocybe*; of these, two (including the type species) are resinicolous. As has recently been expressed, *Sorocybe tenella* and *S. indica* probably do not belong in this genus, but are of unknown placement (Crous et al. 2019). In the same reference, placement of *Sorocybe* in *Herpotrichiellaceae* was only tentatively maintained, due to poor phylogenetic sampling in its close relatives.

Sorocybe oblongispora Tanney & Seifert, in Crous et al., *Persoonia* **43**: 403 (2019).

Holotype: DAOM 867433, Canada: New Brunswick: Charlotte County: Campobello Island, on resin of *Picea rubens*, 26 Sep. 2017, leg. J.B. Tanney; Ex-type culture: DAOMC 251618.

Description: (Crous et al. 2019).

Illustrations: (Crous et al. 2019).

Hosts: *Picea*.

Distribution: North America (Canadian Maritimes, Central Canada?, Southeastern US?).

Molecular data: MN114116 (ITS) & MN114118 (LSU), from ex-type culture. MN114115 (ITS) & MN114117 (LSU), from additional material.

Additional notes: This species is known from two specimens, both collected in about the same locality. Likely the species is more widely distributed but has in the past been misidentified as *S. resinae*. A culture identified as "*S. resinae*" isolated in Quebec held at CMMF is probably this species.

Bunch et al. (2013) reported *Sorocybe resinae* as a root associate of the orchid *Cypripedium acaule*. Since the report is from eastern North America, it likely refers to this species if properly identified. However, no sequence could be found among the supplementary material that closely matched either species of *Sorocybe*; this report may be spurious. Similarly, Asemaninejad et al. (2017) reported *Sorocybe* as part of the fungal community of hummocks in peatlands in Ontario; geography likely indicates this species, but sequences do not appear to have been made available for comparison.

Additional references: (Bunch et al. 2013; Asemaninejad et al. 2017; Crous et al. 2020).

Sorocybe resinae (Fr.) Fr., *Summa veg. Scand.* **2**: 468 (1849).

≡ *Racodium resinae* Fr., *Observ. mycol.* **1**: 216 (1815).

Holotype: B in hb. Link, [Sweden]: Smol. [Småland?], leg. E.M. Fries, examined by Seifert et al., *Stud. Mycol.* **58**: 239 (2007); Isotype: DAOM 41890.

≡ *Dematium resinae* (Fr.) Link, in Willdenow, *Sp. pl. Fifth Edition* **6**(1): 134 (1824).

≡ *Sporocybe resinae* (Fr.) Fr., *Syst. mycol.* **3**(2): 341 (1832), *nom. sanct.* (Fries, *l.c.*).

≡ *Dendryphion resinae* (Fr.) Corda, *Icon. fung.* **6**: 10 (1854).

≡ *Diplococcium resinae* (Fr.) Sacc., *Syll. fung.* **4**: 374 (1886).

≡ *Cephalotrichum resinae* (Fr.) Kuntze, *Revis. gen. pl.* **3**(3): 453 (1898).

≡ *Stysanopsis resinae* (Fr.) Ferraris, *Fl. ital. crypt., Hyphales* **1**(6): 187 (1910).

?= *Dematium nigrum* Link, *Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin* **3**(1): 21 (1809).

≡ *Sporotrichum nigrum* (Link) Link, *Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin* **7**(1): 35 (1816).

≡ *Alytosporium nigrum* (Link) Steud., *Nomencl. bot.* **2**: 55 (1824).

= *Pycnostysanus resinae* Lindau, *Verh. Bot. Vereins Prov. Brandenburg* **45**(2): 160 (1904). Lectotype: B, Deutschland [Germany]: [Saxony-Anhalt]: an Brockenweg, am Dreieckigen Pfahl in Harz, auf erhärteten Fichtenharz, 13 Aug. 1903, leg. G. Lindau, Kabát et Bubák *Fungi Imperfecti Exsiccati* no. 99, examined by Seifert et al., *Stud. Mycol.* **58**: 239 (2007), *designated here* (MBT XXXXXXXX); Isolectotypes: FH, BPI 448957, WIS-F-0081193.

≡ *Stysanus resinae* (Lindau) Sacc., in Saccardo & Saccardo, *Syll. fung.* **18**: 651 (1906).

= *Hormodendrum resinae* Lindau, *Rabenh. Krypt.-Fl. ed. 2, Band 1, Abt. 8* **102**: 699 (1906).

Holotype: B, [Germany: Schleswig-Holstein]: Sachsenwald, auf Harz an *Picea excelsa*, 29 Apr. 1906, leg. O. Jaap, Fl. v. Hamburg 206, examined by Seifert et al., *Stud. Mycol.* **58**: 239 (2007); Isotype: DAOM 41888.

≡ *Cladosporium resinae* (Lindau) G.A. de Vries, *Antonie van Leeuwenhoek J. Microbiol. Serol.* **21**: 167 (1955).

≡ *Hormoconis resinae* (Lindau) Arx & G.A. de Vries, *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Sect. 2* **61**(4): 62 (1973).

= *Herpotrichia resinae* Bres. ex Capp. *nom. inval.* (Art. 38.1), *Ann. Bot. (Rome)* **17**(4): 208 (1927).

Description: (Mel′nik and Popushoĭ 1992; Partridge and Morgan-Jones 2002).

Illustrations: (Barron 1968; Parbery 1969a; Mel′nik and Popushoĭ 1992; Partridge and Morgan-Jones 2002; Seifert et al. 2007; Tanney 2020).

Hosts: *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Tsuga*.

Distribution: Asia (Japan?), Europe (Austria, Belarus, Czechia, Denmark, Finland, Germany, Italy, Poland, Western Russia, Sweden), North America (Pacific Northwest)

Molecular data: EU030275 (ITS) & EU030277 (LSU). Both sequences are from material collected in the PNW, so if PNW material represents a distinct species from that occurring in Europe as suspected by Tanney (2020), these sequences will probably be representative of the new species.

Additional notes: Care must be taken with some of the names above; all names based on *Hormodendrum resinae* have historically been used for a different fungus, now known as *Amorphotheca resinae*. For a discussion of the nomenclatural issues, see the entry under the

latter name, and Seifert et al. (2007). In the list above, Parbery (1969) is listed as giving an illustration of this fungus; this is true, but only of Fig. 16, and not his other illustrations.

The holotype of *P. resinae* indicated previously is not acceptable as such; if the holotype was split for distribution in an exsiccata without knowing which piece specifically Lindau examined, then each of the pieces is better treated as a syntype (Seifert et al. 2007). We lectotypify the examined specimen above.

The presence of this fungus in Denmark and Finland is attested by a number of specimens held at S and UPS.

This fungus was recently reported by Szewczyk et al. (2017) from environmental sequencing of knotwood of *Pinus sylvestris* in Poland; sequences were apparently not published. Similarly, Fukasawa et al. (2019) reported this fungus as a component of the fungal community in decaying *Picea* snags in Japan, again apparently not publishing their sequences.
Additional references: (Lowe 1969; Shaw 1973; Rikkinen 2003a; Bensch et al. 2012; Belomesyatseva and Shabashova 2014; McCune 2017b; Szewczyk et al. 2017; Sun et al. 2018; Fukasawa et al. 2019; Crous et al. 2019, 2020).

Mycocaliciales*: *Sphinctrinaceae

This family is sometimes treated instead as two families, *Sphinctrinaceae* and *Mycocaliciaceae*; the evidence for this interpretation is ambiguous. In this interpretation, all species treated here are assignable to *Mycocaliciaceae*. Both genera containing resinicolous species (*Chaenothecopsis* and *Mycocalicium*) are highly polyphyletic; this group of fungi is badly in need of revision, though characterization of species is proceeding well. This family contains the single largest grouping of closely related resinicolous taxa, though phylogenetic

results show them frequently interspersed among species with other lifestyles (Tibell and Vinuesa 2005; Tuovila et al. 2011a, 2013, 2014; Rikkinen et al. 2014; Beimforde et al. 2017b). It also contains taxa which are not considered resinicolous, but will overgrow very old, hardened resin, such as *Chaenothecopsis nana* (Rikkinen 2003b; Hardman et al. 2017; McCune 2017a).

Statements may be found regarding the high host specificity of these resinicolous species; this seems to be quite true of species growing on angiosperm resin (see Section 1.3), but as the data compiled below suggest (and as previously suggested by Tuovila et al (2011b)), it seems true of a few of the conifer dwellers. Those for which it does seem true are typically reported from one publication; the frequently reported species may occur on as many as five genera of hosts throughout the northern hemisphere. Whether this can be interpreted as suggesting that the species concepts currently employed are overly broad is a matter for further research.

"*Mycocaliciaceae* sp."

A fungus overgrowing resin of *Agathis lanceolata* collected from New Caledonia was recently reported (Beimforde and Schmidt 2011). This fungus was reported growing not only on the surface, but several millimeters into the resin. SEM micrographs were provided illustrating this behavior. A placement in *Mycocaliciaceae* (= *Sphinctrinaceae*) was hypothesized, but it is not clear what this was based on.

Chaenothecopsis Vain., *Acta Soc. Fauna Fl. Fenn.* **57**(1): 70 (1927).

Chaenothecopsis asperopoda Titov, in Titov & Tibell, *Nordic J. Bot.* **13**(3): 316 (1993).

Holotype: LE, Russia: Khabarovsk Krai: Verkhne-Bureinsky region: Dusse-Alin mountains, on exudate of *Picea ajanensis*, 30 Jun. 1990, leg. A.N. Titov 3126; Isotypes: ASU0068077, BC-

Lichen-Caliciales-911668, BM001096817, CANL 111592, DUKE 133060, H, LD 1055868, M-0024939/553040/232291, M-0103226, M-0103227/558536/237016, O 646, OSC, S L2943, TNS 113286, UMFK, UPS L-073803, US 00512739, WIS-L-0121609.

Description: (Titov and Tibell 1993; Tibell and Titov 1995; Selva and Tibell 1999; Tibell and Thor 2003; Titov 2006; McCune 2017a).

Illustrations: (Titov and Tibell 1993; Titov 2006).

Hosts: *Abies*, *Larix*, *Picea*, *Pinus*, *Tsuga*.

Distribution: Asia (China, Eastern Russia, Japan), North America (Canadian Maritimes, Midwestern US, Pacific Northwest).

Molecular data: None available.

Additional notes: This may have been the unnamed resinicolous *Chaenothecopsis* species reported by Goward (1999) from British Columbia; the provided data are sparse, though, so it is not easy to tell.

Additional references: (Tibell 1995; Goward 1999; Wei and Titov 2001; Rikkinen 2003b; Neshataeva et al. 2004; Selva 2013; Gockman et al. 2020).

Chaenothecopsis bitterfeldensis Rikkinen & Poinar, *Mycol. Res.* **104**(1): 8 (2000).

Holotype: GZG.BST.21970, Germany: Bitterfeld, in amber, 1997, AF 9-26.

Description: (Rikkinen and Poinar 2000; Rikkinen et al. 2018).

Illustrations: (Rikkinen and Poinar 2000; Schmidt et al. 2013; Beimforde et al. 2014; Rikkinen and Schmidt 2018; Rikkinen et al. 2018).

Hosts: *Cupressospermum*?.

Distribution: Europe (Germany).

Molecular data: None available.

Additional notes: This fossil taxon was the first resinicolous fossil taxon described. The apothecia of this taxon are clearly growing on a fragment of resin that was then covered by additional resin, and the species is surprisingly well characterized, as hyphae growing in the resin, well preserved one-septate spores, and even germinating spores were observed. Rikkinen et al. (2018) place this species in *Chaenothecopsis* group "D" of Tuovila et al. (2014).

Two additional, similar fossils were recently reported by Tuovila et al. (2013) from Bitterfeld amber and Baltic Amber, and an additional three were reported by Rikkinen et al. (2018). These also were confidently assigned to *Chaenothecopsis* group "D" of Tuovila et al. (2014), but not identified as identical with *C. bitterfeldensis*.

Specimens have been dated between 22 and 35 million years old (Prieto and Wedin 2013).

Additional references: (Tuovila et al. 2013).

Chaenothecopsis claydenii Selva & Tuovila ex J.K. Mitch. *sp. nov.* (MB XXXXXXXX)

Holotype: UMFK, Canada: New Brunswick: Restigouche County: east side of Trout Lake, resinicolous on bark of *Picea* sp., 21 Jul. 2012, leg. S.B. Selva 11076; Isotypes: NY 04181932, NY 04181933.

= *Chaenothecopsis claydenii* Selva & Tuovila *nom. inval.* (Art. 40.2), *Bryologist* **119**(4): 418 (2016).

Description: (Selva and Tuovila 2016).

Illustrations: (Selva and Tuovila 2016).

Hosts: *Picea*.

Distribution: North America (Canadian Maritimes).

Molecular data: None available.

Additional notes: Selva and Tuovila (2016) apparently failed to cite a single holotype, instead listing several gatherings as "holotype." The name is validated here.

Additional references:

Chaenothecopsis diabolica Rikkinen & Tuovila, in Tuovila et al., *Karstenia* **51**(2): 40 (2011).

Holotype: H, USA: Oregon: Benton County: McDonald Research Forest, on resin and resin-soaked lignum of *Abies grandis*, 1998, leg. J. Rikkinen 98363; Isotype: TUR.

Description: (Tuovila et al. 2011b; McCune 2017a).

Illustrations: (Rikkinen 2003c; Tuovila et al. 2011b; McCune 2017a).

Hosts: *Abies*.

Distribution: Europe (Spain), North America (Pacific Northwest).

Molecular data: JX119109 (ITS) & JX119118 (LSU).

Additional notes: This species was described growing among the holotype material of *C. oregana*, but was not recognized when that taxon was described; though the description of *C. oregana* in no part relied on material of *C. diabolica*, several of the photos do correspond to this taxon according to Tuovila et al. (2012).

Additional references: (Tuovila et al. 2012, 2013, 2014; Rikkinen et al. 2014; Beimforde et al. 2017b; Temu et al. 2019).

Chaenothecopsis dolichocephala Titov, in Tibell & Titov, *Bryologist* **28**(4): 551 (1995).

Holotype: LE, Russia: Primorsky Krai: Khasan Region: Kedrovaya padj reserve, on exudate of *Abies holophylla*, Aug. 1990, leg. A.N. Titov 4458; Isotypes: H, M-0024936, UPS.

Description: (Tibell and Titov 1995; Titov 2006; Gudovicheva and Titov 2007; Selva 2010, 2014).

Illustrations: (Tibell and Titov 1995; Titov 2006).

Hosts: *Abies*, *Larix*, *Picea*, *Pinus*, *Tsuga*.

Distribution: Asia (Bhutan, China, Eastern Russia, India), Europe (Western Russia), North America (Central Canada, Maritime Canada, Midwestern US, Northeastern US, Southeastern US).

Molecular data: AY795854 (ITS) & AY795993 (LSU).

Additional notes: This species was possibly grown in culture by Tibell (1997); it is unclear, however, since on page 309 it is stated that this species "exhibited moderate to good vegetative growth but did not produce any anamorphs" and on page 315 it is stated that it "failed to germinate."

Tuovila et al. (2014) suggest that east Asian specimens on *Pinus* may actually be *C. hunanensis*, though they noted that there were still morphological differences. Selva (2016) reported this species on *Pinus* resin from Great Smoky Mountains National Park.

Specimens from India on *Abies* and Bhutan on *Tsuga* are held at UPS. A specimen from Pennsylvania on *Tsuga* is held at KE.

Additional references: (Tibell 1997; Wei and Titov 2001; Tibell and Vinuesa 2005; Tuovila et al. 2011a, 2013, 2014; Rikkinen et al. 2014; Selva 2016; Beimforde et al. 2017b; Temu et al. 2019; Gockman et al. 2020).

Chaenothecopsis edbergii Selva & Tibell, *Bryologist* **102**(3): 381 (1999).

Holotype: UMFK, Canada: British Columbia: Robson Valley, on resin of *Tsuga heterophylla*, 2 Jun. 1995, leg. S.B. Selva 6297a; Isotypes: NY 04181927, UPS.

Description: (Selva and Tibell 1999; Titov 2006; Selva 2010, 2014; McCune 2017a).

Illustrations: (Selva and Tibell 1999; Titov 2006).

Hosts: *Tsuga*.

Distribution: North America (New England, Pacific Northwest, Southeastern US).

Molecular data: None available.

Additional notes: Selva (2014) clarified that previously he (2010) had reported this species from Nova Scotia but is not known to occur there. This presumably applies to his report from 2003 as well (Selva 2003).

This appears to be one of a small number of truly host-specific species of resinicolous *Chaenothecopsis* on gymnosperms; it is only known from hosts in the genus *Tsuga*.

Additional references: (Goward 1999; Selva 2003, 2016).

Chaenothecopsis eugeniae Titov, *Lichenologist* **33**(4): 306 (2001).

Holotype: L-HMAS, China: Sichuan Province: Ganzi Tibetan Autonomous Prefecture: Kanding County: Mount Gongga, on resin of *Abies forrestii*, Oct. 1999, leg. A.N. Titov 6698; Isotypes: LE, M-0024933, UPS.

Description: (Titov 2001, 2006; Selva 2016).

Illustrations: (Titov 2001, 2006).

Hosts: *Abies*, *Picea*, *Tsuga*.

Distribution: Asia (China), North America (Canadian Maritimes, Southeastern US).

Molecular data: None available.

Additional notes:

Additional references: (Wei and Titov 2001; Selva and Tuovila 2016).

Chaenothecopsis golubkovae Tibell & Titov, in Titov & Tibell, *Nordic J. Bot.* **13**(3): 320 (1993).

Holotype: LE, Russia: Krasnodar Krai: Apsheronsk region, on the bark of dead *Abies nordmanniana*, 26 May 1982, leg. A.N. Titov 303; Isotypes: BC-Lichen-Caliciales-911897, BM001096813, CANL 106400, DUKE 133062, H, M-0103231, M-0103232, M-0024937, O 140, OSC, S F109089, TNS 113259, UBC L38509, UMFK, UPS L-023225, US 02482600, WIS-L-0121583.

Description: (Titov and Tibell 1993; Tibell and Titov 1995; Titov 2006).

Illustrations: (Titov and Tibell 1993; Titov 2006).

Hosts: *Abies*, *Picea*, *Pinus*, *Tsuga*.

Distribution: Asia (China, Eastern Russia, India), Europe (Georgia, Western Russia).

Molecular data: AY795859/AY795860 (ITS) & AY795996 (LSU).

Additional notes:

Additional references: (Titov 1998, 2000; Wei and Titov 2001; Tibell and Vinuesa 2005; Tuovila et al. 2011a, 2013, 2014; Rikkinen et al. 2014; Crous et al. 2016; Beimforde et al. 2017b; Temu et al. 2019).

Chaenothecopsis hunanensis Rikkinen & Tuovila, *Mycologia* **106**(5): 995 (2014).

Holotype: H, China: Hunan Province: Dayong County: Zhangjiajie National Forest Park: Fuqiyan, in basal crevice of large *Pinus massoniana*, 15 Sep. 1999, leg. J. Rikkinen 990059.

Description: (Tuovila et al. 2014).

Illustrations: (Tuovila et al. 2014).

Hosts: *Pinus*.

Distribution: Asia (China).

Molecular data: JX122784 (LSU), from the holotype.

Additional notes: This species is listed in the Chinese Macrofungi Red List (Wang et al. 2020).

Additional references: (Tuovila et al. 2013; Wang et al. 2020).

Chaenothecopsis marcineae Selva, *Bryologist* **116**(3): 253 (2013).

Holotype: UMFK, Canada: New Brunswick: Restigouche County, over resin, on *Picea glauca*, 30 Jul. 2012, leg. S.B. Selva 11054; Isotype: NY 04181925.

Description: (Selva 2013).

Illustrations: (Selva 2013; McMullin et al. 2015).

Hosts: *Picea*, *Tsuga*.

Distribution: Europe (Finland), North America (Canadian Maritimes, Central Canada, Midwestern US, New England, Southeastern US).

Molecular data: Not available.

Additional notes:

Additional references: (Deduke et al. 2016; McMullin and Arsenault 2016; Selva 2016; McMullin 2017b, a; Gockman et al. 2020).

Chaenothecopsis mediorossica Titov & Gudov., in Titov, *Mycocalicioid fungi holarct.*: 153 (2006).

Holotype: LE, Russia: Yaroslavl Oblast: Pereslavsky District: National Park Lake Pleshcheyevo, on resin of *Picea abies*, 2006, leg. A.N. Titov 6800.

Description: (Titov 2006).

Illustrations: (Titov 2006).

Hosts: *Picea*.

Distribution: Europe (Western Russia).

Molecular data: Not available.

Additional notes: This species seems to have garnered attention only in Russia, since it is absent from even a treatment purporting to provide worldwide keys of resinicolous mycocalicioid fungi (Selva and Tuovila 2016). This may be because almost all reports have been in Russian language publications.

Additional references: (Muchnik et al. 2007, 2009; Himelbrant et al. 2011, 2016; Notov et al. 2011, 2016; Muchnik 2015).

Chaenothecopsis montana Rikkinen, *Ann. Bot. Fenn.* **40**(6): 447 (2003).

Holotype: H, USA: Oregon: Polk County: Little Sinks Research Natural Area, on exudate and lignum in beaver scars at trunk bases of living *Abies grandis*, 1998, leg. J. Rikkinen 98008; Isotypes: OSC, TUR, UPS.

Description: (Rikkinen 2003c; Titov 2006; Tuovila et al. 2011b; McCune 2017a).

Illustrations: (Rikkinen 2003c; Titov 2006; Tuovila et al. 2011b).

Hosts: *Abies*, *Picea*, *Tsuga*.

Distribution: Europe (Czechia, Finland, Norway, Spain, Sweden, Switzerland), North America (Pacific Northwest).

Molecular data: KF157975 (SSU), JX119105 (ITS), JX119114/KF157987 (LSU), & KF158002 (*RPB2*).

Additional notes: This species was included as a candidate for the Fennoscandian Red List by Tingstad et al. (2017). It was also given as vulnerable in Norway by Holien et al. (2018).

Additional references: (Rikkinen 2003b; Brandrud et al. 2010; Tuovila et al. 2013, 2014; Pang et al. 2014; Rikkinen et al. 2014; Beimforde et al. 2014, 2017b; Crous et al. 2016; Hardman et al. 2017; Tingstad et al. 2017; Holien et al. 2018; Maliček et al. 2018; Ekanayaka et al. 2019; Temu et al. 2019).

Chaenothecopsis neocaledonica Rikkinen, Tuovila & A.R. Schmidt, in Rikkinen et al., *Phytotaxa* **173**(1): (2014).

Holotype: P, [France]: New Caledonia: Province Sud: Yaté, on resin, resin-soaked bark and lignum of *Agathis ovata*, 5 Nov. 2011, leg. J. Rikkinen 010179; Isotypes: H.

Description: (Rikkinen et al. 2014).

Illustrations: (Rikkinen et al. 2014).

Hosts: *Agathis*.

Distribution: Australasia (New Caledonia).

Molecular data: KF815196 (ITS) & KF815197 (LSU), from the holotype.

Additional notes: This is the only resinicolous species in *Mycocaliciales* found on a conifer in *Araucariaceae*, and the only southern hemisphere resinicolous species in *Mycocaliciales*. Likely,

it is extremely localized geographically. Still, similar species should be sought on other species of *Agathis* and on *Araucaria* in the southern hemisphere.

Additional references: (Beimforde et al. 2017b; Temu et al. 2019).

Chaenothecopsis nigripunctata Rikkinen, *Mycologia* **95**(1): 99 (2003).

Holotype: H, USA: Oregon: Linn County: Horse Rock Ridge Research Natural Area, on exudate of *Tsuga heterophylla*, 26 May 1998, leg. J. Rikkinen 98482; Isotypes: UPS, US.

Description: (Rikkinen 2003a; Titov 2006; McCune 2017a).

Illustrations: (Rikkinen 2003a; Titov 2006; McCune 2017a; McMullin 2019).

Hosts: *Abies*, *Picea*, *Pseudotsuga*, *Tsuga*.

Distribution: North America (Pacific Northwest).

Molecular data: JX119103 (ITS) & JX119112 (LSU).

Additional notes:

Additional references: (Rikkinen 2003b; Tuovila et al. 2013, 2014; Rikkinen et al. 2014; Hardman et al. 2017; Beimforde et al. 2017b; Temu et al. 2019).

Chaenothecopsis oregana Rikkinen, *Ann. Bot. Fenn.* **40**(6): 447 (2003).

Holotype: H, USA: Oregon: Benton County: McDonald Research Forest, on exudate and lignum in beaver scar at trunk bases of living *Abies grandis*, 1998, leg. J. Rikkinen 98363 (destroyed); Lectotype: H, USA: Oregon: Lincoln County: H.B. Van Duzer Forest Corridor wayside, on exudate and lignum in beaver scar at trunk base of living *Tsuga heterophylla*, 1998, leg. J. Rikkinen 98333, designated by Tuovila et al., *Karstenia* **52**(2): 74 (2012).

= *Chaenothecopsis zebrina* Rikkinen & Tuovila, in Tuovila et al., *Karstenia* **51**(2): 42 (2011).

Holotype: H, USA: Oregon: Polk County: Little Sinks Research Natural Area, on resin and resin-soaked lignum of *Abies grandis*, 1998, leg. J. Rikkinen 98010a; Isotypes: OSC, TUR.

Description: (Rikkinen 2003c; Titov 2006; Tuovila et al. 2011b; McCune 2017a).

Illustrations: (Rikkinen 2003c; Titov 2006; Tuovila et al. 2011b; Haughland and Martel 2016; Paquette et al. 2019).

Hosts: *Abies*, *Picea*, *Tsuga*.

Distribution: Europe (Spain, Sweden, Switzerland), North America (Central Canada, Pacific Northwest, Prairie Provinces).

Molecular data: None available.

Additional notes: *C. zebrina* was (not explicitly) published as a replacement name for *C. oregana*, since all material in the holotype specimen corresponding to this species was destroyed. The lack of an explicit link between *C. zebrina* and *C. oregana* would seem to make the former legitimate, however, contrary to the opinion of Tuovila et al. (2012). It is still a taxonomic synonym and the correct name for the species is *C. oregana*.

It is somewhat unclear if Titov (2006) illustrated this species, or *C. diabolica*; he does not point out any differences between his description and the protologue, such as ornamented spores, so he may have examined the true *C. oregana* in the holotype prior to its destruction.

This species was included as a candidate for the Fennoscandian Red List by Tingstad et al. (2017).

Additional references: (Rikkinen 2003b; Groner 2010; Tuovila et al. 2012; Tingstad et al. 2017).

Chaenothecopsis penningtonensis Gockman & Selva, in Gockman et al., *Bryologist* **123**(2): 248 (2020).

Holotype: MIN, USA: Minnesota: Beltrami County: Pennington Bog Scientific and Natural Area, corticolous, on lower surface of *Picea mariana* bark chips, 2017, leg. Gockman & Milburn 5481A.

Description: (Gockman et al. 2020).

Illustrations: (Gockman et al. 2020).

Hosts: *Picea*.

Distribution: North America (Midwestern US).

Molecular data: None available.

Additional notes: This is the most recently described resinicolous calicioid fungus and is from a previously under-explored region of North America (the Midwest). This suggests there is more to find, as long as people look in new areas.

Additional references:

Chaenothecopsis proliferatus Rikkinen, A.R. Schmidt & Tuovila, *Fungal Diversity* **58**(1): 203 (2013).

Holotype: H, China: Hunan Province: Dayong County: Zhangjiajie National Forest Park: Fuqijan, on resin, resin-soaked bark, and lignum of *Cunninghamia lanceolata*, 15 Sep. 1999, leg. J. Rikkinen JR990061.

Description: (Tuovila et al. 2013).

Illustrations: (Tuovila et al. 2013).

Hosts: *Cunninghamia*.

Distribution: Asia (China).

Molecular data: JX122783 (LSU).

Additional notes:

Additional references:

Chaenothecopsis resinicola Tibell & Titov, *Bryologist* **28**(4): 553 (1995).

Holotype: LE, Russia: Primorsky Krai: Lazo Region: Lazovsky Reserve, on resin of *Pinus koraiensis*, leg. A.N. Titov 4072; Isotype: UPS.

Description: (Tibell and Titov 1995; Titov 2006; Selva 2010).

Illustrations: (Tibell and Titov 1995; Titov 2006).

Hosts: *Larix*, *Pinus*, *Tsuga*.

Distribution: Asia (China, Eastern Russia), North America (Southeastern US).

Molecular data: AY795867 (ITS).

Additional notes: This species was possibly grown in culture by Tibell (1997); it is unclear, however, as on page 309 it is stated that this species "exhibited rather poor growth and did not produce any anamorph" and on page 315 it is stated that it "failed to germinate."

Additional references: (Wei and Titov 2001; Tibell and Vinuesa 2005; Tuovila et al. 2014; Selva 2016; Temu et al. 2019).

Chaenothecopsis sitchensis Rikkinen, *Bryologist* **102**(3): 366 (1999).

Holotype: H, USA: Oregon: Lane County: Proposed Cape Perpetua Research Natural Area, Cummins Creek, on resin in root crevices of huge *Picea sitchensis*, 19 Mar. 1998, leg. J. Rikkinen 98183; Isotypes: H, OSC, UPS L-105477, US.

Description: (Rikkinen 1999; McCune 2017a).

Illustrations: (Rikkinen 1999, 2003b; Titov 2006; Rikkinen and Schmidt 2018).

Hosts: *Picea*, *Tsuga*.

Distribution: North America (Pacific Northwest).

Molecular data: KF157976 (SSU), JX119102 (ITS), JX119111/KF157988 (LSU), KF157996 (*RPB1*), & KF158003 (*RPB2*).

Additional notes:

Additional references: (Tuovila et al. 2013, 2014; Pang et al. 2014; Rikkinen et al. 2014; Beimforde et al. 2014, 2017b; Ekanayaka et al. 2019; Temu et al. 2019; Hashimoto et al. 2021).

Chaenothecopsis tsugae Rikkinen, *Bryologist* **102**(3): 367 (1999).

Holotype: H, USA: Oregon: Tillamook County: Nestucca River Area of Critical Environmental Concern, on exudate in beaver scar on mature *Tsuga heterophylla*, 6 May 1998, leg. J. Rikkinen 98309; Isotypes: H, OSC, UPS L-105478, US.

= *Chaenothecopsis thujae* Rikkinen ex Selva & Tibell *nom. inval.* (Arts. 39.1, 40.1), *Bryologist* **102**(3): 386 (1999).

Description: (Rikkinen 1999; Selva and Tibell 1999; McCune 2017a).

Illustrations: (Rikkinen 1999; Selva and Tibell 1999; Titov 2006; Rikkinen and Schmidt 2018; McMullin 2019; Bell-Doyon et al. 2021).

Hosts: *Abies*, *Picea*, *Tsuga*.

Distribution: North America (Central Canada, Maritime Canada, Pacific Northwest).

Molecular data: JX119104 (ITS) & JX119113 (LSU).

Additional notes: Selva (2010) clarified that when he and Leif Tibell (1999) employed the name "*C. thujae*," this was merely a *lapsus calami* for *C. tsugae*.

This species was shown to be restricted to stands over 300 years of age in British Columbia by Goward & Arsenault (2018).

Additional references: (Goward 1999; Rikkinen 2003b; Selva 2010, 2013; Tuovila et al. 2013, 2014; Rikkinen et al. 2014; Hardman et al. 2017; Beimforde et al. 2017b; Goward and Arsenault 2018).

Mycocalicium Vain., *Acta Soc. Fauna Fl. Fenn.* **7**(2): 182 (1890).

Mycocalicium sequoiae Bonar, *Madroño* **21**(2): 68 (1971).

Holotype: UC 1403569, [USA]: California: Tulare County: Sequoia National Park: Crescent Meadow, on *Sequoiadendron giganteum*, 1 Jul. 1935, leg. L. Bonar; Isotypes: BPI 683944, BR5020004689334, CUP CaliforniaF.01380, F C0171658F, FH 00995504, G00127960, MICH 62952, MIN 843307, NY 1219089, UPS L-104340, WSP67422.

Description: (Bonar 1971; Tibell and Titov 1995; Titov 2006; McCune 2017a).

Illustrations: (Bonar 1971; Tibell and Titov 1995; Titov 2006).

Hosts: *Sequoia*, *Sequoiadendron*.

Distribution: North America (Pacific Northwest, Southwestern US).

Molecular data: AY796002 (LSU).

Additional notes: This is the only known resinicolous calicioid on resin of conifers in *Cupressaceae*. Overall, species on resin of this family of conifers are fairly rare.

Phylogenetically, this species falls inside the polyphyletic *Chaenothecopsis*, and not particularly close to the type species of *Mycocalicium*, *M. parietinum*. We refrain from proposing a combination in *Chaenothecopsis*, as have other authors, in anticipation of the breakup of *Chaenothecopsis* into segregate genera.

Additional references: (Rikkinen 2003b; Tibell and Vinuesa 2005; Tonouchi 2009; Tuovila et al. 2013, 2014; Rikkinen et al. 2014; Crous et al. 2016).

Verrucariales*: *Verrucariaceae

Spheconisca (Norman) Norman, *Bot. Not.* **1876**(6a): 170 (1876).

≡ *Moriola* B. *Spheconisca* Norman, *Bot. Not.* **1872**(1): 15 (1872).

Spheconisca resinae (Norman) Norman, *Bot. Not.* **1876**(6a): 170 (1876).

≡ *Moriola resinae* Norman, *Bot. Not.* **1872**(1): 14 (1872).

Syntypes: O-F-156000 & O-F-156001, Norway: Troms og Finnmark: Målselv, ad resinam *Pini sylvestris*, leg. J.M. Norman.

Description: (Norman 1872; Migula 1931).

Illustrations: None available.

Hosts: *Picea*, *Pinus*.

Distribution: Europe (Italy, Norway).

Molecular data: None available.

Additional notes: This is a very poorly understood species. It has apparently only been identified by Norman. Its systematic placement is uncertain, and it should be reviewed and illustrated.

DUKE has a specimen from Norman's herbarium which was collected on *Picea* in what is now Italy. Two additional specimens from Italy on *Picea* are held at TRH, also identified by Norman.

Additional references:

Lecanoromycetes

This class does not seem to house any truly resinicolous species, though some foliose and crustose lichens can sometimes be found overgrowing old resin (pers. obs.).

Lecanorales*: *Lecanoraceae

Lecanora Ach., in Luyken, *Tent. hist. lich.*: 90 (1809).

Lecanora cf. *phaeostigma* has been reported from the resin of *Pinus* in Alaska (Spribille et al. 2010). Since it was also reported from the bark, this was probably just a case of a lichen overgrowing resin.

Leotiomycetes

Despite its diversity, this class hosts relatively few resinicolous taxa, almost all of which are poorly understood and in need of revision.

Helotiales

Amorphothecaceae

Amorphotheca Parbery, *Austral. J. Bot.* **17**(2): 340 (1969).

Amorphotheca resinae Parbery, *Austral. J. Bot.* **17**(2): 340 (1969), *nom. cons. prop.* (Rossman et al., *Taxon* **67**(3): 636 (2018).

Holotype: MELU 7130 (IMI 129861×129862), Australia: South Eastern Australia, from soil, leg. D.G. Parbery W1.1×V2.0.

= *Cladosporium avellaneum* G.A. de Vries, *Contr. Knowl. Genus* Cladosporium: 52 (1952).

Holotype: CBS 186.54, Netherlands: Utrecht, isolated from "Nivea" ointment, 19 May 1947, leg. G.A. de Vries; Isotypes: ATCC 11273, IMI 49620.

This species has something of a complicated history, mostly owing to de Vries' (1955) and Parberry's (1969a) misinterpretations of the type specimen of *Hormodendrum resinae*, and the prior use of that name for this fungus by American authors (Christensen et al. 1942; Marsden 1954). Both de Vries and Parbery examined the specimen, growing in association with its synnematous synasexual morph, and found it to be similar to the creosote fungus they were studying (de Vries 1955; Parbery 1969a). Parbery (1969a) also seems to have been confused by a previous statement of the synonymy of *H. resinae* and *Sorocybe resinae*, taking it to imply that they represented the same stage in the life cycle, which they do not (Hughes 1958). This situation has been clarified by a recent paper (Seifert et al. 2007), but does not seem to have been well understood by subsequent authors. In response to continued use of the incorrect names in publications dealing with this fungus and new rules mandating a single correct name for pleomorphic fungi, another recent publication has proposed conservation of the name *Amorphotheca resinae* over *Cladosporium avellaneum*, which has priority (Rossman et al. 2018).

This species has only infrequently been reported from resin. The only first-hand report we could find was that of Christensen et al. (1942), who isolated it from resinous bark and twigs of *Picea pungens*. Otherwise, the fungus grows on a number of substrates, as outlined by other authors (Nicot and Zakartchenko 1966; Parbery 1969b).

Calloriaceae

Micropodia Boud., *Bull. Soc. Mycol. France* **1**: 118 (1885).

Micropodia resinicola (Rehm ex Mouton) Boud., *Hist. classific. discomyc. Europe*: 128 (1907).

≡ *Pezizella resinicola* Rehm ex Mouton, *Bull. Soc. Roy. Bot. Belgique* **36**(2): 16 (1897).

Syntypes: BR5020091647798, FH, M-0206232/596782/266655, M-0206233/596783/266656, NY 03418229, S F12106, S F12107, [Belgium]: prope Liége, in ramulis dejectis *Pini sylvestris* praesertim ad cicatrices et nodos, leg. V. Mouton.

≡ *Belonium resinicola* (Rehm ex Mouton) Rehm, *Ascomyceten* **25**: no. 1218 (1898).

Description: (Mouton 1897).

Illustrations: None available.

Hosts: *Pinus*.

Distribution: Europe (Belgium).

Molecular data: None available.

Additional notes: This fungus is known only from the original gathering, distributed by Rehm in his exsiccata. Its affinities are unclear, and it should be reviewed and illustrated.

Additional references:

Chrysodiscaceae

Chrysodisca Baral, Polhorský & G. Marson, in Baral & Polhorský, *Mycol. Montenegr.* **20**: 81 (2019).

The only member of this monotypic genus, *Chrysodisca peziculoides*, is a yellow discomycete found mostly on species of *Pinus*, but also on *Picea*, in southern and central Europe (Baral and Polhorský 2019). Although it cannot be strictly called resinicolous, largely preferring bark, it is sometimes found growing on resin.

Helotiaceae

Hymenoscyphus Gray, *Nat. arr. Brit. pl.* **1**: 673 (1821).

Hymenoscyphus resinae-piceae Svrček, *Ceská Mykol.* **40**(4): 211 (1986).

Holotype: PRM 842897, [Czechia]: Bohemia centralis [Central Bohemian Region]: Srbsko prope Karlštejn: in colle Doutnáč, ad resinam nigram in codice[?] *Piceae abietis*, 23 Oct. 1966, leg. A. Pilát.

Description: (Svrček 1986).

Illustrations: (Svrček 1986).

Hosts: *Picea*.

Distribution: Europe (Czechia, Germany).

Molecular data: None available.

Additional notes: This species is probably in need of revision, and most likely does not belong to this genus or family. Likely it is more common than it appears based on the reports to date.

Additional references: (Krieglsteiner 1991).

Hyaloscyphaceae

Echinula Graddon, *Trans. Brit. Mycol. Soc.* **69**(2): 255 (1977).

In their recent monograph of *Orbiliomycetes*, Baral et al. (2020) mention an unpublished species, "*Echinula resinicola*" which, based on its epithet and its association with known resinicolous species, is likely resinicolous. It is neither described nor illustrated, and little information about it has been published.

Lachnaceae

Lachnellula P. Karst., *Meddeland. Soc. Fauna Fl. Fenn.* **11**: 138 (1885).

This genus contains a number of plant parasites on conifers, many of which cause wounds which then produce resin. One species, however, does not seem to cause the resin flows it is associated with, and we consider this species resinicolous. This suggests the capacity to shift from a parasitic to a resinicolous lifestyle.

Lachnellula resinaria (Cooke & W. Phillips) Rehm, *Rabenh. Krypt.-Fl. ed. 2, Band 1, Abt. 3* **41**: 864 (1893).

≡ *Peziza resinaria* Cooke & W. Phillips, in Cooke, *Grevillea* **3**(28): 185 (1875).

Syntypes: K(M), [UK]: Wales: Northern Wales: Trefriw, on resin of spruce fir, May 1874, leg. W. Phillips; BPI 658847, FH, M-0229557/656129/310523, NY 1722128, [UK]: Wales: Northern Wales, 1875, leg. W. Phillips.

≡ *Dasyscyphus resinarius* (Cooke & W. Phillips) Rehm, *Ascomyc. lojk.*: 11 (1882).

≡ *Lachnella resinaria* (Cooke & W. Phillips) W. Phillips, *Man. Brit. Discomyc.*: 242 (1887).

≡ *Atractobolus resinarius* (Cooke & W. Phillips) Kuntze, *Revis. gen. pl.* **3**(3): 446 (1898).

≡ *Trichoscypha resinaria* (Cooke & W. Phillips) Boud., *Hist. classific. discomyc. Europe*: 125 (1907).

≡ *Trichoscyphella resinaria* (Cooke & W. Phillips) Dennis, *Mycol. Pap. Commonw. Mycol. Inst.* **32**: 93 (1949).

Description: (Anderson 1902; Dennis 1949; Kujala 1950; Grelet 1951; Seaver 1951; Dharne 1965; Raitviir 1970, 1980; Hanso 1978; Ellis and Ellis 1985; Sacconi 1985; Azbukina 1991; Baral and Matheis 2000; Vesterholt 2000; Minter 2005).

Illustrations: (Anderson 1902; Dennis 1949; Kujala 1950; Dharne 1965; Raitviir 1980; Sacconi 1985; Baral and Matheis 2000; Minter 2005; Raymundo et al. 2013; Mitchell 2017).

Hosts: *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*.

Distribution: Asia (Bhutan, Eastern Russia, Japan), Europe (Austria, Belarus, Czechia, Denmark, Estonia, Finland, France, Germany, Hungary, Italy, Luxembourg, Norway, Poland, Serbia, Spain, Sweden, Switzerland, UK, Western Russia), North America (Canadian Maritimes, Central Canada, Mexico, Midwestern US, New England, Northeastern US, Pacific Northwest, Prairie Provinces, Rocky Mountains, Southeastern US).

Molecular data: MN719894 (ITS+LSU), from Europe; MT913605 (ITS), from North America; AB481246 (ITS), from Asia.

Additional notes: Assuming the three available sequences of this species were correctly identified, this is probably actually a complex of at least three potentially geographically isolated species. More work sequencing expertly identified specimens from around the world is needed before any concrete conclusions can be reached.

European material of this species was shown to have more DNA than its lower elevation congeners by Weber & Bresinsky (1992).

Kikuchi et al. (2009) reported a method for extracting high quality DNA that evidently worked for Japanese material of this fungus, but it is not clear if this was sequenced. A sequence from Japanese material was generated by Hosoya et al. (2010). Another sequence and photos of the culture it was derived from are available from the NARO Genebank Project page, MAFF no. 410530; it does not closely match the sequence generated by Hosoya et al. Judging by the description given by some authors, part of Japanese material identified as *L. resinaria* is likely instead *L. calycina* (Kishi 1998).

Production of an asexual stage in culture was reported by Dharne (1965), and Baral & Matheis (2000) reported observations of an asexual stage as well.

Specimens identified as this species are held at BPI, MU, UC, and WSP from British Columbia, California, Oregon, and Washington on *Larix*, *Picea*, *Pinus*, and *Pseudotsuga*. Specimens from Colorado are held at BPI and NY. BPI also holds a specimen collected in Manitoba on *Picea*, a specimen collected in New York on Picea, a specimen collected in Pennsylvania on *Pinus*, and specimens collected in Norway on *Pseudotsuga*.

Additional references: (Ferdinandsen and Jørgensen 1938; Pilley and Trieselmann 1968; Grand et al. 1975; Svrček 1978; Thind and Sharma 1985; Dennis 1986; Krieglsteiner 1991; Weber 1992; Weber and Bresinsky 1992; Sasaki and Akimoto 1993; Kishi 1998; Schultheis et al. 2001; Ortega et al. 2002; Ayel and van Vooren 2005; Bogacheva 2005, 2012, 2017a, b; Raitviir and Bogacheva 2006; Kobayashi 2007; Tholl et al. 2007; Kahr et al. 2009; Legg 2009; Kikuchi et al. 2009; Goos 2010; Hosoya et al. 2010; Müller et al. 2011; Belomesyatseva and Shabashova 2014; Shishlyannikova 2015; Savić and Karaman 2016; Baral and Polhorský 2019; Crous et al. 2019; Bogacheva and Bukharova 2020; Gorczak et al. 2020).

Pezizellaceae

Ciliolarina Svrček, *Ceská Mykol.* **31**(4): 198 (1977).

There are apparently some undescribed species of *Ciliolarina* occupying resin of *Picea* spp. in the Pacific Northwest. These have been collected by the first author but have also been reported by Tanney (2020). This may be the genus that *Hymenoscyphus resinae-piceae* belongs in. More material needs to be collected and studied.

Incertae sedis

Eustilbum Rabenh., *Hedwigia* **2**(10): 59 (1862).

Eustilbum aureum (Pers.) Seifert & S.E. Carp., *Canad. J. Bot.* **65**(6): 1263 (1987).

= *Bisporella resinicola* (Baranyay & A. Funk) S.E. Carp. & Seifert, *Canad. J. Bot.* **65**(6): 1263 (1987).

Description: (Mitchell et al. In Prep).

Illustrations: (Mitchell et al. In Prep).

Hosts: *Abies*, *Larix*, *Picea*, *Pseudotsuga*, *Tsuga*.

Distribution: Europe (Austria, Czechia, France, Germany, Italy, Luxembourg?, Poland, Slovenia, Switzerland), North America (Canadian Maritimes, Central Canada, New England, Northeastern US, Pacific Northwest, Southeastern US).

Molecular data: See Mitchell et. al. (in prep).

Additional notes: This species in this monotypic genus was recently treated at length by Mitchell et al. (in prep) to which readers are referred. It includes excellent images provided of both states.

A specimen collected on *Abies* or *Picea* in Czechia is held at BPI. Several specimens from Poland are held at WRSL. Two specimens from Slovenia are held at GJO.

Additional references:

Leotiales

Tympanidaceae

***Tympanidaceae* sp.**

A slimy, white discomycete growing on resin of Douglas-fir in British Columbia was reported by Tanney (2020), and an illustration was provided. The species was tentatively assigned to *Tympanidaceae*.

Claussenomyces Kirschst., *Verh. Bot. Vereins Prov. Brandenburg* **65**: 122 (1923).

This genus is in the process of being split up, as it has been shown to be highly polyphyletic (Bien et al. 2019; Baral et al. 2020). Likely, neither of the species treated here belong in this genus; in fact, Baral et al. (2020) demonstrated that *C. kirschsteinianus* belongs in *Helotiales* (as "*Resinomyces kirschsteinianus*").

Claussenomyces kirschsteinianus (Jaap ex Kirschst.) G. Marson & Baral, in Weber, *Biblioth. Mycol.* **140**: 112 (1992).

≡ *Gorgoniceps kirschsteiniana* Jaap ex Kirschst., *Ann. Mycol.* **36**(5-6): 378 (1938). Holotype: B?, [Germany: Brandenburg]: Triglitz, auf einem dürren Ast von *Pinus silvestris* an Harzgallen und den Apothecien von *Biatorina difformis*, Oct. 1912, leg. O. Jaap (destroyed or lost).

≡ *Resinomyces kirschsteinianus* (Jaap ex Kirschst.) Baral & Polhorský *nom. inval.* (Art. 35.1, 41.1), *Mycol. Montenegr.* **20**: 91 (2019).

= *Gorgoniceps kirschsteinii* Jaap *nom. inval.* (Art. 38.1), *Verh. Bot. Vereins Prov. Brandenburg* **64**: 14 (1922).

Description: (Kirschstein 1938).

Illustrations: None available.

Hosts: *Larix*, *Picea*, *Pinus*.

Distribution: Europe (Germany, Luxembourg, Norway, Poland).

Molecular data: KY689628/KY689629/KY689631 (ITS+LSU).

Additional notes: The modern concept of this species appears to be that of Baral & Marson, since they have been involved in almost all reports of this species (Weber 1992). It is somewhat difficult to define the concept of this species, since they have not published a modern description or illustrations. Complicating the case further, type material of this species was probably destroyed in World War II (Robert Lücking, pers. comm.), so a neotypification will be necessary at some point. Kirschstein's (1938) description must suffice until a modern description is provided, with the caveat that asci are mostly eight-spored, not four-spored, per Weber (1992). It seems likely that this will eventually be placed in the new genus "*Resinomyces*."

The first author has seen a specimen of this collected in Norway on *Pinus* which will be deposited in FH.

There is apparently a related, undescribed species, "*Claussenomyces/Resinomyces griseus*" that is mentioned by Capoen (2018), Baral & Polhorský (2019) and Baral et al. (2020). This species is known from Switzerland and France on *Pinus* and *Picea* and is evidently represented by sequences MF099779 and KY689630 (both ITS+LSU). Again, no published descriptions or illustrations are available.

Additional references: (Krieglsteiner 1991; Tholl et al. 1992, 1994, 2000, 2007; Weber 1992; Marson et al. 1996, 1997; Baral and Matheis 2000; Schultheis et al. 2001; Schultheis and Tholl 2003; Capoen 2018; Baral and Polhorský 2019; Baral et al. 2020; Behnke-Borowczyk et al. 2021).

Claussenomyces olivaceus (Fuckel) Sherwood, in Hawksworth & Sherwood, *Canad. J. Bot.* **59**(3): 367 (1981).

≡ *Retinocyclus olivaceus* Fuckel, *Jahrb. Nassauischen Vereins Naturk.* **25-26**: 332 (1871) [1871-2].

Syntypes: FH, G?, K, M-0206278/593676/263879, [Germany: Hessen]: in sylvis ca. Oestrich, ad *Laricis eur.* resinam adultam, vere, leg. K.W.G.L. Fuckel; Syntypes?: BPI 665493, BPI 665494, BPI 665495, CUP Barb.-Boiss.1456, F C0170632F, FH 00995503, MICH 14906, NY 03418042, S F90784, S F90785, TRTC, WSP22475, [Germany: Hessen]: Mittelheimer Aepfelbach, an Harz von *Larix europæa*, in Frühling, leg. K.W.G.L. Fuckel.

≡ *Tromera olivacea* (Fuckel) Sacc., *Syll. fung.* **8**: 470 (1889).

≡ *Tympanis olivacea* (Fuckel) Rehm, *Rabenh. Krypt.-Fl. ed. 2, Band 1, Abt. 3* **32**: 275 (1890) [1896].

≡ *Sarea olivacea* (Fuckel) Kuntze, *Revis. gen. pl.* **3**(3): 515 (1898).

≡ *Biatorella olivacea* (Fuckel) Boud., *Hist. classific. discomyc. Europe*: 157 (1907).

= *Lecidea resinae* f. *cicatricicola* Leight., *Grevillea* **1**(4): 59 (1872) (*fide* Hawksworth & Sherwood, *Canad. J. Bot.* **59**(3): 367 (1981)).

Holotype: K, [UK]: Wales, Bettws-y-Coed, Gwydis Wood, 1872, leg. W.A. Leighton; Isotype?: NY 03418043.

≡ *Biatorella difformis* var. *cicatricicola* (Leight.) H. Olivier, *Mem. Real Acad. Ci. Barcelona, [n.s.]* **11**(5): 8/264 (1914).

Description: (Groves and Wells 1956; Hawksworth and Sherwood 1981; Medardi 2007).

Illustrations: (Leighton 1872; Groves and Wells 1956; Hawksworth and Sherwood 1981; Mitchell 2017; Tanney 2020).

Hosts: *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Thuja*, *Tsuga*.

Distribution: Europe (Austria, Belarus, Denmark, France, Germany, Luxembourg, Norway, Poland, UK), North America (Canadian Maritimes, Caribbean, Central Canada, New England, Midwestern US, Pacific Northwest, Rocky Mountains).

Molecular data: KY661432/KY661433/MW167780 (ITS+LSU), KY633590 (ITS), KY633629 (LSU).

Additional notes: This "species" is probably a complex of several, based on available sequence data.

The first author has seen a specimen on *Pinus* collected in Norway and held at MICH, as part of an isolectotype of *Biatorella coeloplata*. MICH also holds a specimen collected on *Thuja* in Wisconsin, and MIN and NY hold specimens collected in Minnesota on *Pinus*. QFB has two specimens collected on *Picea* in Quebec. FH holds several specimens from Maine, Massachusetts, and Vermont on *Picea* and *Pinus*, mostly quite old. A specimen is also held at NY collected on *Pinus* in the Dominican Republic. This would be an interesting range extension and should be checked. A well-documented (but possibly unpreserved) specimen was found in Denmark; photos can be accessed at https://www.gbif.org/occurrence/2981235323.

Additional references: (Krieglsteiner 1991; Weber 1992; Fernando et al. 1999; Tholl et al. 2000, 2007; Schultheis et al. 2001; Jando and Kukwa 2003; Zalewska et al. 2004; Belomesyatseva and Shabashova 2014; Tanney and Seifert 2018; Bien et al. 2019; Crous et al. 2019; Baral et al. 2020; Behnke-Borowczyk et al. 2021).

Orbiliomycetes*: *Orbiliales*: *Orbiliaceae

All resinicolous entries in this class hail from the monumental, recently published monograph of *Orbiliomycetes* by Baral et al. (2020). This treatment is a significant contribution to the study of resinicolous fungi, with one entirely resinicolous genus and many resinicolous or possibly resinicolous species discussed. A number of other species in this class may be incidentally associated with resin but are not generally considered resinicolous.

Amphosoma Baral, in Baral et al., *Monogr. Orbiliomycetes* **1**: 271 (2020).

Three of the five species treated by Baral et al. (2020) in this genus are resinicolous, but a number of additional undescribed species are known worldwide without a clear link to resin. Interestingly, these three resinicolous species are not most closely related to each other within the genus *Amphosoma*, indicating that this habitat preference may have arisen several times in the genus.

Amphosoma atro-olivaceum Baral & G. Marson, in Baral et al., *Monogr. Orbiliomycetes* **1**: 271 (2020).

Holotype: M-0276401, France: Vaucluse: Mont Ventoux, branch of *P. sylvestris*, 14 Aug. 2009, leg. H.O. Baral & G. Marson.

Description: (Baral et al. 2020).

Illustrations: (Baral et al. 2018, 2020).

Hosts: *Larix*, *Picea*, *Pinus*.

Distribution: Europe (France, Germany, Luxembourg, Poland, Slovakia, Switzerland).

Molecular data: MN151403 (SSU+ITS+LSU), MH221036/KT380069/KT222387 (ITS+LSU), KT380058 (ITS), from paratype specimens.

Additional notes: This species was previously referred to in two publications by Baral et al. (2018) and Baral & Polhorský (2019).

Additional references: (Baral and Polhorský 2019; Witte et al. 2021).

Amphosoma resinicola Baral & G. Marson, in Baral et al., *Monogr. Orbiliomycetes* **1**: 278 (2020).

Holotype: M-0276404, Spain: Teruel: Frías de Albarracín, branch of *Pinus sylvestris*, 29 Sep. 1999, leg. G. Marson.

Description: (Baral et al. 2020).

Illustrations: (Baral et al. 2018, 2020).

Hosts: *Abies*, *Picea*, *Pinus*, *Pseudotsuga*.

Distribution: Europe (France, Liechtenstein, Spain), North America (Prairie Provinces, Rocky Mountains).

Molecular data: KT222388/KT222389 (ITS+LSU), from paratype specimens.

Additional notes: This species was previously illustrated by Baral et al. (2018).

Additional references:

Amphosoma* aff. *resinicola

This species is known from a single specimen and was reported by Baral et al. (2020). It has longer and narrower spores than *A. resinicola*, and significantly deviates genetically, but is otherwise similar. It is known from France, on *Pinus sylvestris*. A published sequence is available, MN151404 (SSU+ITS+LSU).

Hyalorbilia Baral & G. Marson, *Micologia 2000*: 44 (2001).

This genus contains members which grow on various substrates, including woody angiosperms, conifers, herbaceous plants, and even other fungi (Baral et al. 2020). One species, *H. resinae*, is resinicolous. Another species, *H. juliae*, was found once on resin of *Larix*, but more frequently grows on angiosperm bark and other fungi, so cannot be considered truly resinicolous.

Hyalorbilia resinae Baral, in Baral et al., *Monogr. Orbiliomycetes* **1**: 437 (2020).

Holotype: M-0276416, Luxembourg: Mensdorf, branch of *Larix*, on resin, 5 Mar. 2007, leg. G. Marson.

Description: (Baral et al. 2020).

Illustrations: (Baral et al. 2020).

Hosts: *Larix*, *Picea*.

Distribution: Europe (Germany, Luxembourg, Norway, Poland).

Molecular data: None available.

Additional notes: This is the only resinicolous species in this genus; other species have various preferred habitats.

Additional references:

Lecophagus M.W. Dick, *Mycol. Res.* **94**(3): 351 (1990).

This genus contains members mostly occurring on angiosperm hosts but contains one possibly resinicolous species, *Lecophagus pini* (Baral et al. 2020). This species is still poorly known, having only been found twice: once on bark near resin (two apothecia), and once on resin (a single anchoring hypha, but no apothecia). Both specimens were collected in France on *Pinus sylvestris*. More collections should be found to determine whether this species is truly preferentially associated with resin, or the observed association is incidental. Molecular data are not yet available.

Lilapila Baral & G. Marson, in Baral et al., *Monogr. Orbiliomycetes* **1**: 262 (2020).

This genus contains four resinicolous species, of which one is undescribed. The genus seems to be almost entirely restricted to *Picea* and is only found in a small region of southern Europe with the exception of two specimens from Slovakia.

"***Lilapila gallica*** G. Marson, Baral & E. Weber *nom. prov.*"

This species differs from other members of *Lilapila* genetically, but is morphologically indistinguishable (Baral et al. 2020). It is known so far from France on *Picea abies*. Two genotypes are recognized: genotype A, represented by sequences MT367523/MT367524 (SSU+ITS+LSU) and MT367526 (ITS+LSU), and genotype B, represented by sequences MT367527/MT367532 (ITS+LSU).

Lilapila jurana G. Marson, Baral, U. Graf, Gilgen, Wergen & E. Weber, in Baral et al., *Monogr. Orbiliomycetes* **1**: 269 (2020).

Holotype: M-0291754, Switzerland: Jura: Tramelan: Moulin de la Gruère, resinous branch of *Picea abies*, 4 Jun. 2017, leg. J. Gilgen & U. Graf 0406-17UG1.

Description: (Baral et al. 2020).

Illustrations: (Baral et al. 2020).

Hosts: *Picea*.

Distribution: Europe (France, Slovakia, Switzerland).

Molecular data: MH221042 (SSU+ITS+LSU), from the holotype; MK473409/MK473410/MK473411/MT367523/MT367525/MT367528 (SSU+ITS+LSU), MK028715 (ITS), from paratype specimens.

Additional notes:

Additional references:

Lilapila oculispora Baral & G. Marson, in Baral et al., *Monogr. Orbiliomycetes* **1**: 262 (2020).

Holotype: M-0276610, France: Alpes-de-Haute-Provence, Col du Labouret, resinous branches of *Picea abies*, 24 Oct. 1992, leg. G. Marson.

Description: (Baral et al. 2020).

Illustrations: (Baral et al. 2020).

Hosts: *Picea*.

Distribution: Europe (France, Switzerland).

Molecular data: KT222384/KT222413/MH221039/MH221040/MH221041/MT367530 (SSU+ITS+LSU), KY419168/MT367529/MT367533 (ITS+LSU), from paratype specimens.

Additional notes: This species was previously reported by Baral & Matheis (2000) and Baral & Polhorský (2019).

Additional references: (Baral and Matheis 2000; Baral and Polhorský 2019).

Lilapila oculisporella Baral, G. Marson & E. Weber, *Monogr. Orbiliomycetes* **1**: 267 (2020).

Holotype: M-0281047, France: Alpes-de-Haute-Provence: Seyne-les-Alpes, branches of *Pinus sylvestris*, 24 Aug. 1996, leg. G. Marson; Isotype: hb. Baral 5606a.

Description: (Baral et al. 2020).

Illustrations: (Baral et al. 2020).

Hosts: *Picea*, *Pinus*.

Distribution: Europe (France).

Molecular data: MH221043/MH221044/MH221045 (SSU+ITS+LSU), KT222383/KY419169/KY419170/MG372373 (ITS+LSU), KT380057 (ITS), from paratype specimens.

Additional notes: This is thus far the only species of *Lilapila* known to occur on *Pinus* as well as *Picea*. This species was previously reported by Baral & Polhorský (2019) and mentioned by Magyar et al. (2018).

Additional references: (Magyar et al. 2018; Baral and Polhorský 2019)

Orbilia Fr., *Fl. scan.* **22**: 343 (1836).

This cosmopolitan genus contains hundreds of species with varied ecologies (Baral et al. 2020). Of these, one species (*O. olivacea*) might be resinicolous. Other species, including *O.*

aristata, *O. cylindrospora*, and *O. flagellispora*, are sometimes found on resin, but are predominantly found on other substrates.

Orbilia olivacea Baral & G. Marson, *Monogr. Orbiliomycetes* **2**: 1290 (2020).

This species is poorly known, having only been found three times in France on *Pinus* (Baral et al. 2020). In two cases, apothecia were observed on bark at the edge of resinous wounds, and in one case, growing on bark and directly on resin. It is possible that this species is not truly resinicolous, but more material should be collected to verify this. No molecular data are available at present.

Sareomycetes*: *Sareales*: *Zythiaceae

This family has recently been revised by Mitchell et al. (2021), and so for the most part information and citations from that publication will not be repeated. Another recent publication has reached somewhat different conclusions about the higher taxonomy of this family (Hashimoto et al. 2021). In particular, they disagree with the taxonomic conclusions of Beimforde et al. (2020) regarding the erection of a new class, order, and family to accommodate this group of resinicolous taxa, preferring instead to treat these species in *Xylonaceae*, using an expanded six-gene phylogeny showing *Xylonomycetes*+*Sareomycetes* to be monophyletic, *Sarea s. l.* species being among the highest BLAST matches (but still a poor match) for *Trinosporium guianense* (*Xylonaceae*), and morphological observations to argue this.

The second point can be rejected; consistently among the highest BLAST results for *Sarea* and *Zythia* species are *Pycnora* species but presuming that this implies they are most

closely related would result in a contradictory picture, with *Sareomycetes* most closely related to *Pycnoraceae* in *Candelariomycetes*.

The first point is stronger, but in our opinion is still misinterpreted. While this could be interpreted as indicating that *Xylonomycetes* and *Sareomycetes* should be unified in a single class, it seems unwarranted, given the resolution in a phylogeny required to recover *Xylonomycetes*+*Sareomycetes* as monophyletic (nuSSU+LSU+*RPB2* or more genes), to assume they represent the same family. Additionally, *Xylonomycetes* (*Xylona*+*Trinosporium*) is consistently recovered as monophyletic by Hashimoto et al. (2021), and *Sareomycetes* was regularly recovered as monophyletic by Beimforde et al. (2020) and usually recovered as monophyletic by Hashimoto et al. (2021). This second fact may be attributable to poor sampling in *Sareomycetes* by Hashimoto et al. (2021) compared to Beimforde et al. (2020), since the former used essentially 3 and 2 specimens of *Zythia resinae* and *Sarea difformis*, respectively, which produced sequences identical to each other and excluded the sequences generated by the latter authors. Ultimately, we prefer to interpret the phylogenetic results as indicating a sister relationship between *Xylonomycetes* and *Sareomycetes*, pending additional gene marker sequences from *T. guianense* and additional sampling of as-yet-undiscovered close relatives of *Trinosporium* and *Xylona*.

Hashimoto et al. (2021) also argue that the circumscription of *Sareomycetes* by Beimforde et al. (2020) as resinicolous *and* truly polysporous is poor since each feature is not unique to *Sareomycetes*. We would argue that this review indicates that this combination is in fact unique and diagnostic for this class, even as emended by Mitchell et al. (2021). Hashimoto et al. (2021) also propose a circumscription for a broad *Xylonaceae*/*Xylonomycetes*. Diagnostic characters are given as "an endophytic or plant saprobic stage in their lifecycle, sexual morphs

with ascostroma-type ascomata with paraphysoid, bitunicate, polysporic asci with a *Lecanora*-type ascus apex, and asexual morphs with pycnidial conidiomata and enteroblastic conidiogenous cells." Since *Xylona* and *Trinosporium* lack sexual morphs, the unifying features of *Xylonaceae* sensu Hashimoto et al. (2020) must be taken as being endophytic or saprobic on plants, forming pycnidia, and having enteroblastic conidiogenous cells. This combination of features is, for instance, also observed in members of the genus *Pleonectria* in *Sordariomycetes* (Hirooka et al. 2012) and in the order *Phaeomoniellales* in *Eurotiomycetes* (Chen et al. 2015). We also point out that the inclusion of *Atrozythia lignicola* in *Sareomycetes* by Mitchell et al. (2021) further erodes these features, since this species is hyphomycetous and produces fertile branches which divide by basipetal or random septation. Thus, there are no unifying features which characterize all genera in *Xylonaceae* sensu Hashimoto et al. (2021) apart from having an endophytic or plant-saprobic stage in the life cycle. In their comparison of the sexual morphs of *Sareomycetes* to those of other classes, Hashimoto et al. (2021) ultimately conclude that sexual morphs in *Sareomycetes* match those in *Lecanoromycetes* most closely, with the exception that the former lack a thallus. This cannot be accepted as a true differentiating character though, since some members of *Lecanoromycetes* are non-lichenized and thus also lack a true thallus (Baloch et al. 2010; da Silva Cáceres et al. 2020). Thus, this feature also fails to uniquely identify *Xylonomycetes*+*Sareomycetes*. We thus prefer to maintain *Xylonomycetes* and *Sareomycetes* as separate based also on morphological grounds.

In terms of nomenclatural matters, we agree with Hashimoto et al. (2021) that *Sarea resinae* and *Sarea difformis* belong in two genera; the name *Zythia* is also typified by a synonym of *Sarea resinae*, however, and *Zythia* has priority over *Tromera*, making *Zythia* the correct name for this genus (Mitchell and Quijada 2020; Mitchell et al. 2021). This name also typifies

the family name *Zythiaceae*, which has priority over *Sareaceae* and *Xylonaceae*, and thus is the correct name if they are unified.

This said, we acknowledge the excellent observations of apothecial ontogeny in *Sareomycetes* provided by Hashimoto et al. (2021) and consider this an important contribution to the study of this group. The contribution of sequenced and morphologically examined specimens from Asia is also valuable, as are the provided descriptions for Japanese material in the collected lineages.

Atrozythia J.K. Mitch., Quijada, Garrido-Ben. & Pfister, *IMA Fungus* **12**: art. 6, p. 16 (2021).

Atrozythia klamathica J.K. Mitch. & Quijada, in Mitchell et al., *IMA Fungus* **12**: art. 6, p. 17 (2021).

Description: (Mitchell et al. 2021).

Illustrations: (Mitchell et al. 2021).

Hosts: *Chamaecyparis*, *Tsuga*.

Distribution: North America (Pacific Northwest).

Molecular data: sequences available from the holotype and a paratype specimen; see Mitchell et al. (2021).

Additional notes: see Mitchell et al. (2021).

Additional references:

Atrozythia lignicola (Sigler) J.K. Mitch., Garrido-Ben. & Pfister, in Mitchell et al., *IMA Fungus* **12**: art. 6, p. 17 (2021).

Description: (Sigler and Carmichael 1983; Wang and Zabel 1990).

Illustrations: (Sigler and Carmichael 1983; Wang and Zabel 1990).

Hosts: *Picea*, *Pinus*.

Distribution: Europe (Germany, Latvia), North America (Prairie Provinces, Southeastern US).

Molecular data: sequences available from ex-holotype cultures and other cultures; see Mitchell et al. (2021).

Additional notes: This species may or may not be resinicolous; see Mitchell et al. (2021).

Additional references: (Metzler 1997; Lumley et al. 2001; Arhipova et al. 2011)

Sarea Fr., *Syst. orb. veg.* **1**: 86 (1825), *nom. sanct.* (Fries, *Elench. fung.* **2**: 14, 1828).

Sarea coeloplata (Norman) J.K. Mitch., Garrido-Ben. & Quijada, in Mitchell et al., *IMA Fungus* **12**: art. 6, p. 19 (2021).

Description: (Mitchell et al. 2021).

Illustrations: (Mitchell et al. 2021).

Hosts: *Abies*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Thuja*, *Tsuga*.

Distribution: Throughout Europe and North America, also in Antarctica.

Molecular data: see Mitchell et al. (2021).

Additional notes: This species probably occurs wherever northern hemisphere conifers do but has not yet been detected in Asia. In reality, this is two species, but they are so far morphologically indistinct.

Additional references: (Beimforde et al. 2020; Hashimoto et al. 2021).

Sarea difformis (Fr.) Fr., *Elench. fung.* **2**: 14 (1828).

Description: (Hashimoto et al. 2021; Mitchell et al. 2021).

Illustrations: (Hashimoto et al. 2021; Mitchell et al. 2021).

Hosts: *Abies*, *Larix*, *Picea*, *Pinus*, *Tsuga*.

Distribution: Cosmopolitan.

Molecular data: see Mitchell et al. (2021) and Hashimoto et al. (2021).

Additional notes: This species probably occurs wherever northern hemisphere conifers do.

Additional references: (Beimforde et al. 2020; Hashimoto et al. 2021).

Zythia Fr., *Syst. orb. veg.* **1**: 118 (1825).

= *Tromera* A. Massal. ex Körb., *Parerga lichenol*: 453 (1865).

Zythia resinae (Ehrenb.) P. Karst., *Meddeland. Soc. Fauna Fl. Fenn.* **14**: 104 (1887) [1888].

= *Tromera resinae* (Fr.) Körb., *Parerga lichenol.*: 453 (1865).

≡ *Sarea resinae* (Fr.) Kuntze, *Revis. gen. pl.* **3**(3): 515 (1898).

Description: (Hashimoto et al. 2021; Mitchell et al. 2021).

Illustrations: (Hashimoto et al. 2021; Mitchell et al. 2021).

Hosts: *Abies*, *Chamaecyparis*, *Cryptomeria*, *Cupressus*/*Cupressus+Hesperocyparis*, *Juniperus*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, *Taxodium*, *Thuja*, *Thujopsis*?, *Tsuga*.

Distribution: Cosmopolitan.

Molecular data: see Mitchell et al. (2021) and Hashimoto et al. (2021).

Additional notes: This species probably occurs wherever northern hemisphere conifers do.

Additional references: (Beimforde et al. 2020).

Sordariomycetes

This class is relatively poor in resinicolous species, with most recorded being only possibly resinicolous.

Chaetosphaeriales*: *Helminthosphaeriaceae

Endophragmiella B. Sutton, *Mycol. Pap. Commonw. Mycol. Inst.* **132**: 58 (1973).

Endophragmiella resinae P.M. Kirk, *Trans. Brit. Mycol. Soc.* **76**(1): 78 (1981).

Holotype: IMI 231759a, UK: [England]: Devon: Bellever Forest, on old wound of *Picea sitchensis*, 6 Sep. 1978, leg. D.L. Hawksworth 4876.

Description: (Kirk 1981).

Illustrations: (Kirk 1981).

Hosts: *Picea*, unidentified plant.

Distribution: Asia (China), Europe (UK).

Molecular data: None available.

Additional notes: This fungus is poorly known, having only been reported twice; it has not been subjected to molecular analysis, and so its taxonomic position is uncertain. Since the report from China is vague about the host, it is unclear whether it is really resinicolous, or whether the presence of the holotype on resin was largely incidental. Arguing against this is the fact that Kirk (1981) reported that the mycelium was immersed in the substrate.

Additional references: (Ren et al. 2011).

Hypocreales*: *Nectriaceae

Cosmospora Rabenh., *Hedwigia* **2**(10): 59 (1862).

Cosmospora rishbethii (C. Booth) Rossman & Samuels, in Rossman et al., *Stud. Mycol.* **42**: 124 (1999).

≡ *Nectria rishbethii* C. Booth, *Mycol. Pap. Commonw. Mycol. Inst.* **73**: 92 (1959).

This fungus was originally reported as having perithecia "almost immersed in secreted resin" (Booth 1959). Later reports from Asia, Europe, and North America have recovered this fungus on leaves or wood of angiosperms (Thormann et al. 2004; Hirooka et al. 2008) on conifer wood (Baral et al. 2020; Račko et al. 2020), or on wet wood (Chavarria et al. 2010). Specimens in PDD from New Zealand were collected on polypores. Likely, this is not a truly resinicolous fungus. The ex-type strain has been shown to detoxify extractives of Scots pine sapwood, possibly indicating a plant-pathogenic capacity (Martínez-Iñigo et al. 2000). This fungus seems closely related to several genera of fungicolous fungi, not truly placed in *Cosmospora* or *Nectria* (Gräfenhan et al. 2011; Summerbell et al. 2011).

Fusarium Link, *Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin* **3**(1): 10 (1809), *nom. sanct.* (Fries, *Syst. mycol.* **3**(2): 469 (1832)).

Fusarium cavispermum Corda, *Icon. fung.* **1**: 3 (1837).

This species was first reported growing in Bohemia on the resin of *Pinus* (Corda 1837). Since then, it has frequently been reported from Europe as an aquatic hyphomycete growing on angiosperm wood and leaves (Graça et al. 1993; Gulis 1999, 2001), from soil (Nováková et al. 2012), and on untreated pine wood (Gräfenhan et al. 2011). It is thus probably not resinicolous, though it apparently can sometimes tolerate resin. Gräfenhan et al. (2011) have shown that this species does not belong in *Fusarium* but rather is more closely allied to *Cosmospora* and *Dialonectria*.

Thyronectria Sacc., *Grevillea* **4**(29): 21 (1875).

Thyronectria cucurbitula (Tode) Jaklitsch & Voglmayr, *Persoonia* **33**: 201 (2014).

Nectria cucurbitula* f. *resinicola Capp., *Ann. Bot. (Rome)* **17**(4): 202 (1927).

Holotype: PAD?, [Italy]: Como: Rodero, su vecchi tronchi tagliati di *Pinus silvestris*, sullo strato resinoso sgorgato dai canali resiniferi sulla superfice di taglio, 6 Oct. 1926, leg. O. Mattirolo.

Description: (Cappelletti 1927).

Illustrations: None available.

Hosts: *Pinus*.

Distribution: Europe (Italy).

Molecular data: None available.

Additional notes: This fungus is known only from Cappelletti's observations. He was able to grow an asexual stage (assigned by him to *Penicillium*) on resin in culture. When grown on media without resin for a sufficient period of time, this stage apparently lost its ability to grow on resin. Since fungi in *Nectriaceae* and *Aspergillaceae* are not even in the same class, it seems likely that this stage was a contaminant rather than the asexual stage of the nectriaceous fungus he described. In any case, the contaminant appears to have been resinicolous, per Cappelletti's observations. Neither fungus was illustrated, and it is not clear what their true affinities are.

Additional references:

Pleurotheciales*: *Pleurotheciaceae

Monotosporella S. Hughes, *Canad. J. Bot.* **36**(6): 786 (1958).

Monotosporella* cf. *setosa (Berk. & M.A. Curtis) S. Hughes, *Canad. J. Bot.* **36**(6): 787 (1958).

Although *M. setosa* is certainly not resinicolous, having mostly been reported on decaying woody plants, particularly in moist habitats, a fungus extremely similar to it was reported from New Caledonia growing on exuded resin of *Agathis ovata* (Sadowski et al. 2012). The mycelium of this fungus did not appear to penetrate the resin; rather, it was restricted to the surface and small cavities within the resin. Specimens were collected on several occasions, arguing against this being an incidental association. Material should be sequenced to determine if it truly belongs to this species.

Incertae sedis

Several resinicolous fungi have been described which currently cannot be assigned to a particular class in *Ascomycota*. These are treated here.

Gyrocerus Corda, *Icon. fung.* **1**: 9 (1837).

Gyrocerus resinae Jaap, *Ann. Mycol.* **15**(1-2): 123 (1917).

Holotype: ?, [France]: Jura, auf dem Chaumont, auf altem Harz an *Picea excelsa*, 17 Jul. 1910, leg. O. Jaap (location unknown).

Description: (Jaap 1917).

Illustrations: None available.

Hosts: *Picea*.

Distribution: Europe (France).

Molecular data: None available.

Additional notes: This fungus is known only from the type collection, the whereabout of which are unknown. It should be looked for and investigated further to determine its affinities.

Additional references:

Phaeoblastophora Partr. & Morgan-Jones, *Mycotaxon* **83**: 338 (2002).

Phaeoblastophora resinae (Fr.) Partr. & Morgan-Jones, *Mycotaxon* **83**: 339 (2002).

≡ *Myxotrichum resinae* Fr., *Syst. mycol.* **3**(2): 350 (1832), *nom. sanct.* (Fries, *l.c.*).

This taxon was reported by Fries growing on the resin of *Picea abies*, probably in Sweden (Fries 1832). No doubt its occurrence on resin explains why Fries elected to change the epithet from that of Ehrenberg's *Racodium aterrimum*, which Fries listed as a synonym. Since its description by Fries, this species has been reported largely on rotting wood of various angiosperms and gymnosperms in Europe, North America, and Asia under various synonyms (Ellis 1971; Ellis and Ellis 1985; Borowska 1986; Paul et al. 1990; Partridge and Morgan-Jones 2002; Zhang et al. 2012). Thus, it is clear that this species as typically conceived is not resinicolous. However, it does not seem as though material in Fries' herbarium, if it exists, has been examined to determine that his concept is congruent with the modern concept (Hughes 1958). Thus, type material of this taxon should be looked for in Fries' herbarium at UPS to clarify its nature.

Bruceomycetaceae

This family is unplaced at present but contains two apparently related resinicolous fungi. Material should be sequenced to determine the placement of this family.

Bruceomyces Rikkinen, in Tuovila et al., *Karstenia* **52**(2): 74 (2012).

≡ *Brucea* Rikkinen *nom. illegit.* (Art. 53.1), *Ann. Bot. Fenn.* **40**(6): 444 (2003).

Bruceomyces castoris (Rikkinen) Rikkinen, in Tuovila et al., *Karstenia* **52**(2): 74 (2012).

≡ *Brucea castoris* Rikkinen, *Ann. Bot. Fenn.* **40**(6): 444 (2003).

Holotype: H, USA: Oregon: Polk County: Little Sinks Research Natural Area, on resin and resin-soaked lignum of *Abies grandis*, 1998, leg. J. Rikkinen 98010; Isotypes: OSC, UPS.

Description: (Rikkinen 2003c).

Illustrations: (Rikkinen 2003c; Rikkinen et al. 2016).

Hosts: *Abies*, *Tsuga*.

Distribution: North America (Pacific Northwest).

Molecular data: None available.

Additional notes: As discussed by Rikkinen (2003c) and Rikkinen et al. (2016), this fungus is generally calicioid in appearance and habit, but is morphologically distinct from extant genera in several ways. Molecular data are needed to place it conclusively, and thereby place the family it typifies.

Additional references: (Rikkinen 2003b; Tuovila et al. 2012).

Resinogalea Rikkinen & A.R. Schmidt, in Rikkinen et al., *Ann. Bot. Fenn.* **53**(3-4): 207 (2016).

Resinogalea humboldtensis Rikkinen & A.R. Schmidt, in Rikkinen et al., *Ann. Bot. Fenn.* **53**(3-4): 207 (2016).

Holotype: P, [France]: New Caledonia: Province Sud: Mont Humboldt Nature Preserve, on semi-hardened resin of *Araucaria humboldtensis*, 9 Nov. 2011, leg. J. Rikkinen JR010168a; Isotypes: GOET GZG.BST.21892, H.

Description: (Rikkinen et al. 2016).

Illustrations: (Rikkinen et al. 2016; Beimforde et al. 2017a).

Hosts: *Araucaria*.

Distribution: Australasia (New Caledonia).

Molecular data: None available.

Additional notes: This is one of only six known fungi growing on resin of hosts in Araucariaceae, of which only three are described. It is morphologically similar to *Bruceomyces castoris*, which supports Rikkinen et al.'s (2016) placement of both genera in the same family. Beimforde et al. (2017a) have suggested that this fungus is spread by the beetles that feed on its host, causing resin flows to occur. All attempts to culture this fungus failed.

Additional references:

Section 1.3

Fungi on Water-Insoluble Angiosperm Exudates

Compared to fungi on gymnosperm resins, the fungi on angiosperm exudates represent a much more poorly understood group. In addition to resins chemically similar to those of gymnosperms, angiosperms produce gums, latexes (a mixture of gums and resins), phenolics or kinos, and viscins (Gedalovich-Shedletzky et al. 1989; Langenheim 2003; Lambert et al. 2008). These are spread across a number of unrelated families and vary in solubility. Gums are water

soluble, and frequently dissolve in nature. Kinos as well are soluble in water when fresh, but can dry into a less soluble form if they do not dissolve first; despite this, one species at least is known from a kino. The majority of the remaining species are from resins, and two are known from mistletoe viscin.

Due to the varied nature of angiosperm exudates and the scattered literature, this cannot be considered a complete review of fungi from all angiosperm exudates; we are confident, however, that it is a reasonable review of fungi known from water-insoluble angiosperm exudates. Perhaps of interest, all these fungi are found in *Eurotiomycetes*, compared to the widely varied taxonomic placements of fungi on conifer resin.

Ascomycota*: *Pezizomycotina*: *Eurotiomycetes

Eurotiales

Aspergillaceae

Aspergillus P. Micheli ex Haller, *Hist. stirp. Helv.* **3**: 113 (1768), *nom. sanct.* (Fries, *Syst. mycol.* **3**(2): 383 (1832)).

A fungus was recently found penetrating the resin and forming sclerotia in resin beads of *Hymenaea verrucosa* in Madagascar (Delclòs et al. 2020). While not sequenced or formally described, the fungus was illustrated and preliminarily identified as a species of *Aspergillus*.

Trichocomaceae

Talaromyces C.R. Benj., *Mycologia* **47**(5): 681 (1955).

Talaromyces resinae (Z.T. Qi & H.Z. Kong) Houbraken & X.C. Wang, in Houbraken et al., *Stud. Mycol.* **95**: 91 (2020).

≡ *Penicillium resinae* Z.T. Qi & H.Z. Kong, *Acta Mycol. Sin.* **1**(2): 103 (1982).

Holotype: HMAS 42799, China: Guizhou Province: Guiyang, isolatus e resinae *Eucalyptus tereticornis*, Oct. 1977, leg. Q.-T. Chen; Ex-type cultures: AS 3.4387, ATCC 60349, CBS 324.83, DT 027-G5.

Description: (Qi and Kong 1982).

Illustrations: (Qi and Kong 1982).

Hosts: *Eucalyptus*.

Distribution: Asia (China).

Molecular data: MT079858 (ITS), MN969442 (*BenA*), MT066184 (*CaM*), & MN969221 (*RPB2*), from ex-type culture.

Additional notes: This is the only fungus known to grow on a kino. It is apparently known only from the type collection, and thus its ecology is somewhat mysterious; certainly, its host is native to Australia and not China, so the question arises as to which region it is native to. It should be sought out again and studied in greater depth.

Penicillium asperosporum has apparently been misinterpreted several times as either related to this species (Stolk and Samson 1986), or as the correct name for it (Frisvad and Filtenborg 1990; Frisvad et al. 1990; Houbraken and Samson 2011). As pointed out by Houbraken et al. (2014), this was likely due to an apparent clerical error at the Westerdijk Fungal Biodiversity Institute which resulted in the ex-type strain of *Penicillium resinae* stored there being mislabeled as instead the holotype of *P. echinosporum* (https://wi.knaw.nl/page/fungal_display/29562). Unfortunately, Houbraken et al. (2014) also misinterpreted *P. resinae* as a synonym of *P. purpurescens* due to an incorrect *RPB2* sequence

(Houbraken et al. 2020). *P. resinae* seems to be a good species at present and is correctly placed in *Talaromyces*.

Additional references: (Stolk and Samson 1986; Frisvad and Filtenborg 1990; Frisvad et al. 1990; Houbraken and Samson 2011; Houbraken et al. 2014, 2020).

Mycocaliciales

Sphinctrinaceae

As with the resinicolous species on conifers, this family hosts a significant group of species occurring on angiosperm exudates. Unlike the species on conifers, however, present indications are that the angiosperm exudate species, including both those on viscin and resin, form a monophyletic group related to *Sphinctrina* (Messuti et al. 2012; Tuovila et al. 2013, 2014; Rikkinen et al. 2014; Beimforde et al. 2017b). Likely in the future, this will be split off into a distinct genus. Again, the species placed in *Mycocalicium* rather than a broad *Chaenothecopsis* are probably placed there due to artificial generic boundaries that need resolution.

Chaenothecopsis Vain., *Acta Soc. Fauna Fl. Fenn.* **57**(1): 70 (1927).

Chaenothecopsis khayensis Rikkinen & Tuovila, *Mycologia* **103**(3): 611 (2011).

Holotype: H, Ghana: Bobiri Forest Reserve, on exudate of *Khaya ivorensis*, 13-25 May 2004, leg. J. Rikkinen JR04G058.

Description: (Tuovila et al. 2011a, 2014).

Illustrations: (Tuovila et al. 2011a).

Hosts: *Khaya*.

Distribution: Africa (Ghana).

Molecular data: JX122785 (ITS), from holotype material. HQ172895 (LSU), from paratype(?) material.

Additional notes: Tuovila et al. (2011) noted a hyphomycete growing on the surface of the resin associated with this fungus. However, this could not be verified by culture or sequencing of material. These authors also posited a link between this fungus and boring insects causing the resin flows on its hosts.

This fungus was erroneously listed in the Checklist of Fungi in China and the Red List of China's Biodiversity - Macrofungi, presumably due to the inclusion of a description of *C. khayensis* by Tuovila et al. (2014) (Wang et al. 2020).

Additional references: (Messuti et al. 2012; Tuovila et al. 2013, 2014; Rikkinen et al. 2014; Beimforde et al. 2017b; Temu et al. 2019; Wang et al. 2020).

Chaenothecopsis pallida Rikkinen & Tuovila, in Tuovila et al., *Mycologia* **106**(5): 996 (2014).

Holotype: H, China: Hunan Province: Xinning County: Shunhuangshan National Forest Park: Li Zhu Jiang Valley, in basal crevice of large *Ailanthus altissima*, 24 Sep. 2001, leg. J. Rikkinen 010652.

Description: (Tuovila et al. 2014).

Illustrations: (Tuovila et al. 2014).

Hosts: *Ailanthus*.

Distribution: Asia (China).

Molecular data: JX122779 (ITS) & JX122781 (LSU), from holotype material.

Additional notes:

Additional references: (Tuovila et al. 2013; Rikkinen et al. 2014; Beimforde et al. 2017b).

Chaenothecopsis perforata Rikkinen & Tuovila, in Tuovila et al., *Mycologia* **106**(5): 992 (2014).

Holotype: H, China: Hunan Province: Xinning County: Shunhuangshan National Forest Park: Zheng Jiang Valley, on branches of *Rhus chinensis*, 24 Sep. 2001, leg. J. Rikkinen 010540.

Description: (Tuovila et al. 2014; Gockman et al. 2019).

Illustrations: (Tuovila et al. 2014; Gockman et al. 2019).

Hosts: *Rhus*.

Distribution: Asia (China), North America (Central Canada, Mexico, Midwestern US, Northeastern US, Southeastern US).

Molecular data: None available.

Additional notes: This species is listed in the Red List of China's Biodiversity - Macrofungi (Wang et al. 2020). It has apparently been observed in Mexico on *Rhus* sp. (https://www.inaturalist.org/observations/31088226). It is apparently much more widely distributed in North America than in Asia, and it would not be surprising if it turned out that there was an earlier name for this species based on North American material.

Additional references: (Curtis 2019; Ladd 2019; Brinker 2020; Wang et al. 2020; Gockman et al. 2020).

Chaenothecopsis quintralis Messuti, Amico, Lorenzo & Vidal-Russ., in Messuti et al., *Mycologia* **104**(5): 1224 (2012).

Holotype: BRCU 05233, Argentina: Río Negro: San Carlos de Bariloche: Parque Municipal Llao-Llao, on dung of *Dromiciops gliroides* [containing seeds of *Tristerix corymbosus*], 1 Feb. 2009, leg. G.C. Amico.

Description: (Messuti et al. 2012).

Illustrations: (Messuti et al. 2012).

Hosts: *Tristerix*.

Distribution: South America (Argentina).

Molecular data: JQ267741 (LSU), from holotype material.

Additional notes: Messuti et al. (2014) describe this fungus as coprophilous, but it is more likely (particularly given that another species, *Mycocalicium viscinicola*, has a similar ecology), that this species is rather utilizing the viscin of *Tristerix corymbosus* seeds in the dung. However, the fact that this species is consistently observed on the seeds which have passed through the digestive system of *Dromiciops gliroides* suggests that this animal may play an important part in its life cycle beyond dispersing it.

Additional references: (Rikkinen et al. 2014; Tuovila et al. 2014; Beimforde et al. 2017b).

Chaenothecopsis resinophila Rikkinen & Tuovila, in Tuovila et al., *Mycologia* **106**(5): 991 (2014).

Holotype: H, China: [Hunan Province]: Sangzhi County: Badagongshan National Nature Reserve: Nan Mu Ping, in trunk crevices of *Kalopanax septemlobus*, 23 Sep. 2000, leg. J. Rikkinen 000424.

Description: (Tuovila et al. 2014).

Illustrations: (Tuovila et al. 2014).

Hosts: *Kalopanax*.

Distribution: Asia (China).

Molecular data: JX122780 (ITS) & JX122782 (LSU), from holotype material.

Additional notes: This species is listed in the Red List of China's Biodiversity - Macrofungi (Wang et al. 2020).

Additional references: (Tuovila et al. 2013; Rikkinen et al. 2014; Beimforde et al. 2017b; Temu et al. 2019; Wang et al. 2020).

Chaenothecopsis schefflerae (Samuels & D.E. Buchanan) Tibell, *Acta Univ. Upsal., Symb. Bot. Upsal.* **27**(1): 158 (1987).

≡ *Mycocalicium schefflerae* Samuels & D.E. Buchanan, *New Zealand J. Bot.* **21**(2): 163 (1983).

Holotype: PDD 42005, New Zealand: Northland: Whangarei, on bark of living tree of *Schefflera digitata*, 17 Mar. 1980, leg. I. Hood; Isotypes: NY 01219087, NY 01219088, ZT; Ex-type cultures: ATCC 11679, CBS 113957, ICMP 21682.

Description: (Samuels and Buchanan 1983; Tibell 1987; Tibell and Titov 1995; Beimforde et al. 2017b).

Illustrations: (Samuels and Buchanan 1983; Tibell 1987; Beimforde et al. 2017b; Rikkinen and Schmidt 2018).

Hosts: *Pseudopanax*, *Schefflera*.

Distribution: Australasia (New Zealand).

Molecular data: KY499951-KY499966 (ITS) & KY499967 (LSU).

Additional notes: Samuels and Buchanan (1983) reported an asexual state of this fungus in cultures derived from ascospores. This was also reported by Beimforde et al. (2017). The former authors also reported formation of the sexual state in culture, which was not replicated by the latter authors.

The later authors also reported that, despite the initial report from *Schefflera*, they were only able to find it in the field on species of *Pseudopanax*, and posited that the host was possibly misidentified by the original authors; this could probably be resolved by examining sections of the wood in the holotype. In any case, the species is apparently identical from all hosts tested, though some morphological differences were observed by Beimforde et al. (2017). These authors also mentioned that it was likely that this species is insect-dispersed.

Beimforde et al. (2017) mentioned that they sequenced an ex-type culture, but it is not clear if these sequences are publicly available, and the mentioned ITS phylogeny is not presented in their paper.

De Lange et al. (2018) listed this as known from one location, but this is no longer true. Additional references: (Tibell 1995; De Lange et al. 2018; Temu et al. 2019).

Chaenothecopsis tristis (Körb.) Titov, in Titov & Tibell, *Mycotaxon* **70**: 472 (1999).

≡ *Calicium triste* Körb., *Syst. lich. Germ.* **4**: 308 (1855).

Syntypes: in or ex Herb. Zwackh-Holzhausen, [Germany: Saxony-Anhalt]: bei Blankenburg, an alten Laubholzstämmen, leg. G.E.L. Hampe.

≡ *Calicium pusillum* subsp. *triste* (Körb.) Nyl., *Syn. meth. lich.* **1**(2): 157 (1860).

≡ *Calicium pusillum* var. *triste* (Körb.) Boistel, *Nouv. fl. Lich.* **2**: 262 (1903).

≡ *Calicium subtile* f. *triste* (Körb.) Eitner, *Jahresber. Schles. Ges. Vaterl. Cult.*

88(2b): 52 (1911) [1910].

≡ *Calicium floerkei* var. *triste* (Körb.) Zahlbr., *Cat. lich. univ.* **1**(4): 601 (1922).

≡ *Mycocalicium triste* (Körb.) Keissl., *Rabenh. Krypt.-Fl. ed. 2.* **9.1.2**(5): 672 (1938).

Description: (von Keißler 1938; Titov and Tibell 1999; Titov 2006).

Illustrations: (Titov and Tibell 1999; Titov 2006).

Hosts: *Acer*, *Alnus*, *Tilia*.

Distribution: Europe (Germany, Western Russia).

Molecular data: None available.

Additional notes: As stated by Koerber (1863) and Titov & Tibell (1999), original material was apparently collected by Hampe on a lightning-struck *Acer* in Germany. He evidently recollected material from the same location, as Hampe material from multiple years is present in BR, FH, LE, M, PC, and UPS and was issued by Massalongo (1856) in one of his exsiccatae. A lectotype should probably be chosen from material in or from Zwackh-Holzhausen's herbarium; if none exists, a neotype may be required. Von Keißler (1938) also reported that Brandt collected material in the same locality, on *Alnus*; he had examined Körber's material at L, so his identification is probably reliable. Neither von Keißler nor Notov and Himelbrant (2017) mention fire or lightning damage to the host trees, though it was noted by Titov & Tibell (1999) in the newer specimen they examined.

This fungus is apparently reliably known from only three locales; as Koerber (1863) and von Keißler (1938) stated, earlier reports by Nylander (1857, 1860) and Eitner (1911) seem to have been misidentifications. The nature of the exudate this fungus grows on is unclear.

Additional references: (Massalongo 1856; Nylander 1857, 1860; Koerber 1863; Eitner 1911; Notov and Himelbrant 2017).

Mycocalicium Vain., *Acta Soc. Fauna Fl. Fenn.* **7**(2): 182 (1890).

Mycocalicium chaudharii V.P. Tewari & D.C. Pant, *Mycologia* **58**(1): 58 (1966).

Holotype: BHUPP 15, [India: Uttar Pradesh: Varanasi]: Benaras Hindu University, on exudate of *Mangifera indica*, 15 Oct. 1963, leg. V.P. Tewari; Isotypes: CUP, IMI 104673, URM.

Description: (Tewari and Pant 1966; Tibell and Titov 1995).

Illustrations: (Tewari and Pant 1966; Tibell and Titov 1995).

Hosts: *Mangifera*.

Distribution: Asia (India).

Molecular data: None available.

Additional notes:

Additional references:

Mycocalicium viscinicola A. Funk & Kuijt, *Canad. J. Bot.* **60**(2): 191 (1982).

Holotype: DAVFP 22523, Ecuador: Azuay Province: near Cuenca, in viscin coating of seed of *Tristerix longibracteatus*, 27 May 1979, leg. J. Kuijt.

Description: (Funk and Kuijt 1982; Tibell and Titov 1995).

Illustrations: (Funk and Kuijt 1982; Tibell and Titov 1995).

Hosts: *Tristerix*.

Distribution: South America (Ecuador, Peru).

Molecular data: None available.

Additional notes: Funk and Kuijt (1982) observed sterile fungal masses in the specimens they had which they posited were related of this fungus. This connection has not been proven, however.

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Section 1.4

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Chapter 2

Sareomycetes cl. nov.: a new proposal for placement of the resinicolous genus *Sarea* (*Ascomycota*, *Pezizomycotina*)

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Section 2.1

Abstract

Resinicolous fungi constitute a heterogeneous assemblage of fungi that live on fresh and solidified plant resins. The genus *Sarea* includes, according to current knowledge, two species, *S. resinae* and *S. difformis*. In contrast to other resinicolous discomycetes, which are placed in genera also including non-resinicolous species, *Sarea* species only ever fruit on resin. The taxonomic classification of *Sarea* has proven to be difficult and currently the genus, provisionally and based only on morphological features, has been assigned to the *Trapeliales* (*Lecanoromycetes*). In contrast, molecular studies have noted a possible affinity to the *Leotiomycetes*. Here we review the taxonomic placement of *Sarea* using sequence data from seven phylogenetically informative DNA regions including ribosomal (ITS, nucSSU, mtSSU, nucLSU) and protein-coding (*rpb1*, *rpb2*, *mcm7*) regions. We combined available and new sequence data with sequences from major *Pezizomycotina* classes, especially *Lecanoromycetes* and *Leotiomycetes*, and assembled three different taxon samplings in order to place the genus

Sarea within the *Pezizomycotina*. Based on our data, none of the applied phylogenetic approaches (Bayesian Inference, Maximum Likelihood and Maximum Parsimony) supported the placement of *Sarea* in the *Trapeliales* or any other order in the *Lecanoromycetes*. A placement of *Sarea* within the *Leotiomycetes* is similarly unsupported. Based on our data, *Sarea* forms an isolated and highly supported phylogenetic lineage within the "*Leotiomyceta*". From the results of our multilocus phylogenetic analyses we propose here a new class, order, and family, *Sareomycetes*, *Sareales* and *Sareaceae* in the *Ascomycota* to accommodate the genus *Sarea*. The genetic variability within the newly proposed class suggests that it is a larger group that requires further infrageneric classification.

Section 2.2

Introduction

Many conifers and angiosperms have developed resin-based defence mechanisms to deter herbivores and microbial pathogens (Farrell et al. 1991; Gershenzon and Dudareva 2007; Howe and Schaller 2008). The sticky resin seals injuries in the trees and acts as a biochemical barrier due to terpenoid and phenolic compounds (Bednarek and Osbourn 2009; Rautio et al. 2011; Sipponen and Laitinen 2011; Seyfullah et al. 2018). However, certain fungi have developed resistance against toxic resin compounds (Rautio et al. 2011; Adams et al. 2013), and are able to colonize fresh and solidified resin (Tuovila et al. 2013). Resinicolous fungi represent a polyphyletic assemblage of ascomycetes which grow exclusively on tree resins (Tuovila 2013; Rikkinen et al. 2016).

Resinicolous fungi occur scattered throughout many classes within the *Ascomycota*. Most resinicolous fungi described to date are ascomycetes within the order *Mycocaliciales* (*Eurotiomycetes*) (e.g. Rikkinen 2003; Rikkinen et al. 2014; Tuovila et al. 2011a, 2011b, 2012; Tuovila 2013). *Sorocybe resinae* (*Chaetothyriales*, *Herpotrichiellaceae*) and its synasexual morph *Hormodendrum resinae* (Seifert et al. 2007), and *S. oblongispora* (Crous et al. 2019), represent asexual *Eurotiomycetes* that are also often found on resin. The association of these fungi with conifer resin has existed for at least 35 M years as evidenced by fossilized specimens in Palaeogene amber (Rikkinen and Poinar 2000; Tuovila et al. 2013; Beimforde et al. 2014; Rikkinen and Schmidt 2018). While other resinicolous fungi have not received as much recent attention, a significant number occurs in other classes. *Dothideomycetes* contains at least six resinicolous species: *Helicoma resinae*, *Mytilinidion resinae*, *M. resinicola*, *Strigopodia batistae*, *S. resinae*, and *Torula resinicola*. *Leotiomycetes* boasts a similar number, with at least six resinicolous species: *Bisporella resinicola*, *Claussenomyces kirschsteinianus*, *C. olivaceus*, *Hymenoscyphus resinae-piceae*, *Lachnellula resinaria*, and *Micropodia resinicola*. A similar number of fungi are also currently not satisfactorily placed. Fungi such as *Gyrocerus resinae* and *Moriola resinae* have not been collected in over a century, while more recently collected fungi such as *Bruceomyces castoris* and *Resinogalea humboldtensis* are classified based on morphological characters due to the lack of molecular data (Rikkinen et al. 2016). Among this group of poorly placed fungi, two widely collected discomycetes in the genus *Sarea* are also found.

Sarea resinae and *S. difformis* are both found fruiting exclusively on conifer resins and often co-occur on the same substrate. These two fungi are the only presently known species in the genus *Sarea*, which was erected by Fries in 1825. In contrast to other resinicolous

discomycetes, which are placed in genera also including wood rotting species or parasites, *Sarea* species only ever fruit on resin. Both species are common in northern latitudes where they are usually found on resins of *Picea* and *Pinus* species, but also on other genera of *Pinaceae* including *Abies*, *Larix* and *Pseudotsuga* (Hawksworth and Sherwood 1981), *Cedrus* (Malençon 1979) and *Tsuga* (Baranyay 1966). They have also been reported from exudates of *Cupressaceae s. l.* such as *Chamaecyparis* (Ayers 1941; Suto 1985), *Cupressus* (Hawksworth and Sherwood 1981; Garrido-Benavent 2015), *Cryptomeria* (Suto 1985) and *Juniperus* (Petrini and Carroll 1981) indicating a relatively broad host range.

Little has been conclusively shown about the ecology and evolutionary origin of the genus *Sarea* so far. Species of the genus have variously been treated as lichen symbionts (Mudd 1861; Koerber 1865; Nylander 1866; Ohlert 1870; Hasse 1898; 1908; Cappelletti 1924; Fink 1935; Watson 1948; Etayo 1996; Bartkowiak and Bennett 2015) or mild to serious parasites (Kujala 1950; Conners 1967; Smerlis 1973; Funk 1981; Kobayashi and Zhao 1989; Kuz'michev et al. 2001; Safronova and Palnikova 2010; Bazhina and Aminev 2012; Safronova and Sorokin 2013). Currently they are mostly treated as saprobes (Hawksworth and Sherwood 1981; Wirth 1995; Gadgil and Dick 1999; Suto 2000; Robertson 2002; Czyżewska et al. 2005; Kukwa et al. 2008; Lõhmus et al. 2012; Łubek and Jaroszewicz 2012; Szymczyk et al. 2014; Garrido-Benavent 2015; Motiejūnaitė 2015; Yatsyna 2015; Himelbrant 2016; Kuznetsova et al. 2016; McMullin and Lendemer 2016), but additionally have been regarded as endophytes (Petrini and Carroll 1981; Petrini and Fisher 1988; Kowalski and Kehr 1992; Giordano et al. 2009; Koukol et al. 2012; Sanz-Ros et al. 2015).

The taxonomy of *Sarea* and its systematic assignment within the *Pezizomycotina* is still poorly resolved. Previously, *Sarea* species were placed in genera belonging to *Lecanoromycetes*,

Leotiomycetes, and *Pezizomycetes*, including *Biatora*, *Biatoriella*, *Lecidea*, *Tympanis*, *Biatoridium*, *Pezicula* and *Peziza* (Hawksworth and Sherwood 1981). Hawksworth & Sherwood (1981) solved nomenclatural issues and provided detailed morphological descriptions of both *Sarea* species and placed the genus within *Agyriaceae*. Successive molecular studies suggested a relationship of *Sarea* to clades presently placed in *Leotiomycetes* (Reeb et al. 2004; Wang et al. 2006, 2009; LoBuglio and Pfister 2010; Miadlikowska et al. 2014), as opposed to earlier morphological placement within *Lecanoromycetes*, but these authors could not satisfactorily place the genus into any class within *Pezizomycotina*. Based on morphological traits, Lumbsch & Huhndorf (2010) and Hodkinson & Lendemer (2011) provisionally placed *Sarea* within *Trapeliaceae* (*Lecanoromycetes*). However, the difficulty of excluding potential homoplasy of morphological traits is well known in fungal systematics (e.g. Berbee and Taylor 1992; Schmitt et al. 2005; Lumbsch et al. 2007) and many studies show that morphological synapomorphies do not consequently correspond to monophyletic groups (e.g. Lumbsch et al. 2007; Prieto et al. 2013).

In this study, we aim to revise the current placement of *Sarea* in *Trapeliales* (*Lecanoromycetes*) with molecular data. Additionally, we aim to test the earlier suggestions of a placement within *Leotiomycetes* and calculate a phylogenetic hypothesis of *Sarea* and representatives of most *Pezizomycotina* classes. Only ribosomal sequences (nucLSU, nucSSU and 5.8S rDNA) of *Sarea* were available for phylogenetic studies so far and these may have provided insufficient information for accurate classification into the *Pezizomycotina*. Here we use seven phylogenetically informative DNA regions represented by ribosomal (ITS, nucSSU, mtSSU, nucLSU) and protein-coding (*rpb1*, *rpb2*, *mcm7*) sequences, of which four are new to the research community. Most sequences were obtained from in vitro cultures of *Sarea resinae*

and *S. difformis* isolated from resin flows of *Picea abies* (Norway spruce). We combined the new sequence data with present sequences from major classes in *Pezizomycotina* in three different taxon samplings and applied the most current approaches including Bayesian Inference, Maximum Likelihood and Maximum Parsimony for the phylogenetic calculations.

Section 2.3

Material and Methods

Subsection 2.3.1

Biological Material

Specimens of *Sarea difformis* and *S. resinae* originate from resin soaked bark or fresh, semi-solidified resin flows of *Picea abies*, *Pseudotsuga menziesii* and *Abies sp.* from coniferous forests in Finland, Germany and New Zealand. Sampled trees produced resin in response to mechanical damage due to animal or human activity or in response to microbial infections causing resinous canker lesions. Analysed specimens were deposited in the New Zealand Fungarium (PDD), Landcare Research in Auckland and in Helsinki (H). The collection data are provided in Table 2.1. GenBank accession numbers are provided in the supplementary data Table 2.S1.

Subsection 2.3.2

Light Microscopy

Taxon	Voucher	Substrate	Locality	Collection
Sarea difformis s.l.	CB093	resin, *Picea abies*	Göttingen, Lower Saxony, Germany	University of Helsinki (H), Helsinki
Sarea difformis s.l.	JR6451	resin, *Picea abies*	Finland	University of Helsinki (H), Helsinki
Sarea resinae s.l.	CB094	resin, *Picea abies*	Göttingen, Lower Saxony, Germany	University of Helsinki (H), Helsinki
Sarea resinae s.l.	JR6450	resin, *Picea abies*	Finland	University of Helsinki (H), Helsinki
Sarea resinae s.l.	PDD117345	resin, *Pseudotsuga menziesii*	Dunedin, Otago, New Zealand	New Zealand Fungarium (PDD) Collection, Auckland
Sarea resinae s.l.	PDD117343	resin, *Abies* sp.	Manapouri, Southland, New Zealand	New Zealand Fungarium (PDD) Collection, Auckland

Table 2.1. List of *Sareomycetes* examined in this study with information to their substrate, collection locality, voucher number and collection where the specimens are deposited.

Fungal specimens were studied and imaged under a Carl Zeiss StereoDiscovery V8 dissection microscope and a Carl Zeiss AxioScope A1 compound microscope equipped with Canon EOS 5D digital cameras. All images (Fig. 2.1) represent digitally stacked photomicrographs obtained from up to 50 focal layers merged with the software package HeliconFocus v. 6.33 Pro (Helicon Soft Limited, Kharkiv, Ukraine). For Fig. 2.1D, incident and transmitted light were used simultaneously. To study hyphal growth inside the resin bodies, samples were embedded in epoxy resin EpoTek 301-2 (Epoxy Technology, Inc; Massachusetts) and ground using gradually fine-grained emery paper. Ascomatal details of *Sarea resinae* and *S. difformis* (Fig. 2.1E–H) were studied under 40× to 100× magnification using 100× oil-immersion

Figure 2.1. Light micrographs of *Sarea difformis* and *S. resinae*. A. Ascomata of *S. difformis* and B. *S. resinae*; C. Young ascoma of *S. resinae* arising on a fresh resin flow; D. Cross-section of *S. resinae* showing hyphal growth into the liquid resin; E. Ascus and paraphyses of *S. difformis*; F. Young ascus of *S. difformis*; G. Asci and paraphyses of *S. resinae*; H. Young ascus of *S. resinae*. Scale bars: 1 mm (A, B), 500 µm (C, D), 10 µm (E, G), 5 µm (F, H).

objective, sometimes with an additional 1.6-fold magnification (Fig. 2.1H).

Subsection 2.3.3

Cultivation

Ascospore germination was performed on solid malt yeast extract agar (MYA; 20 g malt extract, 2 g yeast extract, 20 g agar on 1,000 mL distilled water, pH = 6.5–7), malt extract agar (MEA; 20 g malt extract, 1 g peptone, 20 g glucose, 20 g agar in 1,000 mL distilled water, pH = 5–5.5) and potato dextrose agar (PDA; pre-formulated media, Carl Roth, Germany, pH = 5.6 ± 0.2) treated with 50 mg / mL penicillin G and streptomycin to prevent bacterial growth. For spore isolation, ascomata of *Sarea difformis* and *S. resinae* were removed from the resinous substrate and transferred to double cavity glass slides containing a drop of sterile 0.9 % NaCl2 solution. Contaminations were removed under a Carl Zeiss Stemi 2000-C stereomicroscope and the ascomata were transferred to the edge of the second cavity and gently crushed with a flamed needle to liberate the spores. The spores were further diluted in 200–300 µL sterile 0.9 % NaCl2 solution, transferred on the fungal media and incubated at 25–30 °C for up to 24 mo in the dark.

Subsection 2.3.4

DNA Isolation, Amplification and Sequencing

For DNA extraction, ascomata of *Sarea difformis* and *S. resinae* from environmental samples were cleaned of macroscopical contaminations under a Carl Zeiss Stemi 2000- C stereomicroscope, shock frozen with liquid nitrogen and crushed using a glass micromortar and

pestle. Cultures of both species isolated from *Picea abies* were freeze dried (Christ, Alpha 1–4 LDplus, Osterode, Germany) and subsequently pulverized in Eppendorf tubes using plastic pestles. DNA was isolated from the fungal material using the Invisorb Spin Plant Mini Kit (Stratec, Berlin, Germany) by following the manufacturer's protocol, but modified by incubating the samples over night at 52 °C to ensure the lysis of the fungal cell walls. For phylogenetic analysis, we amplified parts of four protein coding and four ribosomal DNA regions. The protein coding genes represent the RNA polymerase II largest (*rpb1*) and second largest subunit (*rpb2*), the *tsr1* gene, a gene required for rRNA accumulation during biogenesis of the ribosome (Gelperin et al. 2001, Schmitt et al. 2009) and the *mcm7* gene, a DNA replication licensing factor required for DNA replication initiation and cell proliferation (Moir et al. 1982, Kearsey & Labib 1998). Ribosomal DNA regions include the small and large nuclear ribosomal subunit (18S rDNA and 28S rDNA respectively), the mitochondrial small ribosomal subunit (mtSSU) as well as the nuclear internal transcribed spacer region (ITS). DNA regions were isolated and amplified from in vitro cultures of *Sarea difformis* and *S. resinae* in order to exclude the amplification of DNA from potential contaminates of environmental samples. The nuclear ITS regions of the cultures and environmental samples were compared to make sure that the cultures correspond to the correct environmental sample.

Polymerase chain reaction (PCR) was conducted using Taq DNA polymerase (Promega, Madison, WI) by following the manufacturer's recommendations. Fungal specific primers and PCR conditions used to amplify the gene regions for phylogenetic analysis of this study are provided in Table 2.S2. PCR products were purified using MSB® Spin PCRapace (Invitek, Berlin, Germany) and sequenced in both directions with a MegaBACE 1000 automated sequencing machine and DYEnamic ET Terminator Cycle Sequencing Kit (Amersham

Biosciences, Little Chalfont, UK). Sequences were assembled and edited with BioEdit v. 5.0.9 (Hall 1999).

Subsection 2.3.5

Reference Data Sets

We combined the new ribosomal and protein coding sequences with data from the National Center for Biotechnology Information (NCBI). In total, seven marker sequences were used for the phylogenetic analyses. Since few *tsr1* sequences are available in GenBank we excluded the new, high quality *tsr1* sequences from our phylogenetic analyses in order to avoid a high percentage of missing data in any of the included gene/DNA regions. Accession numbers for all sequences used for the molecular analyses are provided in Table 2.S1. Three different taxon samplings were assembled:

1. *Trapeliales*/*Helotiales*: To assess whether or not the morphological similarities of *Sarea* and *Trapeliales* can be substantiated with molecular data we assembled a data set including members of the *Trapeliales* (*Lecanoromycetes*) and *Helotiales* (*Leotiomycetes*). Additionally, we included representatives of the recently proposed classes *Xylonomycetes* and *Candelariomycetes* because in our preliminary analyses (data not shown) included representatives of these two classes often grouped with *Sarea* when additional *Pezizomycotina* classes were included in the phylogenetic analyses. The operculate ascomycetes *Peziza arvernensis* and *P. varia* were used as outgroup. The representative dataset consists of 66 taxa with a total 1,295 base pairs of which 449 represent variable sites from the ITS region and 846 sites from the nucLSU. In addition to the sequences of

Sarea difformis and *S. resinae* that we generated in this study, we incorporated some available ITS and nucLSU sequences from GenBank.

2. *Lecanoromycetes*: To assess whether or not the current (morphological) classification of *Sarea* in *Lecanoromycetes* can be confirmed with molecular data we assembled a taxon sampling which broadly corresponds to the well-balanced dataset by Prieto et al. (2013). The dataset comprises 96 taxa and includes 3,862 variable sites from four ribosomal (ITS, nucSSU, mtSSU, nucLSU) and two protein coding (*mcm7*, *rpb1*) sequences.
3. *Pezizomycotina*: To place *Sarea* within *Pezizomycotina* we assembled a taxon sampling including representatives of all major ascomycete classes except *Laboulbeniomycetes*, *Xylobotryomycetes* and *Coniocybomycetes* because preliminary analyses (data not shown) have shown that these classes are unlikely to be closely related to *Sarea*. Many of the implemented genes were compiled in a previous study by James et al. (2006). The dataset consists of 103 taxa including 160 base pairs of the ITS region, 916 sites from the small ribosomal subunit (nucSSU), 1,057 sites from the large ribosomal subunit (nucLSU), and 900 sites from the *rpb2* gene. All reference data sets are available via Treebase http://purl.org/phylo/treebase/phylows/study/TB2:S25817.

Subsection 2.3.6

Phylogenetic Analyses

Phylogenetic hypotheses were calculated with the three most current approaches: Bayesian Inference, Maximum Likelihood and Maximum Parsimony. All analyses were performed on the CIPRES Science Gateway v. 3.3 (Miller et al. 2010). For each dataset, included

genes were aligned separately by using MAFFT v. 6 (Katoh and Toh 2008) sometimes with subsequent manual adjustment to minimize the number of possible false homologies using BioEdit v. 5.0.9. (Hall 1999) and SeaView v. 4 (Gouy et al. 2010). Unalignable regions and introns were excluded by using the mask function in BioEdit v. 5.0.9. For each dataset, genes were combined in a super matrix using BioEdit v. 5.0.9.

Maximum Likelihood search for the most likely tree was accomplished using RAxML VI-HPC (Stamatakis 2006; Stamatakis et al. 2008) by applying a GTR model of molecular evolution, 1,000 ML bootstrap replicates and the Gamma model of rate heterogeneity by letting RAxML optimize individual α-shape parameters and base frequencies for 6 separate gene partitions.

Maximum parsimony (MP) was performed using PAUP v. 4.0b10 (Swofford 1991, 2002) by treating gaps as missing characters, and by applying 1,000 random addition sequences (RAS), TBR (tree bisection reconnection) branch-swapping and MULTREES option. To assess statistical support of the clades, non-parametric bootstrapping (Felsenstein 1985) was performed with heuristic searches.

Bayesian analyses were performed using Markov Chain Monte Carlo (MCMC) in MrBayes v. 3.1.2 (Ronquist and Huelsenbeck 2003). Best fitting substitution models for each gene were chosen separately from seven substitution schemes included in the software package jModeltest v. 2.1.1 (Darriba et al. 2012), and models were chosen according to the Bayesian information criterion (BIC, Schwarz 1978).

Analyses were run using four chains for 5–10 M generations each, sampling parameters every 500 to 1,000 generations. Average standard deviations of split frequency (ASDSF) lower than 0.01 were interpreted as indicative of independent MCMC convergence.

Section 2.4

Results

Subsection 2.4.1

Phylogenetic Analyses

The phylogenetic tree obtained from the *Trapeliales*/*Helotiales* data (Fig. 2.2) displays well-supported clades of *Sarea*, *Trapeliales*, *Helotiales*, *Candelariomycetes* and *Xylonomycetes* from the Bayesian, Maximum Likelihood and Maximum Parsimony analyses. *Xylobotryomycetes* were placed as a sister clade to the remaining classes included in this taxon set (data not shown), which means that a relationship with *Sarea* is not likely. We therefore excluded *Xylobotryomycetes* in our further analysis. Both Bayesian and Maximum Likelihood approaches place *Sarea* as second order sister group to *Lecanoromycetes* with low node support (35 ML-BS and 61 PP). In each of the three applied methods *Sarea* species clustered in a well-supported clade (84 ML-BS, 99 PP, 77 MP-BS) and *S. difformis* (89 ML-BS, 100 PP, 89 MP-BS) and *S. resinae* (100 ML-BS, 100 PP, 100 MP-BS) build well-supported groups in this clade.

The phylogenetic hypothesis resulting from the six-gene *Lecanoromycetes* dataset is shown in Fig. 2.3. The topology of the resulting phylogeny is generally congruent with the analysis of Prieto et al. (2013) and members of currently defined *Pezizomycotina* classes group in well-supported clades. With three methods (Bayesian, MP and MB) *Sarea* was placed outside the *Lecanoromycetes*, but was placed inside the ‘‘*Leotiomyceta*’’ with unanimous support (99 ML-BS, 100 PP, 91 MP-BS). Maximum Parsimony analysis did not resolve relationships between the classes of *Pezizomycotina* and relationships between members of *Lecanoromycetes*

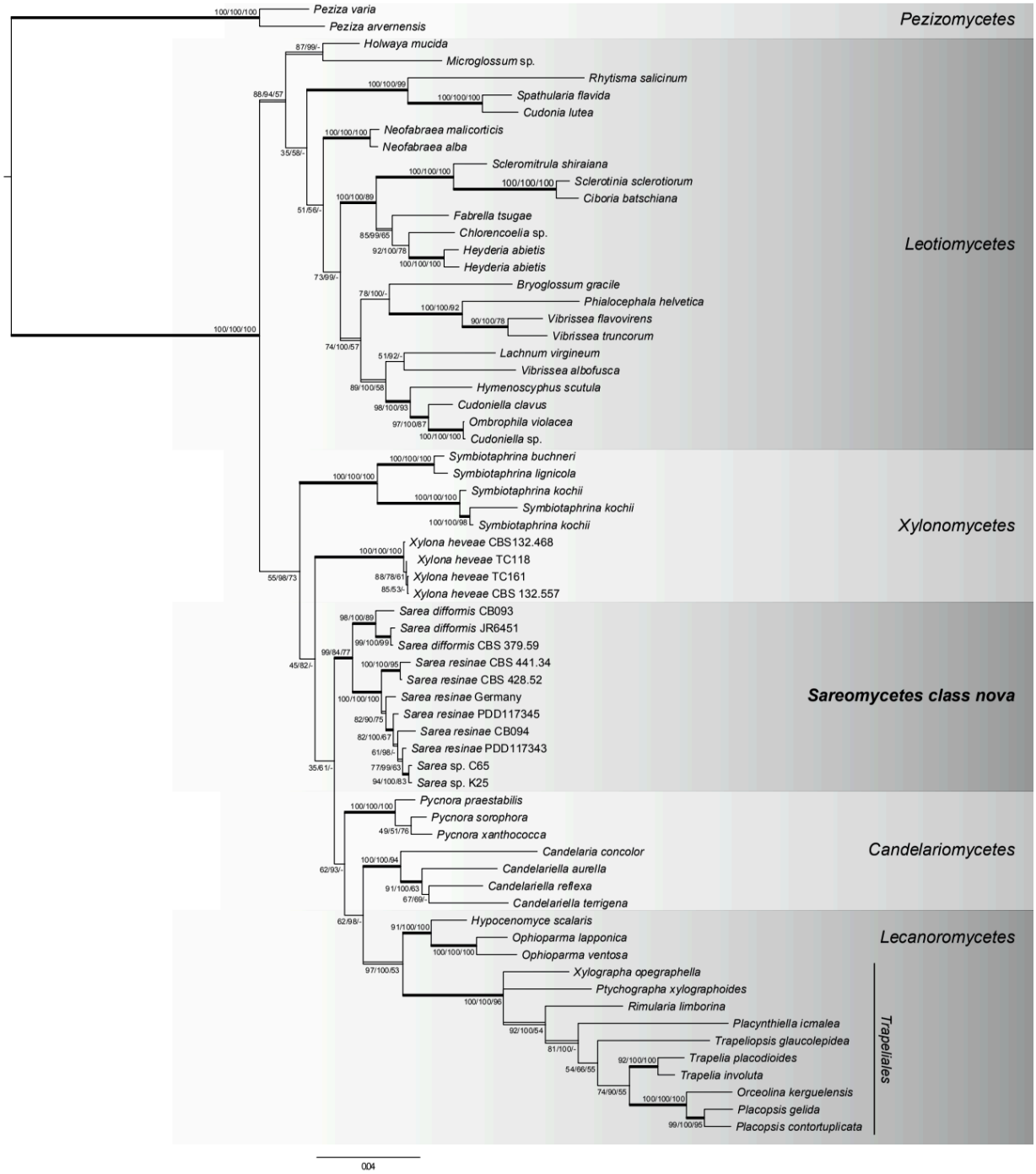

Figure 2.2. Phylogenetic relationships of *Sarea*, *Trapeliales* and *Helotiales* based on two ribosomal genes (ITS, nucLSU) obtained from Bayesian, Maximum Likelihood and Maximum Parsimony (MP) analysis. Posterior Probabilities (PP), ML- and MP-Bootstraps are represented by the first, second and third numbers associated with internodes. Branches in bold indicate PP ≥ 95 %, and both ML and MP bootstrap values ≥ 70 %. Double lined branches indicate significant support obtained by two out of the three analyses. Scale = number of substitutions per site.

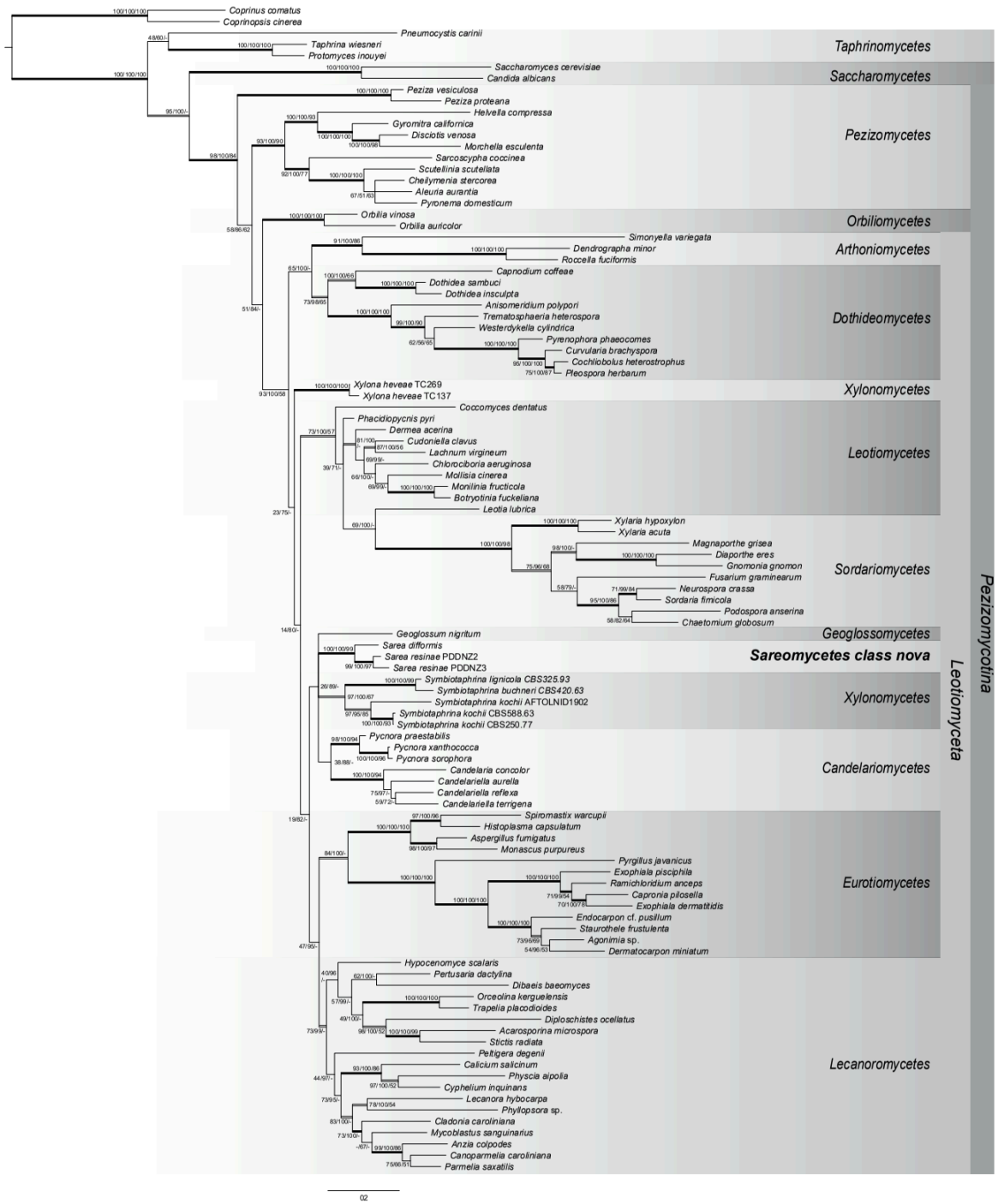

Figure 2.3. Phylogenetic relationship of *Sarea* and *Lecanoromycetes* based on six genes (ITS, mtSSU, nucSSU, nucLSU, *mcm7*, *rpb1*) obtained from Bayesian, Maximum Likelihood and Maximum Parsimony (MP) analysis. Taxon sampling broadly corresponds to the data set by Prieto et al. (2013). Posterior Probabilities (PP), ML- and MP-Bootstraps are represented by the first, second and third numbers associated with internodes. Branches in bold indicate PP ≥ 95 %, and both ML and MP bootstrap values ≥ 70 %. Double lined branches indicate significant support obtained by two out of the three analyses. Scale = number of substitutions per site.

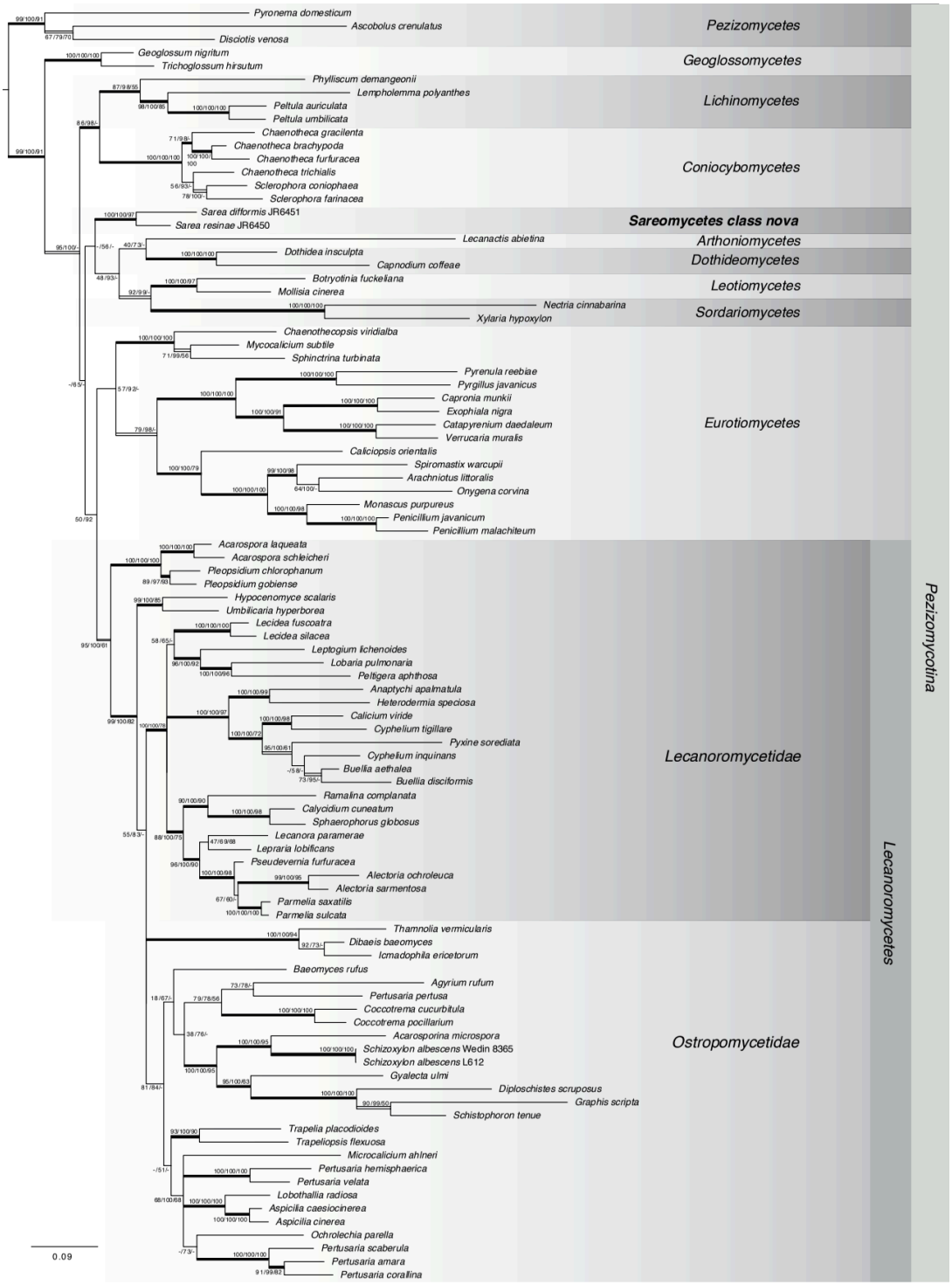

Figure 2.4. Phylogenetic relationship of *Pezizomycotina* based on four genes (ITS, nucSSU, nucLSU, *rpb2*) obtained from Bayesian, Maximum Likelihood and Maximum Parsimony (MP) analysis. Posterior Probabilities (PP), ML- and MP-Bootstraps are represented by the first, second and third numbers associated with internodes. Branches in bold indicate PP ≥ 95 %, and both ML and MP bootstrap values ≥ 70 %. Double lined branches indicate significant support obtained by two out of the three analyses. Scale = number of substitutions per site.

were only partly resolved. Bayesian analysis grouped *Sarea* as sister group to the clade including *Dothideomycetes*-*Arthoniomycetes* and *Leotiomycetes*-*Sordariomycetes* with low support (56 PP), but Maximum Likelihood analysis grouped *Sarea* as sister group of the *Coniocybomycetes*-*Lichinomycetes* clade with only very low node support (15 ML-BS).

The phylogenetic hypothesis obtained from our four-gene dataset of Pezizomycotina is shown in Fig. 2.4. With some exceptions, the topology of the phylogenetic tree broadly corresponds to other large-scale phylogenies of *Ascomycota* (e.g. Reeb et al. 2004; James et al. 2006; Schoch et al. 2009a, 2009b; Beimforde et al. 2014). In our analysis *Xylonomycetes* forms two separate groups with *Symbiotaphrina* placed in the clade also including *Candelariomycetes* and the here-proposed new class *Sareomycetes*. However, these results are not congruent with the phylogenomic study of Gazis et al. (2016) which indicate that *Symbiotaphrinales* represent the sister clade to *Xylonomycetales*. Otherwise, members of currently defined *Pezizomycotina* classes group in well-supported clades and show relationships between the major classes of ascomycetes that have been described in other studies, such as *Arthoniomycetes*-*Dothideomycetes*, *Leotiomycetes*-*Sordariomycetes* and *Lecanoromycetes*-*Eurotiomycetes*. Maximum Parsimony did not resolve the relationships between the *Pezizomycotina* classes, but both Bayesian Inference and Maximum Likelihood placed *Sarea* in a clade also including *Geoglossomycetes*, *Candelariomycetes* and *Xylonomycetes*. This group, however, is only indicated by low node support (26 ML-BS, 89 PP).

Subsection 2.4.2

Taxonomy

Justified by the distinct phylogenetic position of *Sarea* from other ascomycetes in our multilocus gene calculations and by the unique combination of ecological and morphological characteristics of the fungal group, we here propose a novel class, order, and family in the *Ascomycota* to accommodate the genus *Sarea*: *Sareomycetes*, *Sareales* and *Sareaceae cl.*, *ord. et fam. nov.*

Sareomycetes Beimforde, A.R. Schmidt, Rikkinen & J.K. Mitch., *cl. nov.* (MB831369).

Sareales Beimforde, A.R. Schmidt, Rikkinen & J.K. Mitch., *ord. nov.* (MB831372).

Sareaceae Beimforde, A.R. Schmidt, Rikkinen & J.K. Mitch., *fam. nov.* (MB831373).

Type genus: *Sarea* Fr., *Syst. orb. veg.* **1**: 86 (1825), *nom. sanct.* (Fries, *Elench. fung.* **2**: 14, 1828); Type species: *Sarea difformis* (Fr.) Fr., *Elench. fung.* **2**: 14 (1828) (lectotype); Type specimen: K, **Germany**: Bavaria: im Wald bei Sugenheim, an Fichten [*Picea* sp.] auf ausgeflossenem Harze, 1871, leg. H. Rehm Ascomyceten No. 577 (neotype).

Etymology: The name of the class, order, and family are derived from the name of the type genus, *Sarea* Fr.

Description of the class, order, and family: Multispored, non-lichenized ascomycetes with resinicolous ecology, *ascomata* apothecial, scattered, formed exclusively on conifer resin, ascohymenial, sessile to short stipitate, pale to deep orange or black, the pigment localized at least in granules in the epithecial layer and marginal extracellular material as well as in oily inclusions in the interior tissues or in patches in the extracellular matrix, fleshy and gelatinous when fresh, becoming coriaceous when dry; excipulum paraplectenchymatous, composed of radiating hyphae immersed in a gel; subhymenium gelatinous, of interwoven hyphae forming a *textura intricata*, hyaline to brownish or coloured by intracellular pigments. *Hymenial elements* sometimes lightly bluing in KOH. Paraphyses numerous, often containing numerous oily

inclusions, pigmented or not, filiform; septate, mainly unbranched but sometimes anastomosing and often becoming forked near the apices; apices slightly swollen and embedded in gel to form an epithecium-like layer. *Asci* with croziers, multispored, clavate with thick multilayered walls, not fully functionally bitunicate, the outermost layer amorphous and gelatinous, turning blue in IKI and Melzer's reagent with or without pretreatment in KOH, but staining more intensely after pretreatment, the innermost layer forming a thick apical cap pierced by a central pore, lacking a reaction in IKI and Meltzer's with or without KOH pretreatment. *Ascospores* numerous, spherical, minute, hyaline, smooth-walled, thin- to thick-walled, aseptate. *Asexual morphs* pycnidial, arising singly or in small groups, on conifer resin, superficial or immersed, subglobose, more or less concolourous with their sexual morph, walls composed of interwoven plectenchymatous hyphae forming a *textura intricata*, hyphae gelatinized or not, walls sometimes convoluted and appearing multilocular in section; ostiolate and papillate when young and expanding with age due to extrusion of conidia or opening by breakdown or tearing of the upper wall to form an irregular hole. *Conidiophores* lining the cavity of the pycnidium, hyaline, short, branched or not and septate at the base, bearing one to three conidiogenous cells. *Conidiogenous cells* enteroblastic, phialidic, not proliferating or sometimes with one to four short proliferations, lageniform to cylindrical, tapering towards the apex, hyaline, smooth-walled, with a minute collarette and channel but marked periclinal thickening. *Conidia* abundantly produced, slimy or forming slimy masses, subglobose when mature but somewhat pyriform when young, sometimes slightly angular due to mutual compression, aseptate, hyaline to pale brown, more or less smooth-walled, thin- or thick-walled, more or less isodiametric with the ascospores of the sexual morph, usually containing a single minute guttule not disappearing in KOH.

Notes: The description above was modified from the generic description of *Sarea* and the specific descriptions for *Sarea resinae* and *S. difformis* published in Hawksworth & Sherwood (1981). Hawksworth and Sherwood (1981) also discussed the nomenclatural situation of *Sarea* in extraordinary detail. As no type species was designated for *Sarea* by Fries (1822, 1825, 1828), Kuntze (1898) lectotypified *Sarea* by *Peziza difformis*. Neither Kuntze (1898) nor Fries (1822, 1828) mentioned any locality of the described specimens and no original material is known to exist, and therefore Hawksworth & Sherwood (1981) selected a neotype for the name *Peziza difformis*, which is stored in the Royal Botanical Garden, Kew, England UK. Hawksworth & Sherwood (1981) also designated a lectotype for *Sarea resinae* (≡ *Peziza resinae*), which is stored in the Acharius Herbarium in the University of Helsinki Herbarium in Helsinki. Specimens examined: *Sarea difformis* CB093 (H), *Sarea difformis* JR6451 (H), *Sarea resinae* CB094 (H), *Sarea resinae* JR6450 (H), *Sarea resinae* PDD117343, *Sarea resinae* PDD117345. Information about the substrate, collection locality, voucher number and collection where the specimens are deposited is listed in Table 2.1.

Section 2.5

Discussion

Subsection 2.5.1

Phylogeny

According to our phylogenetic results (Figs 2.2–2.4) *Sarea* does not belong in *Trapeliales* (*Lecanoromycetes*) — as the current taxonomic classification suggests (Lumbsch and Huhndorf

2010; Hodkinson and Lendemer 2011) — and cannot be classified within *Lecanoromycetes*. All of our analyses placed *Sarea* in the clade of inoperculate euascomycetes which corresponds to the rankless ‘‘*Leotiomyceta*’’ (Eriksson and Winka 1997) with unanimous support, but none satisfactorily assigned it to any of the existing classes in "*Leotiomyceta*".

Based on morphological similarities, previous studies placed the two *Sarea* species in various genera of *Lecanoromycetes*, for instance *Biatorella* within *Acarosporaceae*, *Biatora* in *Ramalinaceae*, or *Lecidea* within *Lecideaceae*. Nannfeldt (1932) placed both as species of *Tromera* within *Lecanorales* due to their thick ascus walls and the presence of an epithecium and amyloid reaction in the hymenium. Hawksworth & Sherwood (1981) also assigned *Sarea* to *Lecanoromycetes* because it resembles *Agyrium rufum* (*Agyriaceae*) in ascus structure, pigmentation and excipular structure.

Like *Sarea*, most genera in which *Sarea* was previously classified also include species with polyspored asci. True polyspory (= meiosis followed by several mitoses generating more than 100 spores, Gueidan et al. 2015) occurs in many other species in *Lecanoromycetes*. In the past, *Acarosporaceae* was characterized by its true polyspory (Gueidan et al. 2015), but molecular studies revealed that lichenized polysporous species do not form a monophyletic group and that polysporous asci evolved several times within lichenized species (Reeb et al. 2004; Aptroot and Schumm 2012). However, true polyspory has also evolved in non-lichenized genera such as *Deltopyxis* (Baral and Marson 2012), *Podospora* (Mirza and Cain 1969), *Thelebolus* (de Hoog et al. 2005) and *Tromeropsis*. The last was shown to be congeneric to *Symbiotaphrina* in *Xylonomycetes* (Baral et al. 2018). It is not known if the polyspory is linked to ecological environmental conditions, but it is noticeable that many polyspored species occur in xeric habitats (Sherwood 1981).

The polyspored asci, apothecial ascomata and the nonlichenized resinicolous ecology are fundamental characters of all *Sarea* species. *Claussenomyces olivaceus* also possesses polyspored asci while occurring on resin. However, in contrast to *Sarea*, its ascospores (ascoconidia) arise from septate primary ascospores (Medardi 2007).

Another feature that Hawksworth & Sherwood (1981) did not mention is the distribution of pigments in *Sarea resinae*. The pigment may be located in the excipulum, subhymenium, hymenium, and apothecial surface, and can vary in intensity to the point of being absent in some structures between clades of *S. resinae*. Additionally, the excipular cells may vary in tightness between *Sarea* clades and differences in stipe length, presence and amount of granular material at the margins of the cups appear, depth of hymenium or thickness of epithecium seem to be other variable features between *Sarea* clades. However, these features are variable also based on environmental conditions and developmental stages.

Previous classifications of *Ascomycota* emphasized the morphology and development of the ascoma, and especially similar ascus structures and the mechanisms of spore release. Since then, molecular methods have revolutionized phylogenetic systematics of fungi (e.g. Lutzoni et al. 2004; Hibbett et al. 2007; Schoch et al. 2009a; Miadlikowska et al. 2006; Prieto et al. 2013). Lumbsch et al. (2007) pointed out that the ascus types in *Trapeliaceae* and *Agyriaceae* are phylogenetically misleading, since the ascus type of *Agyrium* agrees with those of *Trapeliaceae*, but the morphological similarities are inconsistent with molecular analyses. They excluded *Sarea* from their phylogenetic study since molecular data rather suggested a placement outside *Ostropomycetidae*.

In molecular approaches, potential sources of error include undetected (e.g. homoplasy, Goloboff et al. 2008) or wrongly inferred substitutions (e.g. long branch attraction, Bergsten

2005), polymorphism and gene specific evolution. Because most species have not been sequenced and/or even discovered to date (Blackwell 2011), taxon sampling biases also have to be considered (e.g. Cusimano et al. 2012). Often new gene sequences, such as the *tsr1* genes of Sarea generated in this study, are difficult to include in phylogenetic analyses, because they are underrepresented in GenBank. However, in the future more use could be made from genome extractions provided that the quality of the genes can be guaranteed. In any case, morphological and physiological traits provide additional diagnostic and biological information and should not be disregarded in current classifications (e.g. Hibbett et al. 2007).

We provide the first phylogenetic study of *Sarea* that includes molecular data from protein coding and ribosomal gene regions. Our results are consistent with previous molecular studies in that *Sarea* was placed within the clade of inoperculate euascomycetes, but could not be assigned to any of the currently defined classes in *Ascomycota*. Giraldo et al. (2014) reported affiliations of *Sarea* with *Lecanoromycetes*, but this was only based on data from a single gene (nucLSU) and the placement had no statistical support. Only a few other studies (Lutzoni et al. 2004; Reeb et al. 2004; Wang et al. 2006, 2009; Miadlikowska et al. 2014) supported the placement of *Sarea* outside *Lecanoromycetes* and an affiliation of *Sarea* with the *Leotiomycetes* was found by Reeb et al. (2004) and Wang et al. (2006). Here we cannot confirm an affiliation of *Sarea* with the *Leotiomycetes* (Figs 2.2–2.4), nor can we suggest a well-supported affiliation to any other class within "*Leotiomyceta*". However, in previous phylogenetic studies (Reeb et al. 2004; Wang et al. 2006) as well as our own, relationships between *Sarea* and other *Pezizomycotina* classes were indicated by only low node support and we therefore cannot assume a closer relationship of these taxon groups. It is rather the case that taxon groups of uncertain affiliations (including *Sarea*) in the assembled taxon sets cluster together (long branch attraction,

Bergsten 2005, 1978) and it is likely that the placement of *Sarea* as sister taxon to *Leotiomycetes* in previous studies is just coincidence.

Our phylogenetic results (Figs 2.2–2.4) show that *Sarea* does not belong to *Lecanoromycetes* as currently assigned. Based on the information from the seven DNA regions, *Sarea* cannot be assigned to any of the classes of *Pezizomycotina*, but forms an isolated and highly supported lineage within "*Leotiomyceta*". We therefore propose to recognize this group formally as the new class, order, and family *Sareomycetes*, *Sareales* and *Sareaceae*.

Section 2.6

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Section 2.7

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Chapter 3

Conservation Proposals

This chapter consists of two publications coauthored with Dr. Luis Quijada to correct nomenclatural issues in the genera *Zythia* and *Dendrostilbella*. The latter genus has been treated in *Claussenomyces*, which houses several resinicolous members, per Chapter 1. These proposals were published in Taxon and can be accessed at https://doi.org/10.1002/tax.12328 ((2762) Proposal to conserve the name *Cytospora resinae* (*Zythia resinae*) with a conserved type (*Ascomycota*), J.K. Mitchell & L. Quijada, Taxon 69/5, Copyright © 2020, International Association for Plant Taxonomy, John Wiley & Sons Ltd) and https://doi.org/10.1002/tax.12330 ((2763) Proposal to conserve the name *Dendrostilbella prasinula* against *Stilbum viridipes*, *Belonidium viridiatrum*, and *B. clarkei* (*Ascomycota*), J.K. Mitchell & L. Quijada, Taxon 69/5, Copyright © 2020, International Association for Plant Taxonomy, John Wiley & Sons Ltd).

Section 3.1

(2762) Proposal to conserve the name *Cytospora resinae* (*Zythia resinae*) with a conserved type (*Ascomycota*)

(2762) *Cytospora resinae* Ehrenb., *Sylv. Mycol. Berol.*: 28. 5 Nov 1818, nom. cons. prop.

Typus: Sweden in Fries, Scleromyceti Suec. [exs.] No. 37 (UPS No. F-541757; isotypus: FH barcode 00964792), typ. cons. prop.

The need for this proposal arises from the existence of three nomenclaturally independent species names, all with the epithet "*resinae*", and all now regarded as applicable to the same species. Two, *Lecidea resinae* Fr. and *Sphaeria resinae* Fr., published simultaneously (Fries 1815), were thought by Fries to be different species occurring in the same habitat and not to be confused. Subsequent authors have demonstrated that these two names are based upon morphs of the same species (Ayers 1941; Hawksworth and Sherwood 1981). The third, *Cytospora resinae* Ehrenb. (Ehrenberg 1818: 28), has long been considered a synonym of *Sphaeria resinae*, but, although Ehrenberg was aware of Fries's *Observationes mycologicae*, for example suggesting (l.c.) that perhaps all of *Sphaeronaema* Fr., published therein, might be included in his new genus *Cytospora*, the evidence is that he did not intend to base *C. resinae* on an already existing name, listing it as "*resinae* mihi" (l.c.: 15) and including it in his "Specierum novarum index" (l.c.: 31–32). Consequently, the provisions of Art. 41.4 of the ICN (Turland et al. 2018) to treat a name as a new combination cannot be applied as that was evidently not Ehrenberg's "presumed intent".

Sarea Fr. (Fries 1825) is a genus of widespread, nonpathogenic, resinicolous discomycetes (Hawksworth and Sherwood 1981). *Cytospora resinae* Ehrenb. has long been considered an anamorphic synonym of its most commonly reported species, *Sarea resinae* (Fr.) Kuntze (1898), based ultimately on *Lecidea resinae* Fr. (Fries 1815, 1823; Körber 1865; Hawksworth and Sherwood 1981) that has, as noted, to be treated as an independent use of the epithet "*resinae*" from that of Ehrenberg. Recent work (Mitchell et al. 2021) has found that the species to which these names apply falls outside the genus *Sarea* as typified by Hawksworth & Sherwood (1981) by *Peziza difformis* Fr. (Fries 1822) and that the generic name *Zythia* Fr. (Fries 1825) should be revived to accommodate it.

Although von Höhnel (1915) first proposed as type of *Zythia*, *Z. elegans* (De Not.) Fr. (Fries 1849), based on *Sphaeronaema elegans* De Not. (de Notaris 1845), this is not a species name referred to by Fries in the protologue (indeed not validly published until 20 years later), nor is *Zythia* a sanctioned name, and so *Z. elegans* is not eligible as type. The next published typification is that by Clements & Shear (1931), who cited the type as "*Z. resinae* (Ehrb.) Fr.", which, as Fries never published that combination, whether based on *Cytospora resinae*, *Lecidea resinae*, or *Sphaeria resinae*, must be interpreted as referring to *Z. resinae* (Ehrenb.) P. Karst. (Karsten 1887). As Fries (1825), in the protologue of *Zythia*, only cited "*Sphæronæmata* priora in S. M., forsan & *Sphæria Resinæ* &c" (i.e., the first species of *Sphaeronaema* from his *Systema Mycologicum* account [Fries 1823] and *Sphaeria resinae*), it is open to question whether he "definitely included" (Art. 10.2) the type of *C. resinae* Ehrenb. in *Zythia*, although he had treated the name as a synonym of *Sphaeria resinae* in his *Systema Mycologicum* (Fries 1823). The proposed conservation will resolve this question and confirm the choice by Clements & Shear.

The generic name *Zythia* was until recently generally applied to a group of some 60 species of unrelated pycnidial fungi (Redlin and Rossman 1991; Koukol et al. 2018). *Zythia* is listed as *incertae sedis* in *Ascomycota* in one recent classification (Wijayawardene et al. 2018) and was not included by Jaklitsch et al. (2016) in their classification of *Ascomycota*. The genus was also excluded from the most prominent treatment of the coelomycetes (Sutton 1980). Thus, it may be considered to have been abandoned until its present resurrection as the earliest generic name available for *Sphaeria resinae* (Mitchell et al. 2021). The family name, *Zythiaceae* Clem. (Clements 1909) is based on this generic name. It too is not in current use but should be taken up as an earlier synonym of *Sareaceae* Beimforde et al. (2020).

Karsten (1887) made the combination *Zythia resinae* (Ehrenb.) P. Karst. explicitly based on *Cytospora resinae*, but he listed *Sphaeria resinae* as a synonym, citing it from the sanctioning work (Fries 1823), rather than the earlier protologue (Fries 1815), published three years before Ehrenberg's name. Similar confusion exists in the work of other authors (von Thümen 1880; von Höhnel 1915; Clements and Shear 1931). This may be attributable to confusion, or even ignorance, regarding the true protologue of *Sphaeria resinae*, with authors appearing to consider Fries's (1823) now sanctioned binomial as a combination based on Ehrenberg's (1818) name. The later starting date for the nomenclature of fungi was not apparently a factor as that rule only existed between the Brussels Rules (Briquet 1912) and the Leningrad Code (Stafleu et al. 1978). Recent authors have disagreed as to whether Ehrenberg's name was a combination based on *Sphaeria resinae* Fr. (Hawksworth and Sherwood 1981) or a new species (Braun 2016). As noted above, it is not possible to consider it a new combination, even under Art. 41.4.

The issue has become important because recent work (Mitchell et al. 2021) has indicated that the current concept of *Sarea resinae* encompasses a large number of possible cryptic species with little detectable morphological variation, several of which occur in Scandinavia and several in central Europe, some with overlapping distributions. *Cytospora resinae* was described from Hasenheide and Grunewald in Berlin (Ehrenberg 1818), whereas the type of *Sphaeria resinae* is from Sweden. It is thus possible that at some point in the future, *Cytospora resinae*, for which no type has been designated, but for which Braun (2016) reports original material at Berlin and Halle (B 700016297, HAL 3029 F), may no longer be treated as conspecific with *Sphaeria resinae*. This will inevitably lead to confusion, since treating both species in the same genus (they are undoubtedly congeneric) will require a nomen novum for one or the other. In the case of treatment in the genus *Zythia*, this will result in the unfortunate necessity of replacing the

older Friesian name. It will likely also complicate further the confusion existing already in the literature.

To avoid these eventualities, we propose here to conserve the name *Cytospora resinae* with the lectotype of *Sphaeria resinae* selected by Hawksworth & Sherwood (1981) as conserved type. While material from Fries's *Scleromyceti Sueciae* exists in several herbaria, determining which specimens may be considered isolectotypes is complicated by the fact that Fries issued two editions of his exsiccata (Holm and Nannfeldt 1963) and the lectotype selected by Hawksworth and Sherwood (1981) is from the first edition. The only other first edition containing a specimen of *Sphaeria resinae* known to the authors is housed in FH (Pfister 1975), still bound in the original booklets, and we cite this specimen here as an isolectotype of *Sphaeria resinae* and an isotype of the proposed conserved type of *Cytospora resinae*. This change in type will have the effect of rendering the two names homotypic, preventing future confusion. It will also correct most of the existing nomenclatural irregularities without the need for any new combinations or replacement names.

Section 3.2

(2763) Proposal to conserve the name *Dendrostilbella prasinula* against *Stilbum viridipes*, *Belonidium viridiatrum*, and *B. clarkei* (*Ascomycota*)

(2763) *Dendrostilbella prasinula* Höhn. in *Oesterr. Bot. Z.* **55**: 22. Jan 1905, nom. cons. prop.

Lectotypus (hic designatus, MBT 393276): [Austria. Lower Austria:] Wiener Wald, Glaskogel, Morsches Carpinus H[olz], 7 Jul 1904, von Höhnel (FH barcode 00965330).

(=) *Stilbum viridipes* Boud. in *Rev. Mycol. (Toulouse)* **9**(36):158. 1 Oct 1887, nom. rej. prop.

Lectotypus (hic designatus, MBT 393308): [icon in] Boudier, *Rev. Mycol. (Toulouse)* **9**(36): t. LXIV ('XLIV') fig. 2. 1 Oct 1887.

(=) *Belonidium viridiatrum* Sacc. & Fautrey in *Bull. Soc. Mycol. France* **16**: 22. 1900, nom. rej. prop.

Holotypus: France. Côte-d'Or, In ligno putri Quercus, 1899, ?Saccardo 45 (PAD).

(=) *Belonidium clarkei* Massee & Crossl. in *Naturalist (Hull), ser. 3* **1901**: 181. 1 Jun 1901, nom. rej. prop.

Holotypus: United Kingdom. North Yorkshire, Whitby, Mulgrave Woods, On damp, rotten wood, Sep 1900, Clarke (K).

Claussenomyces Kirschst. (Kirschstein 1923) is a widespread genus of presumed saprobic discomycetes found in various habitats (Ouellette and Korf 1979; Tholl et al. 2000; Gamundí et al. 2004). The genus contains 19 species and has been placed in *Tympanidaceae* (*Leotiomycetes*) (Jaklitsch et al. 2016; Wijayawardene et al. 2018). The name *Claussenomyces* is also protected against *Dendrostilbella* Höhn. (von Höhnel 1905; https://naturalhistory2.si.edu/botany/codes-proposals/). Published analyses indicate that the genus *Claussenomyces* is polyphyletic (Bien et al. 2019), and further analyses have shown that the type, *Claussenomyces jahnianus* Kirschst., is not related to *C. prasinulus* (pers. obs.). *Claussenomyces prasinulus* (P. Karst.) Korf & Abawi (1971), based on *Peziza prasinula* P. Karst. (Karsten 1869), one of the more commonly encountered species, may be recognized in a separate genus, for which the name *Dendrostilbella* Höhn. is available.

Dendrostilbella is a genus of synnematous hyphomycetes (Seifert 1985) typified by *Dendrostilbella prasinula* Höhn. (Clements and Shear 1931). From its first publication by von Höhnel (1905), *D. prasinula* has been known to be the conidial state of *Claussenomyces prasinulus* (then known as *Coryne prasinula* (P. Karst.) P. Karst.). A formidable number of additional heterotypic synonyms have been compiled by Iturriaga (1991) and Seifert (1985). Seifert also gives as a possible synonym *Stilbum viridipes* Boud. (Boudier 1887). He stated that he was unable to find type material in PC, and that the description and illustration (designated here as lectotype) by Boudier possess two qualities arguing against a synonymy of the species with *Dendrostilbella prasinula*: (1) that Boudier illustrated the spores as ellipsoid rather than cylindrical, as typical for *D. prasinula*, and (2) that Boudier, familiar with the teleomorph, made no mention of the association of the newly described anamorphic state with the previously described teleomorph. The second point is explicable: though often associated, the teleomorphic and anamorphic states of these fungi are not always associated, so it is simply possible that Boudier never encountered them together and had no cause to consider them related. This still leaves the first point, which unfortunately cannot be resolved unless original material is found. We agree with Seifert in treating this name as a nomen dubium, but nevertheless feel it is necessary to propose it here for rejection given its high probability of being a heterotypic synonym.

These heterotypic synonyms, all little-known, create complications when determining the proper name for the combination of *Peziza prasinula* P. Karst. in *Dendrostilbella*. Applying Art. 11.4 of the ICN (Turland et al. 2018), the correct name for this fungus should be "*Dendrostilbella viridiatra*", based upon *Belonidium viridiatrum* Sacc. & Fautrey (Saccardo and Fautrey 1900), which would require a new combination, or would be *Dendrostilbella viridipes*

(Boud.) Höhn. (von Höhnel 1905), based upon *Stilbum viridipes* Boud., if that name is accepted as a synonym. In addition to the necessary change in the fairly well-known generic name for this fungus, the epithet would change as well in both cases. Thus, a commonly known species would not only be found in an unfamiliar genus but also with a new epithet.

A further complication is that there is some indication that this is a species complex, with several similar apothecial species, but only one associated with *Dendrostilbella prasinula* (pers. obs.). The holotype of *Peziza prasinula* in H (barcode H6039409) lacks an anamorphic state, so to verify whether this is the species associated with *D. prasinula*, the syntypes of that name in von Höhnel's herbarium were examined for the presence of the teleomorph.

Both syntypes of *Dendrostilbella prasinula* in the von Höhnel Herbarium at FH (00950956 & 00965330) were found upon searching. Of these, the first is very poor, with little or no material of either the anamorphic or teleomorphic states remaining in the packet. The original slides of the anamorph prepared by von Höhnel of this specimen and studied by Seifert (1985) are quite good, though, and illustrate the required diagnostic characters well, but do not resolve whether this species is truly linked with Karsten's *Peziza prasinula*. In contrast, the second specimen, previously thought lost, has only a poor slide, but the specimen itself is excellent, containing copious material of both the anamorphic and teleomorphic states. The apothecia in this specimen are in good agreement with the holotype of *P. prasinula*, and we are satisfied that they are conspecific. We thus designate this specimen the lectotype of *D. prasinula*.

We propose here to conserve the name *Dendrostilbella prasinula* Höhn. against the synonyms *Belonidium viridiatrum* and *B. clarkei* Massee & Crossl. (in Naturalist (Hull), ser. 3, 1901: 181. 1901), as well as a nomen dubium considered by Seifert (1985) to be a possible synonym, *Stilbum viridipes* Boud. This would allow *Dendrostilbella prasinula* to be used as the

correct name of this fungus, and would remove the necessity of creating a new, confusing combination or taking up a currently dubious name for this well-known fungus. Because the type specimen of *D. prasinula* is conspecific with the holotype of *P. prasinula*, there should be no need to shift the type of either name to clarify application, and they are unlikely ever to be considered separate, necessitating publication of a nomen novum.

Section 3.3

Acknowledgments

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Section 3.4

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Chapter 4

Sareomycetes: more diverse than meets the eye

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Section 4.1

Abstract

Since its resurrection, the resinicolous discomycete genus *Sarea* has been accepted as containing two species, one with black apothecia and pycnidia, and one with orange. We investigate this hypothesis using three ribosomal (nuITS, nuLSU, mtSSU) regions from and morphological examination of 70 specimens collected primarily in Europe and North America. The results of our analyses support separation of the traditional *Sarea difformis s.lat.* and *Sarea resinae s.lat.* into two distinct genera, *Sarea* and *Zythia*. *Sarea* as circumscribed is shown to conservatively comprise three phylospecies, with one corresponding to *Sarea difformis s.str.* and two, morphologically indistinguishable, corresponding to the newly combined *Sarea coeloplata*. *Zythia* is provisionally maintained as monotypic, containing only a genetically and morphologically variable *Z. resinae*. The new genus *Atrozythia* is erected for the new species *A. klamathica*. *Arthrographis lignicola* is placed in this genus on molecular grounds, expanding the concept of *Sareomycetes* by inclusion of a previously unknown type of asexual morph. Dating analyses using additional marker regions indicate the emergence of the *Sareomycetes* was

roughly concurrent with the diversification of the genus *Pinus*, suggesting that this group of fungi emerged to exploit the newly-available resinous ecological niche supplied by *Pinus* or another, extinct group of conifers. Our phylogeographic studies also permitted us to study the introductions of these fungi to areas where they are not native, including Antarctica, Cape Verde, and New Zealand and are consistent with historical hypotheses of introduction.

Section 4.2

Introduction

Conifers, particularly in the families *Araucariaceae*, *Pinaceae*, and *Cupressaceae*, produce resins in their tissues (Langenheim 2003) as part of a complex defence system to protect against herbivores (Smith 1961; Rudinsky 1966; van Buijtenen and Santamour 1972), pathogenic fungi (Whitney and Denyer 1969; Gibbs 1972; Hart et al. 1975; Yamada 2001), protists (Krupa and Nylund 1972; Bunny and Tippett 1988), and bacteria (Hemingway and Greaves 1973; Hartmann et al. 1981). To protect against fungi, resins have the potential to act in several different manners. First, they present a physical barrier to penetration by fungal hyphae (Verrall 1938; Shain 1971; Rishbeth 1972; Prior 1976). When soft, resin can flow, trapping fungal hyphae and spores; when hard, the resin is difficult to penetrate. Furthermore, the components of the resin can inhibit the growth of fungi, acting as a chemical barrier (Cobb et al. 1968; Hintikka 1970; De Groot 1972; Fries 1973; Väisälä 1974; Chou and Zabkiewicz 1976; Bridges 1987; Yamamoto et al. 1997). Despite this apparently inhospitable environment, a number of so-called "resinicolous" fungi have evolved to exploit this niche (Cappelletti 1924; Selva and Tuovila 2016).

The study of fungi growing on conifer resins has a long history, dating back to the fathers of mycology (Persoon 1801; Fries 1815, 1822). The first species described was *Helotium aureum*, described in 1801 by Christiaan Persoon, though he made no mention of the resinicolous habit (Seifert and Carpenter 1987). Thus, the first author to describe fungi dwelling on resin was Elias Fries, who described three such fungi in 1815. *Sphaeria resinae* and *Lecidea resinae* were described as sharing the same habitat and easily confused; these were later determined to represent the asexual and sexual morphs of the same fungus, currently known as *Sarea resinae* (Ayers 1941; Hawksworth and Sherwood 1981). The third species, *Racodium resinae*, described from *Picea* resin, is a synnematous hyphomycete now called *Sorocybe resinae* (Seifert et al. 2007). These three Friesian species were followed by *Cytospora resinae*, described by Ehrenberg (1818); this was later determined to be a synonym of Fries' *Sphaeria resinae* (Fries 1823; von Thümen 1880). The last of these early species was described in 1822, again by Fries, as *Peziza difformis,* currently known as *Sarea difformis*. No additional new resinicolous taxa were noted until Arnold (1858).

The two species assigned to the genus *Sarea*, *S. resinae* and *S. difformis*, are the most commonly collected and reported of these resinicolous fungi. A search of the Global Biodiversity Information Facility (GBIF) database for *S. resinae* yielded 1261 records, and one for "*Sarea resinae*" on Google Scholar 249 results; *S. difformis* gave 519 records and 196 results, respectively. In contrast, *Sorocybe resinae* gives only 24 records and 56 results (accessed 13 July 2020). In addition to frequent reports, the two *Sarea* species have also been a subject of some interest regarding their systematic placement, which has been unclear (Reeb et al. 2004; Miadlikowska et al. 2014). A recent study resolved the uncertainty and has supported the erection of a new class in *Pezizomycotina*, *Sareomycetes* (Beimforde et al. 2020). This study, as

well as a recent study that yielded 31 endolichenic isolates of *Sarea* species (Masumoto and Degawa 2019), have illustrated that both *Sarea* species are genetically diverse. This pattern is present in published sequences of both *Sarea* species deposited in public repositories. Sequence similarity and phylogenetic analyses also suggest that *Arthrographis lignicola*, though morphologically unlike *Sarea* species, is a close relative (Giraldo et al. 2014). This, combined with the wide distributions of these species, suggest a higher than known diversity, both obvious and cryptic, in *Sareomycetes*. The aim of this study is to assess this diversity.

To assess this diversity within *Sareomycetes*, an integrative taxonomic approach was employed. Fresh and fungarium specimens of orange (*Sarea resinae*) and black (*S. difformis*) species from around the world were borrowed or collected and examined morphologically. Where possible, DNA was extracted, and several regions amplified and sequenced. Two multi-locus datasets were assembled to explore species boundaries and their phylogenetic relationships and to provide further insights on the evolutionary history of *Sareomycetes* on a temporal and spatial scale.

Section 4.3

Materials and Methods

Subsection 4.3.1

Specimens Examined and Microscopic Examination

During the course of this study, a number of specimens of *Sarea* were collected and examined by us. The host range and distribution of these specimens was broad, with collections

from the United States (California, Georgia, Maine, Massachusetts, Minnesota, New Hampshire, Rhode Island, and Vermont) made by J.K.M. and collections from Austria, Cape Verde, Spain, and Switzerland made by I.G.-B. Further specimens were collected by and lent by Tomás J. Curtis (Ohio), Alden C. Dirks (Michigan, Wisconsin), Michael Haldeman (Idaho, Washington), Jason M. Karakehian (Maine, Massachusetts, Newfoundland), Elizabeth Kneiper (Maine, Massachusetts), Jiří Malíček (Czechia), Rubén Negrín Piñero (Canary Islands), Donald H. Pfister (Dominican Republic), Michaela Schmull (New York), Judi Thomas (Missouri), Per Vetlesen (Norway), and Andrus Voitk (Newfoundland); these specimens are deposited in FH, KE, MICH, VAL, and several personal herbaria. Further specimens of *Sarea* and other critical materials from the following fungaria were studied: B, CANL, DUKE, FH, H, K, LD, MICH, NCSLG, NY, TFM, TNS, and TROM.

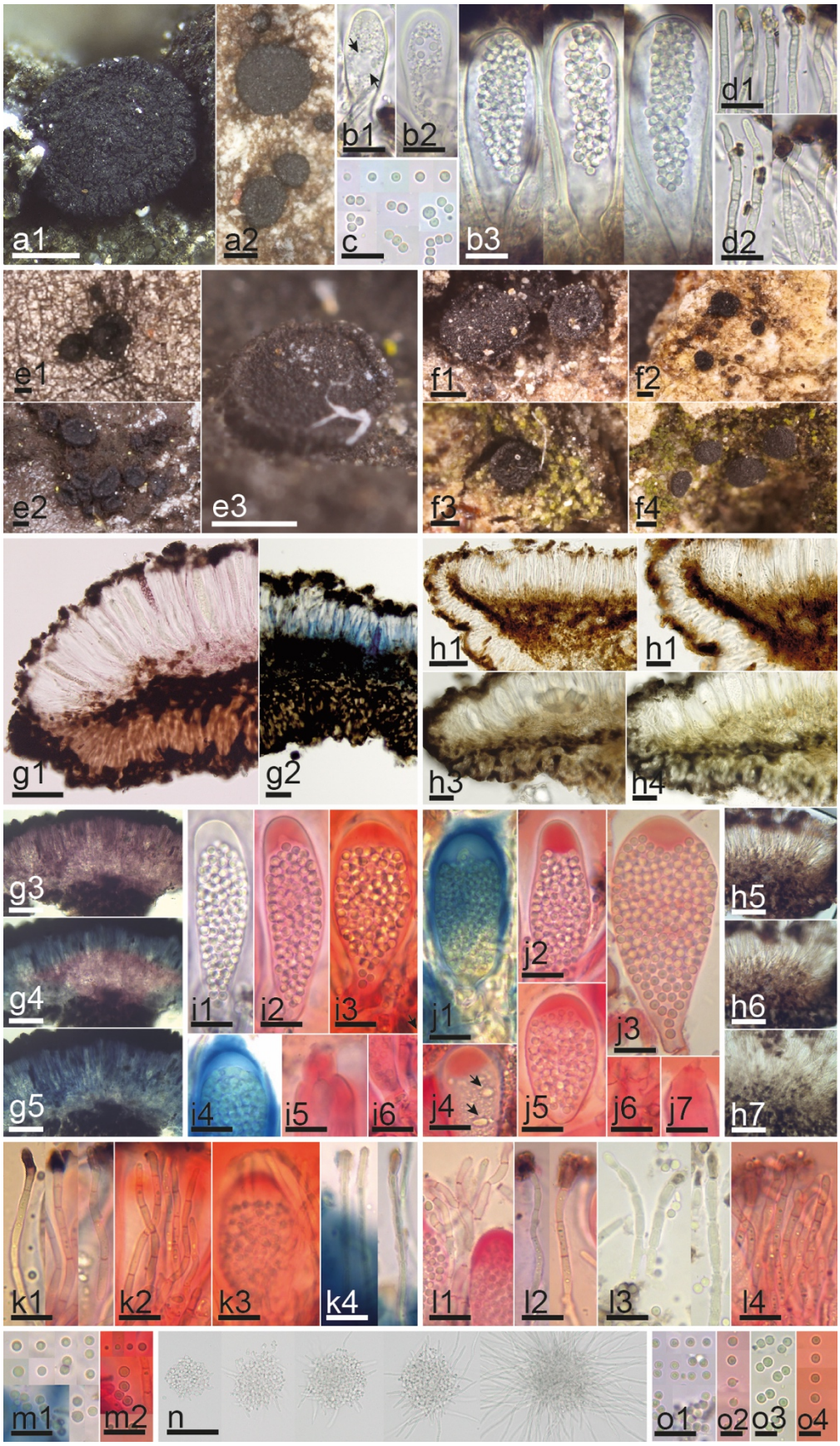
Microscopic examination of hymenial elements was conducted using free-hand sections cut under a dissecting microscope (Wild M5; Leica Geosystems, Heerbrugg, Switzerland) and of the excipulum using sections made on a freezing microtome. Microtome sections were prepared by stabilizing water-hydrated apothecia on a freezing stage (Physitemp BFS-MP; Physitemp Instruments, Clifton, NJ) with a diluted gum arabic solution and sectioning with a sliding microtome (Bausch & Lomb Optical, Rochester, NY) set at approximately 25 µm. The resulting sections were applied serially to a clean glass slide and allowed to adhere by drying in the remaining gum arabic. Slides were prepared under a dissecting microscope (Olympus SZX9; Olympus Corporation, Tokyo, Japan) and studied with a compound microscope (Olympus BX40; Olympus Corporation, Tokyo, Japan). Digital images were captured with an Olympus XC50 USB camera (Olympus Corporation, Tokyo, Japan). Hand sections were studied with a compound microscope (Motic B1; Motic, Hong Kong, China). Except for two fresh collections

studied alive in tap water (Fig. 4.1, b1-d2, Fig. 4.2, b1-d3) and a culture studied on potato dextrose agar (PDA) (Fig. 4.1, n), all the other specimens (Fig. 4.1, g1-m2, o1-o4, Fig. 4.2, e2-e9, f2-f9, g2-g9, h2-h9, i2-i9, j2-j9, k2-k9, l2-l9, m2-m9, Fig. 4.3, b1-d4), were pre-treated in 5% KOH prior to morphological studies. Melzer's reagent (MLZ) was used to test amyloidicity and Congo red (CR) to contrast cells walls. Images were captured with a Moticam 2500 USB camera and processed with the software Motic images Plus 2.0 (Motic, Hong Kong, China). The 95% confidence intervals of the median were calculated with SPSS 15.0 (SPSS, Chicago, IL) for each morphological feature. Measurements are given as follows: (the smallest single measurement) smallest value for percentile of 95% - largest value for percentile of 95% (largest single measurement). Whenever possible, biometric values are based on ≥10 measurements for each character on an individual specimen.

Subsection 4.3.2

Culturing

Some specimens were grown in axenic culture. Cultures were generated from discharged ascospores. A living apothecium was placed oriented upward on a dab of petroleum jelly on a filter paper. This assemblage was then placed in the lid of an upside-down, sterile petri dish containing either PDA or cornmeal agar (CMA) prepared according to the manufacturer's instructions (HiMedia Laboratories, Mumbai, India). The filter paper was saturated with water, and the chamber sealed with Parafilm (Bemis Company, Neenah, WI). After incubation at room temperature for one or two days, the lid was removed and replaced with another sterile lid. The culture was then allowed to grow at 25°C for up to one month before sampling. Once sampled,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←**Figure 4.1.** Morphological features of *Sarea* spp. **a1–d2** Fresh collection and living asci, ascospores and paraphyses of *Sarea coeloplata*. **e–o** Comparative morphology between *S. difformis* (e, g, i, k, m, n) and *S. coeloplata* (f, h, j, l, o). **e–f** Dry or rehydrated apothecia on substrate. **g–h** Median section of apothecium with ectal and medullary excipulum and changes after adding KOH. **i–j** Mature asci with ascus dehiscence and base with croziers. **k–l** Paraphyses. **m & o** Ascospores. **n** Ascospore shoot in culture and hyphal germination. Reagents: H_2O = b1–3, c, d1–2; g1, h1, h3, n; KOH = g2–5; h2, h4–7, i1, l3, o3; KOH+CR = i2–3, i5–6, j2–7, k1–3, l1–2, l4, m2, o2, o4; KOH+MLZ = i4, j1, k4, m1, o1. Scale bars: 200 µm = a1–2, e1–3, f1–4; 50 µm = g1–5, h1, h5–7, n; 10 µm = b1–3, c, d1–2, h2–4, i1–6, j1–7, k1–4, l1–4, m1–2, o1; 10 µm = o2–4. Collections: BHI-F925 = f3, h3–7, j3, l3, o3; IGB454 = f1–2; IGB457 = j5–7, l1, o1; IGB448 = h1–2; JM0007 = e1, i1–2, i4–6, k4, m1–2; JM0009.2 = i3, k1–3; JM0010.1 = g3–5; JM0011 = f4, j1, j4, l4, o4; JM0132 = a1–2, b1–3, c, d1–2, n; JM0072.1 = j2, l2, o2; JM0074.1 = e3; JMEK = e2; PV-D836 = g2; Rehm *Ascomyceten* 577 (FH 00995483) = g1.

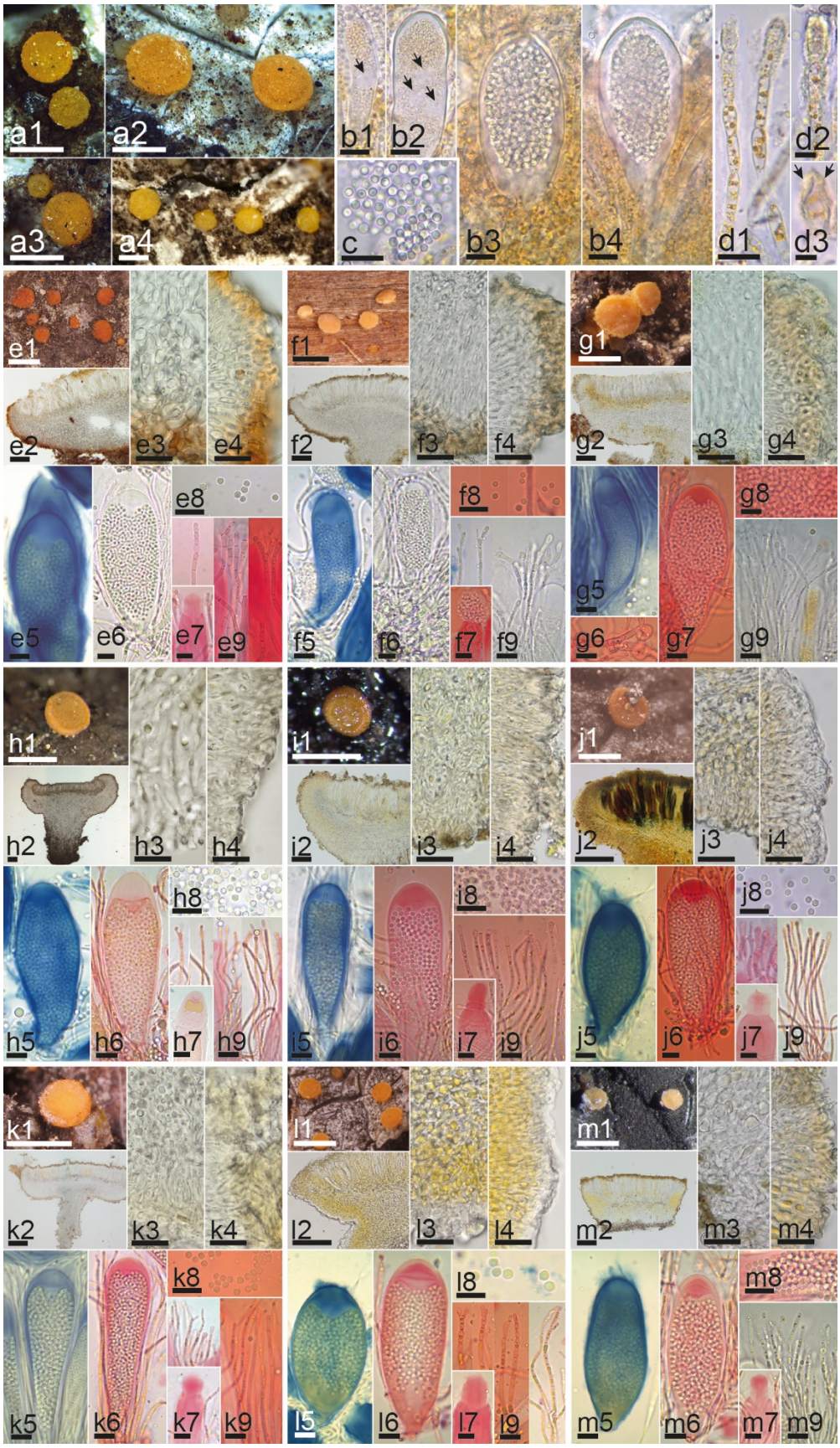
→**Figure 4.2.** Morphological features of *Zythia resinae*. **a1–d3** Fresh collection and living asci, ascospores and paraphyses. From e to m each letter represents the morphology of one specimen for each different clade (Fig. S1): **e1–9** Clade 3, **f1–9** Clade 2, **g1–9** Clade 1, **h1–9** Clade 5, **i1–9** Clade 6, **j1–9** Clade 8, **k1–9** Clade 12, **l1–9** Clade 13, **m1–9** Clade 9. Numbers after the letter e to m indicate different morphological features: 1. Dry apothecia, 2. Median section of apothecium, 3–4. Excipular cells. 5–7. Asci, 8. Ascospores, and 9. Paraphyses. Reagents: H_2O = b1–4, c, d1–3; KOH = e2–4, e6, e8, f2–4, f6, f9, g2–4, g9, h2–4, h8, i2–4, j3–4, j8, k3–4, l3–4, m3–4, m9; KOH+CR = e7, e9, f7–8, g6–8, h6–7, h9, i6–9, j6–7, j9, k2, k6–9, l6–7, l9, m6–8; KOH+MLZ = e5, f5, g5, h5, i5, j2, j5, k5, l2, l5, l8, m2, m5. Scale bars: 500 µm = a1–4; e1, f1, g1, h1, i1, j1, k1, l1, m1; 100 µm = e2, f2, g2, h2, i2, j2 k2, l2, m2; 20 µm = e3–4, f3–4, g3–4, h3–4, i3–4, j3–4, k3–4, l3–4, m3–4; 10 µm = b1–4, c, d1, e5–9, f5–9, g5–9, h5–9, i5–9, j5–9, k5–9, l5–9, m5–9; 5 µm = d2–3. Collections: 17121601 = m1–9; HJMS11998 = i1–9; JM0120 = h1–9; JM0014 = l1–9; JM0131 = a1–4, b1–4, c, d1–3; JM0006 = j1–9; JM0065.1 = k1–9; LD1356193 = e1–9; PV-D836-Ba = g1–9; TNS-F-41522 = f1–9.

cultures were not preserved.

Subsection 4.3.3

DNA Extraction, PCR, and Sequencing

DNA extractions were performed from axenic culture when available and from fresh or preserved apothecia or pycnidia otherwise. Fresh or plentiful dried material was extracted by grinding 1-2 apothecia, 3-4 pycnidia, or a rice grain-sized slice of a culture and employing the DNeasy Plant Mini Kit (QIAGEN, Venlo, The Netherlands) following the manufacturer's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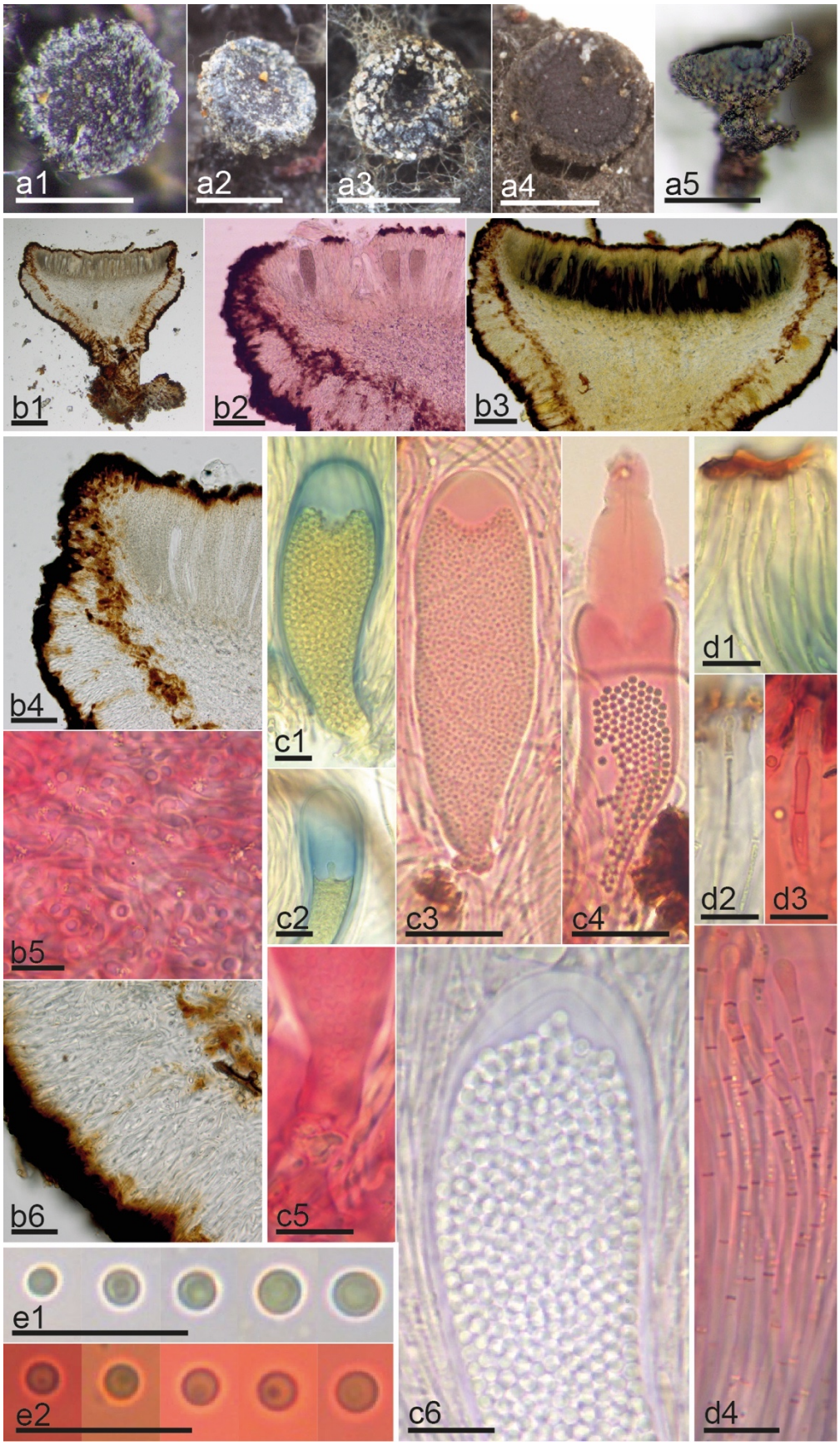
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←**Figure 4.3.** Morphological features of *Atrozythia klamathica*. **a1–5** Dry apothecia. **b1–6** Median section of apothecium with details of excipulum: b4. Ectal excipulum at margin, b5. Medullary excipulum, b6. Ectal excipulum at lower flanks. **c1–6** Morphological variation of asci: c1–2. Amyloid walls, c3. multispored mature ascus, c4. Ascus dehiscence, c5. Perforated crozier, c6. Details of ascus walls. **d1–4** Paraphyses. **e1–2** Ascospores. Reagents: H_2O = b4, b6; KOH = b1, c6, e1; KOH+CR = b2, b5, c3–5, d1, d3–4, e2; KOH+MLZ = b3, c1–2, d2. Scale bars: 500 µm = a1–5; 200 µm = b1; 100 µm = b2–3; 50 µm = b4, b6, c3–4; 10 µm = b5, c1–2, c5–6, d1–4, e1–2. Collections: JM0068 = a1–2, a5, b1–6, c5–6, d2–4, e1; Haldeman 2748 = a3–4, c1–4, d1, e2.

recommendations. Preserved or scanty material was extracted by grinding .25-2 apothecia or 2-3 pycnidia and employing the QIAamp DNA Micro Kit (QIAGEN), again following the manufacturer's recommendations.

Three rDNA regions were amplified: the internal transcribed spacer regions plus 5.8S gene (nuITS), the nuclear large subunit ribosomal RNA gene (nuLSU), and the mitochondrial small subunit ribosomal RNA gene (mtSSU). For older material, nuITS was obtained in two parts by employing the primer pairs ITS1-F (Gardes and Bruns 1993) + 5.8S (Vilgalys and Hester 1990) and 5.8S-R (Vilgalys and Hester 1990) + ITS4 (White et al. 1990). For other extractions nuITS+nuLSU was amplified in one or two pieces, using the primer pairs ITS1-F + LR5 (Vilgalys and Hester 1990), ITS1-F + LR3 (Vilgalys and Hester 1990) and LR0R (Rehner and Samuels 1994) + LR5, or ITS1-F + ITS4 and LR0R + LR5. The region mtSSU was amplified using the primer pair mrSSU1 + mrSSU3R (Zoller et al. 1999). For our dating analysis, two additional genes were obtained for a small subset of fresh specimens, the nuclear small subunit ribosomal RNA gene (nuSSU) and the second largest subunit of RNA polymerase II gene (*RPB2*). The nuSSU was obtained employing the primer pair NS1 + NS4 (White et al. 1990). *RPB2* was amplified in two pieces, employing the primer pairs fRPB2-5F + fRPB2-7cR and fRPB2-7cF + fRPB2-11aR (Liu et al. 1999). All primers were purchased from Integrated DNA Technologies (Coralville, IA).

When nuITS+nuLSU was amplified in a single piece, REDExtract-N-Amp PCR ReadyMix (Sigma-Aldrich, St Louis, MO) was used; when amplified in multiple parts or amplifying nuSSU, EconoTaq DNA Polymerase (Lucigen, Middleton, WI) was used. Amplification was performed for mtSSU and *RPB2* using Q5 High-Fidelity DNA Polymerase (New England BioLabs, Ipswich, MA). All PCR reactions were performed using 5 µL of full strength, 1/10 dilution, or 1/100 dilutions of the DNA extracts as templates in a total reaction volume of 25 µL and utilised either a Mastercycler ep Gradient (Eppendorf, Hamburg, Germany) or a C1000 Touch Thermal Cycler (Bio-rad, Hercules, CA). All PCR protocols are included in Appendix A.

PCR products sometimes contained multiple bands. In these cases, the band of interest was excised from a 2% agarose gel and purified using either a QIAquick Gel Extraction Kit (QIAGEN) or a Monarch DNA Gel Extraction Kit (New England BioLabs). Otherwise, single-band PCR products were purified with a QIAquick PCR Purification Kit (QIAGEN) or a Monarch PCR & DNA Cleanup Kit (New England BioLabs). In the case of faint PCR products, reamplification was performed using 5 µL of a 1/100 dilution of the previous PCR product as template in a total reaction volume of 25 µL using the same polymerase, primers, reaction recipe, and cycling parameters as previously.

In preparation for sequencing, all purified products were run on a 1% agarose gel with 0.0001% GelRed Nucleic Acid Stain, 10,000× in Water (Biotium, Hayward, CA) added for DNA visualisation and using Gel Loading Dye Purple (6×), no SDS (New England BioLabs). UV photographs of gels were taken with an AlphaImager EP (Alpha Innotech, San Leandro, CA), and band fluorescence was estimated using the AlphaView software (Alpha Innotech). Purified PCR product concentration was assessed by comparison with the fluorescence of the bands in

Low DNA Mass Ladder (Invitrogen, Carlsbad, CA) run on the same gel. All PCR products of all genes were sent to GeneWiz Inc. sequencing facilities (Cambridge, MA) for Sanger Sequencing. The forward and reverse sequences from each PCR product were edited and a consensus sequence generated using Sequencher v. 5.1 (GeneCodes, AnnArbor, MI). All sequences were submitted to GenBank, with accession numbers listed in Table 4.S1. Our alignments were submitted to TreeBase (S27765).

Subsection 4.3.4

Assembling Published *Sareomycetes* Sequences

Sequences of species in *Sareomycetes*, either already identified or identified by us through BLAST similarity, are available on public databases such as GenBank, UNITE (Nilsson et al. 2019), and the NARO Genebank Microorganism Search System (Genebank Project 2020). Those nuITS sequences used from these databases were restricted to complete or nearly complete (>450 bp). The identified sequences were obtained by searching GenBank and the NARO Genebank Microorganism Search System for *Sarea*, *Sarea resinae*, *Sarea difformis*, or *Arthrographis lignicola* and downloading those sufficiently complete nuITS and nuLSU sequences (71 and 19 sequences, respectively).

Unidentified and misidentified sequences were found by searching GenBank using the Nucleotide Basic Local Alignment Search Tool (BLAST) (Altschul 1997) with nuITS, nuLSU, and mtSSU sequences derived from morphologically identified specimens. The "distance tree of results" feature was employed, with sequences identified as *Lecanoromycetes* species excluded from consideration. The remaining sequences on branches with or adjacent to identified

Sareomycetes sequences were downloaded and identified by comparison to further sequences of identified specimens. This yielded an additional 30 sequences. Two of these were discarded because they were identified as chimeric by BLASTing their nuITS1 and nuITS2 portions separately. This method was used to determine that KF274061 consists of a nuITS1 region from *Sarea resinae s. lat.* and a nuITS2 region from an unidentifiable fungus with affinities to *Leotiomycetes*, and KM104053 consists of a nuITS1 region from *Sarea difformis s. lat.* and a nuITS2 region from *Sarea resinae s. lat.* In addition, the UNITE database was searched by examining sequences unique to the UNITE database included in the 8 species hypotheses for the genus *Sarea* and the 11 species hypotheses for the genus *Arthrographis*. These were downloaded and identified by comparison with sequences of identified specimens; low similarity sequences were discarded. In this way, 8 sequences were identified.

Host, locality, and specimen/culture strain data were determined for all published sequences by consulting the information provided in the source database, relevant publications, and relevant culture collection databases (*e.g.*, ATCC 2020; Westerdijk Fungal Biodiversity Institute 2020; University of Toronto 2021). These data as well as accession numbers and updated identifications are included in Table 4.S1.

Subsection 4.3.5

Sequence Alignments

MAFFT v. 7.308 (Katoh 2002; Katoh and Standley 2013) was used to generate a multiple sequence alignment (MSA) independently for each marker with the following parameters: the FFT-NS-I x1000 algorithm, the 200PAM / k = 2 scoring matrix, a gap open penalty of 1.5 and an

offset value of 0.123. The resulting alignments were manually optimised in Geneious v. 9.0.2 (a) to replace gaps at the ends of shorter sequences with an IUPAC base representing any base ("N"), and (b) to trim ends of longer sequences in the nuITS MSA that included part of the 18S–28S ribosomal subunits. The software GBlocks v. 0.91b (Castresana 2000) was used to automatically remove ambiguously aligned regions in the nuITS and mtSSU MSAs using the least stringent parameters but allowing gaps in 50% of the sequences.

Subsection 4.3.6

Phylogenetic Tree Inference

The online version of RAxML-HPC2 hosted at the CIPRES Science Gateway (Stamatakis 2006; Stamatakis et al. 2008; Miller et al. 2010) was used to estimate a three-locus phylogeny under a Maximum Likelihood (ML) framework based on a dataset comprising specimens with at least two available sequenced markers. Several specimens of *Pycnora* were included as outgroup to root phylogenetic trees. Prior to concatenation, and to test for topological incongruence among sequence datasets, we inferred ML trees independently for each locus with RAxML-HPC2, using 1,000 bootstrap pseudoreplicates, and assumed bootstrap values ≥70 % as significant for conflicting relationships among the same set of taxa (Mason-Gamer and Kellogg 1996). Because no conflicts were detected, the RAxML analysis was conducted using the GTRGAMMA substitution model for the four delimited partitions (nuITS1+2, 5.8S, nuLSU, mtSSU) and 1,000 rapid bootstrap pseudoreplicates were implemented to evaluate nodal support. Evolutionary relationships were additionally inferred in a Bayesian context using MrBayes v. 3.2.6 (Ronquist et al. 2012). Optimal substitution models and partition schemes for these four

sequence data partitions were estimated with PartitionFinder v. 1.1.1 (Lanfear et al. 2012) considering a model with linked branch lengths and the Bayesian Information Criterion (BIC). This analysis favoured the SYM+Γ model for the nuITS1+2 partition, the K80+I+Γ for the 5.8S+nuLSU, and the HKY+I+Γ for the mtSSU. The analysis was then conducted with two parallel, simultaneous four-chain runs executed over 5×10^7 generations starting with a random tree, and sampling after every 500th step. The first 25% of data were discarded as burn-in, and the 50% majority-rule consensus tree and corresponding posterior probabilities were calculated from the remaining trees. Average standard deviation of split frequencies (ASDSF) values below 0.01 and potential scale reduction factor (PSRF) values approaching 1.00 were considered as indicators of chain convergence. Tree nodes showing bootstrap support (BP) values equal or higher than 70 % (RAxML analysis) and Bayesian posterior probabilities (PP) equal or higher than 0.95 (MrBayes analysis) were regarded as significantly supported. Phylogenetic trees were visualised in FigTree v. 1.4 (Rambaut 2012) and Adobe Illustrator CS5 was used for artwork.

Subsection 4.3.7

Species Discovery-Validation Approach

Based on the existence of well-delimited and highly supported clades in the three-locus phylogenetic tree inferred above, we conducted a preliminary exploration of species boundaries independently for the orange and black *Sarea*. To this end, we used the distance-based Automatic Barcode Gap Discovery method (ABGD) (Puillandre et al. 2012), restricting the analyses to specimens with available data for the fungal barcode nuITS. The analyses used the Kimura two-parameters (K2P) model to estimate genetic distances, a transition/transversion

value of 3.95 (orange *Sarea*) and 3.07 (black *Sarea*) calculated with MEGA v.5.2 (Tamura et al. 2011), a *Pmax* of 0.01, and different values for the relative gap width (*X*). Subsequently, the Bayes Factor Delimitation (BFD) method, which allows for topological uncertainty in gene trees and incongruences among gene trees, was chosen to compare two species boundary hypotheses generated for the black *Sarea* on the basis of our morphological study of the specimens, and the ABGD and phylogenetic results (Table 4.1). *BEAST (Heled and Drummond 2010; Drummond et al. 2012) was used to build the two competing models. These comprised a three-locus dataset in which specimens with identical sequences were removed to avoid sequence redundancies; the number of specimens left was 85, including outgroup specimens. The same optimal substitution models and partition schemes selected in the MrBayes analysis were used for the *BEAST analyses except for the substitution model TrNef+I+Γ, which was preferred for the 5.8S+nuLSU partition. An uncorrelated relaxed lognormal molecular clock was chosen for the three markers

Table 4.1. Species delimitation hypotheses in *Sarea.*

	Distinct species	Motivation	Path Sampling		Stepping-Stone	
			Ln (Marginal Likelihood)	2ln (Bayes Factor)	Ln (Marginal Likelihood)	2ln (Bayes Factor)
Model 1 (three *Sarea* spp.)	*Sarea difformis* / *S. coeloplata* 1 / *S. coeloplata* 2	Morphological observations and three-locus phylogenies (RAxML and MrBayes)	**-7867.9101**	**N/A**	**-7868.3128**	**N/A**
Model 2 (two *Sarea* spp.)	*Sarea difformis* + *S. coeloplata* 1 / *S. coeloplata* 2	ABGD nuITS	-7873.5589	11.2976	-7874.1365	11.6474

Marginal likelihood and Bayes factor values for two alternative species delimitation hypotheses in *Sarea* and their motivation. The best model is highlighted in bold.

based on a preliminary assessment of the adequacy of strict clocks in MEGA 5.0 (Tamura et al. 2011) (see Table 4.S2). The mean clock rate was fixed to 1.0 for nuITS whereas rates were co-estimated for nuLSU and mtSSU under a uniform prior (1×10^{-5}, 5). A birth-death process tree prior was imposed after conducting preliminary Bayes factors comparisons of Maximum Likelihood Estimates (MLE) calculated with Path Sampling and Stepping-Stone (Lartillot and Philippe 2006; Xie et al. 2011) for models implementing alternative tree priors (see Table 4.S2). By using this tree prior we accommodated incomplete sampling and speciation of nodes in the topology. The *BEAST analyses used a piecewise linear and constant root model for population size (Grummer et al. 2014). Hyperpriors for the birth-death process tree prior and species population mean were given an inverse gamma distribution with an initial value of 1 or 0.1, shape parameter of 1 or 2 and scale of 1 or 2, respectively. Default (but informative) priors were given for the remaining parameters across all analyses. Finally, *BEAST runs of 1.5×10^8 generations, saving every 15,000th tree, were performed using the CIPRES Science Gateway (Miller et al. 2010). Tracer v.1.7 (Rambaut et al. 2018) was used to check for convergence, assumed if effective sample sizes (ESS) were > 200. Then, MLE for the two species boundary models were calculated using Path Sampling and Stepping-Stone, with default settings. Bayes Factors were calculated following Hedin et al. (2015). 2lnBF > 10 indicate very strong evidence against a model as compared with the best (Kass and Raftery 1995).

Subsection 4.3.8

Estimating the Age of the Crown Node of *Sareomycetes*

To infer the age of the crown node of class *Sareomycetes*, a six-locus dataset was compiled using sequences from nine *Sarea s.lat*. specimens and sequences retrieved from GenBank representing major clades in the *Ascomycota* tree of life. For ascomycete taxa compilation, we followed Pérez-Ortega et al. (2016), Lutzoni et al. (2018) and Voglmayr et al. (2019). Together with the four basidiomycete species included as outgroup, the final dataset consisted of 169 taxa (Table 4.S3).

Alignments of the nuSSU, nuLSU, mtSSU, *RPB1*, *RPB2* and *tef1-α* were carried out in MAFFT v. 7.308 as implemented in Geneious v. 9.0.2 using the same algorithm parameters as above. Manual optimisation of the resulting MSAs consisted in removing clearly ambiguously aligned and intronic regions in rDNA marker datasets (nuSSU, nuLSU, and mtSSU), as well as non-coding regions (introns) in the protein-coding markers (*RPB1*, *RPB2*, and *tef1-α*). Sequences of the latter three datasets were also translated into amino acids to spot misaligned regions generating stop codons. Finally, "N"s were used to fill gaps at the ends of shorter sequences. The resulting alignment lengths were: nuSSU (1629 bp), nuLSU (1305 bp), mtSSU (651 bp), *RPB1* (1100 bp), *RPB2* (2001 bp), *tef1-α* (1209 bp), for a total length of 7895 bp. PartitionFinder v. 1.1.1 was used to estimate the optimal number of partitions of the data along with their corresponding best-fitting nucleotide substitution model using the linked branch lengths option and the Bayesian Information Criterion for model selection. Eight independent data blocks were suggested: (1) nuSSU; (2) nuLSU; (3) *tef1-α* codon1; (4) *tef1-α* codon2, *RPB1*-codon2, *RPB2*-codon2; (5) *tef1-α* codon3; (6) *RPB2*-codon1, *RPB1*-codon1; (7) *RPB2*-codon3, *RPB1*-codon3; and (8) mtSSU. The GTR+I+Γ substitution model was selected for all partitions but 1 (SYM+I+Γ), 2 (TRN+I+Γ), 3 (HKY+I+Γ), and 5 (GTR+Γ). Before assembling the six-locus dataset, potential topological conflicts among markers were visually explored on single-locus

ML phylogenetic trees calculated with the online version of RAxML-HPC2 with 1,000 bootstrap pseudoreplicates conducted to retrieve nodal support values.

Among all available fossils that may be used to calibrate a class-wide fungal phylogeny (Lücking and Nelsen 2018; Samarakoon et al. 2019), we chose six ascomycete fossils, whose details and associated reference publications are in Table 4.S4. Divergence times and a tree topology were then co-estimated in BEAST v. 1.8.1. XML files were prepared in BEAUti v 1.8.1 (Drummond et al. 2012) using the above-mentioned six-locus dataset with the corresponding partitions and nucleotide substitution models. Additional settings included selection of an uncorrelated lognormal relaxed clock for each marker and a birth-death prior, and the use of a rooted, strictly-bifurcating ML topology obtained in RAxML as a starting tree. This ML tree was previously transformed into ultrametric using the function *chronos* in the R package *ape* (Paradis et al. 2004). In the prior settings step, we forced the co-estimation of the average rate of evolution of each locus by setting the priors for the *ucld.mean* parameter to uniform (10^{-5}, 0.01). The taxa and prior distributions used to set the fossil calibrations are detailed in Table 4.S4. Fourteen independent BEAST runs of 200 million generations each were carried out, logging parameters and trees every 2×10^4 generations. Then, Tracer v. 1.7 was used to check for convergence and mixing, making sure that ESS were well above 200. After implementing an adequate burn-in portion to the sampled trees in each run, a total of 8×10^4 remaining trees were combined in a single file using LogCombiner v1.8.1 (Drummond et al. 2012). Because the resulting file exceeded 6 GB and could not be handled by TreeAnnotator v.1.8.1 (Drummond et al. 2012), we implemented a custom script to generate ten files with 4×10^4 randomly drawn trees each. These were then processed with TreeAnnotator v.1.8.1 to generate ten maximum clade credibility trees with annotated median node heights. Age estimates in million years ago

(Ma), 95% High Posterior Density (HPD) intervals, and average substitution rates for markers reported in this study are the result of averaging over these ten annotated tree files.

Subsection 4.3.9

Inferring a Timeframe for the Diversification of *Sareomycetes*

We implemented a secondary calibration approach in BEAST v.1.8.1 on the concatenated three-marker dataset used in the BFD analysis (see section "Species discovery-validation approach") to estimate a temporal context for the diversification of the main lineages of *Sareomycetes*. First, a time estimate of 120.88 Ma (181.35–75.76 Ma, 95 % HPD) was used to calibrate the crown node of *Sareomycetes* based on results of our previous six-locus dating analysis. This calibration was set as a prior using a normal distribution (mean = 120.88, stdev = 35); average substitution rates for the three loci (nuITS, nuLSU and mtSSU) were co-estimated under a uniform prior (10^{-5}, 0.01). For comparison, we additionally estimated divergence ages using four different substitution rates: (a) a mtSSU rate of 3.28×10^{-10} s/s/y inferred for the *Sareomycetes* clade in the six-locus dating approach, (b) a nuLSU rate of 2.68×10^{-10} s/s/y inferred for the *Sareomycetes* clade as well, (c) a nuITS rate of 2.52×10^{-9} s/s/y calculated for the fungal order *Erysiphales* by Takamatsu and Matsuda (2004), and (d) a nuITS rate of 3.41×10^{-9} s/s/y calculated for the lichenised fungal genus *Melanohalea* by Leavitt et al. (2012). For all analyses, clock models were set identical to the BFD analyses whereas tree priors were set to “Coalescent: Constant size” to account for the increased amount of intraspecific diversity included in the dataset. The run consisted of 7.5×10^7 generations, saving every 7500th tree. A

25% of burn-in was selected in the TreeAnnotator step and chronograms were drawn with FigTree v. 1.4.

Section 4.4

Results

Subsection 4.4.1

Molecular Sequence Data

Molecular data were obtained from 70 collections. From these, we produced 212 sequences: 70 nuITS, 63 nuLSU, 61 mtSSU, 9 *RPB2*, and 9 nuSSU (Tables 4.S1 & 4.S3). The nuITS alignment of the 202 sequences produced *de novo* and downloaded from GenBank was 524 bp long; 192 positions were variable and 38 were singleton sites. After processing the alignment with GBlocks, 482 positions (91% of the original alignment) were retained in 24 selected blocks; 172 positions were variable and 33 were singleton sites. The nuLSU alignment comprised 92 sequences and was 914 bp in length; the number of variable and singleton sites were 87 and 21, respectively. The original mtSSU alignment was composed of 75 sequences and 977 positions, of which 253 were variable and 21 were singleton sites. The use of GBlocks trimmed the alignment to 691 bp (70% of the original alignment), displaying 152 variable and ten singleton positions. Last, the concatenated three-locus (nuITS, nuLSU and mtSSU) dataset used for (a) estimating a phylogeny, (b) species validation with the BFD method, and (c) inferring the timing of diversification of *Sareomycetes* was composed of 87 specimens of which

63 had data for the three loci. The total number of bp was 2088, including 398 variable and 75 singleton sites.

Subsection 4.4.2

Phylogenetic Reconstructions

The single-locus phylogenies produced with RAxML had lnL values of -3158.2564 (nuITS), -2229.9957 (nuLSU) and -2375.8252 (mtSSU). The nuITS and mtSSU phylogenies showed strong nodal support for (a) a clade including all orange *Sarea s.lat*. (hereafter referred to as *Zythia resinae*; see section "Taxonomy" below), and (b) a clade assigned to the new genus *Atrozythia* (see section "Taxonomy" below) including two species composed of a few specimens each (Figs 4.S1-4.S3). The two taxa referenced below as *Sarea coeloplata* 2 and *S. difformis s.str*. also formed well delimited and highly supported clades in these two phylogenies; however, *S. coeloplata* 1 was monophyletic with high support only in the mtSSU topology. A supported sister relationship was found for *Zythia* and *Atrozythia*, whereas a clade comprising the three *Sarea* species was only supported in the mtSSU topology, in which *S. coeloplata* 1 and *S. difformis* appeared as sister species. The nuLSU phylogeny only delimited the *S. coeloplata* 2 clade with support, and a specimen assigned to the new species *A. klamathica* was found interspersed in a non-supported clade including *Z. resinae* specimens (Fig. 4.S2). No clear relationships among the main nuLSU lineages were inferred. On the other hand, three-locus phylogenies inferred with RAxML and MrBayes showed high support (100 % BP, PP = 1) for the clades comprising the genera *Zythia*, *Atrozythia* and *Sarea* (Fig. 4.4). In *Zythia*, these two phylogenetic reconstruction methods were not coherent in delimiting well-supported subclades;

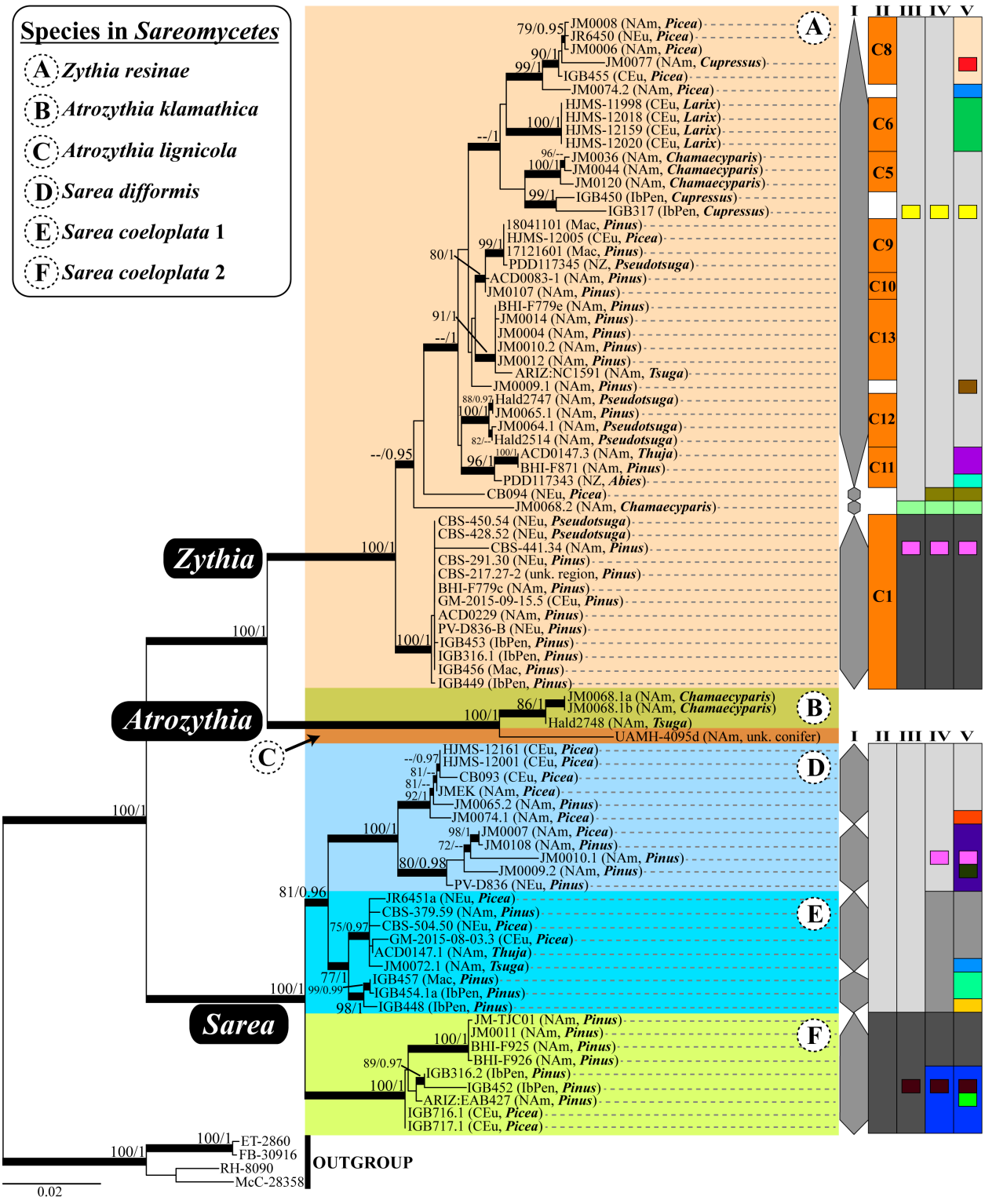


Figure 4.4. Three-locus RAxML phylogram of *Sareomycetes* with different species delimitation scenarios for *Zythia* and *Sarea*. Phylogram based on a three-locus matrix (nuITS, nuLSU and mtSSU) that depicts relationships among lineages within *Sareomycetes*. The voucher code, the geographic region, and the tree host genus on which each specimen occurred are provided.

Coloured boxes delineate the different taxa (genus, species) considered in the present study; full Latin names are available in the legend on the upper-left corner. Bold branches denote high nodal support in the RAxML (bootstrap values ≥ 70%) and/or Bayesian (PP ≥ 0.95) analyses. On the right margin of *Zythia*, species delimitation schemes are based on tree branch lengths and clade support (column I), ecology and distribution (II), and the ABGD 6 (III), 10 (IV) and 24 (V) putative species solutions. On the right margin of *Sarea*, the schemes are based on tree branch lengths and clade support (column I), and the ABGD 2 (II), 3 (III), 7 (IV) and 16 (V) putative species solutions.

only a basal lineage containing samples from Northern and Central Europe, North America, the Iberian Peninsula, and Macaronesia (Cape Verde Is.) showed strong nodal support by both methods, whereas the Bayesian method provided support for at least three inner nodes. The *Atrozythia* clade was split into two well-supported clades, one corresponding to the new species *A. klamathica* (see section "Taxonomy" below), and the other to *A. lignicola*. The *Sarea* clade segregated in three well delimited and supported subclades, each corresponding to a different species: *S. difformis* and *S. coeloplata* 1 and 2. All three lineages are distributed across the Northern Hemisphere (North America and Europe) and occur mainly on *Pinus* and *Picea* resin. Interestingly, in *S. coeloplata* 1, samples from the Iberian Peninsula and Macaronesia (Cape Verde Is.) formed a well-supported subclade sister to the bulk of North American and Northern-Central European specimens. This situation also occurred, although not so markedly, in *S. coeloplata* 2.

Subsection 4.4.3

Species Delimitation

Based on the topology (*i.e.*, branch lengths) and clade support obtained with the three-locus dataset, at least four lineages in *Zythia* (orange specimens) and five in *Sarea* (epruinose black specimens) might correspond with different species (grey column on the right margin of

Fig. 4.4). The ABGD analyses conducted on nuITS datasets of those genera did not reveal clear barcode gaps. In *Zythia*, ABGD rendered 6, 10, 24 and 52 different partitions (*i.e.*, putative species) when the relative gap width (*X*) was set to 0.5 (Figs. 4.S1, 4.S4), but initial and recursive partitions only converged in the 52-partitions solution. With *X*=1, convergence was found for 1 and 52-partition solutions. In agreement with our morphological data and due to difficulties discussed below in the section "Mixed collections", we hereafter conservatively considered the existence of only one *Zythia* species for assessing genetic polymorphism and phylogeographic structure and calculating neutrality tests. In *Sarea*, although a barcode gap was not strictly found, ABGD analyses using varying levels of *X* (0.5, 1 and 1.5) rendered 2, 3, 6, 7, 16 and 34 different partitions when the relative gap width (*X*) was set to 0.5 and 1 (Figs 4.S1, 4.S5). The two-partition solution suggested the combination of specimens assigned to *S. difformis* and *S. coeloplata* 1 into one single partition (Fig. 4.S5). As this solution contradicted our morphological observations of specimens suggesting the existence of three species in *Sarea*, a hypothesis in agreement with the multi-locus phylogenetic results, we compared the two alternative species delimitation models with the BFD method. Marginal likelihood values for the considered models calculated through Path Sampling and Stepping-Stone are shown in Table 4.1. Bayes factor comparisons favoured the three species model over the two species model.

Subsection 4.4.4

Genetic Polymorphism, Neutrality Tests and Phylogeographic Structure

Genetic diversity indices, such as the numbers of segregating sites and haplotypes, were greater for *Zythia resinae* than for any *Sarea* species across different markers (Table 4.2). The

Table 4.2. Polymorphism statistics and neutrality tests for *Sarea* spp. and *Zythia resinae*

Dataset	n	bp	Gaps/missing	*s*	*h*	*Hd*	π (JC)	Tajima's *D*	Fu's *Fs*
nuITS									
Sarea coeloplata 1	22	482	48	17	14/20	0.948	0.00662	-1.41635	-7.954(**)
Sarea coeloplata 2	15	483	31	17	7/12	0.838	0.01186	0.05176	0.91
Sarea difformis	17	482	28	31	13/13	0.956	0.01754	-0.58929	-2.987
Zythia resinae	118	511	115	71	48/68	0.96	0.02835	-0.55575	-12.831(*)
nuLSU									
Sarea coeloplata 1	8	909	382	4	4/7	0.786	0.00251	-0.62573	-0.674
Sarea coeloplata 2	8	907	381	13	4/6	0.75	0.00803	-0.84352	1.756
Sarea difformis	10	908	415	9	7/7	0.911	0.00548	-0.67784	-2.631
Zythia resinae	32	906	226	34	16/17	0.897	0.0114	-0.32928	-1.648
mtSSU									
Sarea coeloplata 1	5	741	35	12	4/4	0.9	0.00973	1.30583	0.98
Sarea coeloplata 2	8	740	17	14	4/4	0.75	0.01013	1.74512	3.209
Sarea difformis	11	750	72	33	6/8	0.8	0.01919	0.61079	3.46
Zythia resinae	40	691	36	35	14/18	0.931	0.01301	0.08728	-0.796

*: 0.01<p-value<0.05; **: p-value<0.01

Polymorphism statistics and neutrality tests results for each marker (nuITS, nuLSU and mtSSU), and *Sarea* spp. and *Zythia resinae*. Columns contain the number of sequences (n), their length (in bp), the number of positions in the alignment with gaps and missing data, the number of segregating sites (*s*), the number of haplotypes (*h*; value after vertical bar was calculated considering gaps in the alignment), haplotype diversity (*Hd*), nucleotide diversity (π) using the Jukes and Cantor (1969) correction, and results of neutrality tests.

nucleotide diversity index behaved in a similar way except for the mtSSU marker: though four times as many specimens of *Z. resinae* as *S. difformis* were included in their respective analyses, *S. difformis* showed slightly higher values than *Z. resinae*. Haplotype diversity values were comparable among species and markers, although *S. coeloplata* 2 consistently showed lower values. However, these results must be interpreted with caution due to the uneven number of studied specimens for each species: for example, *Z. resinae* incorporated three to eight times more individuals in the analyses than the remaining species. Neutrality tests gave significant negative values of Fu's *Fs* in *S. coeloplata* 1 and *Z. resinae* based on nuITS data (Table 4.2), indicating a population expansion. Negative values of Tajima's *D* and Fu's *Fs* were also obtained for the same species as well as *S. difformis* using the nuLSU dataset; however, these were not statistically significant. Tajima's *D* tests of mtSSU data generated positive values for all species, but these were not significant as well.

Tokogenic relationships among the 48 nuITS haplotypes of *Zythia resinae* revealed no geographic structure as haplotypes from North America, Northern/Central Europe and Eastern Asia were widespread across the network (Fig. 4.5A). Identical haplotypes were shared among widely distant regions: (a) North America and Eastern Asia; and (b) North America, the whole of Europe, and the Macaronesian islands. The two studied New Zealand haplotypes were not closely related: whereas one was relatively close to a haplotype shared between North America and Eastern Asia, the other was linked to a haplotype shared between Northern/Central Europe and the Macaronesia. The Caribbean haplotype was close to a North American one. As for *Sarea s.lat.*, the network delimited the three considered species well (Fig. 4.5B). These showed differing levels of intraspecific diversity. For instance, haplotypes of *S. difformis* were separated from each other by a higher number of mutations than haplotypes of *S. coeloplata* 1 and 2. At the

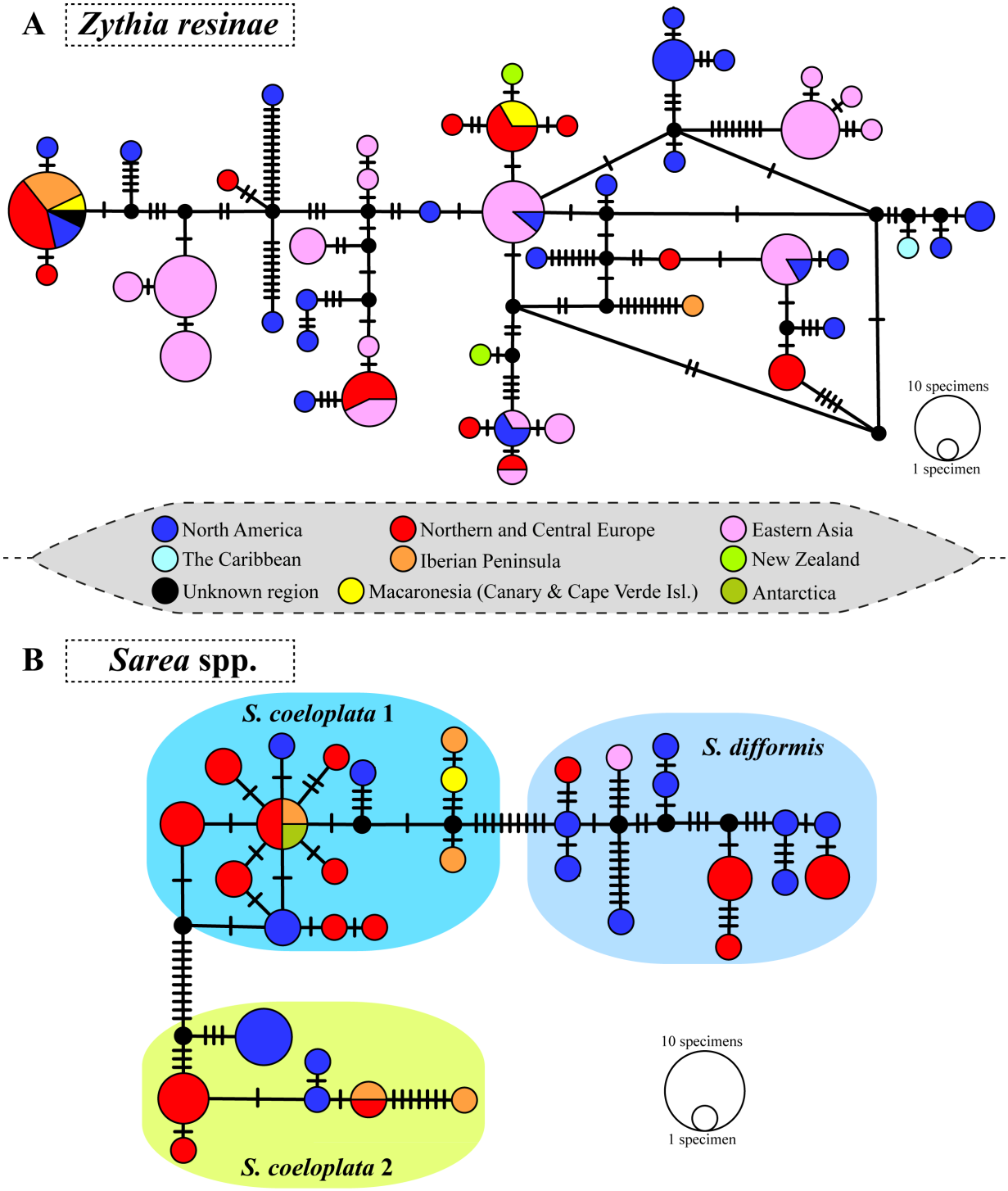


Figure 4.5. Statistical parsimony networks for *Zythia resinae* and *Sarea* spp. haplotypes. **A** *Zythia resinae*. **B** *Sarea* spp. Haplotypes were coloured according to the geographic origin of specimens (a legend is provided for reference). In B, a coloured box is used to delimitate each species within *Sarea*. The sizes of the circles in the networks are proportional to the numbers of individuals bearing the haplotype; black-filled smaller circles indicate missing haplotypes. Mutations are shown as hatch marks.

geographical scale, whereas haplotypes from many of the considered Northern Hemisphere regions were widespread across the network, we found no haplotypes shared between widely distant localities, except for an Antarctic haplotype shared with Northern/Central Europe and the Iberian Peninsula. These observations may also be due to the limited number of specimens studied compared to the scenario revealed for *Z. resinae*. Finally, in *S. coeloplata* 1 and 2, some Iberian Peninsula and Macaronesian haplotypes showed an increased number of separating mutations; further, *S. coeloplata* 1 haplotypes from these two regions were closely related.

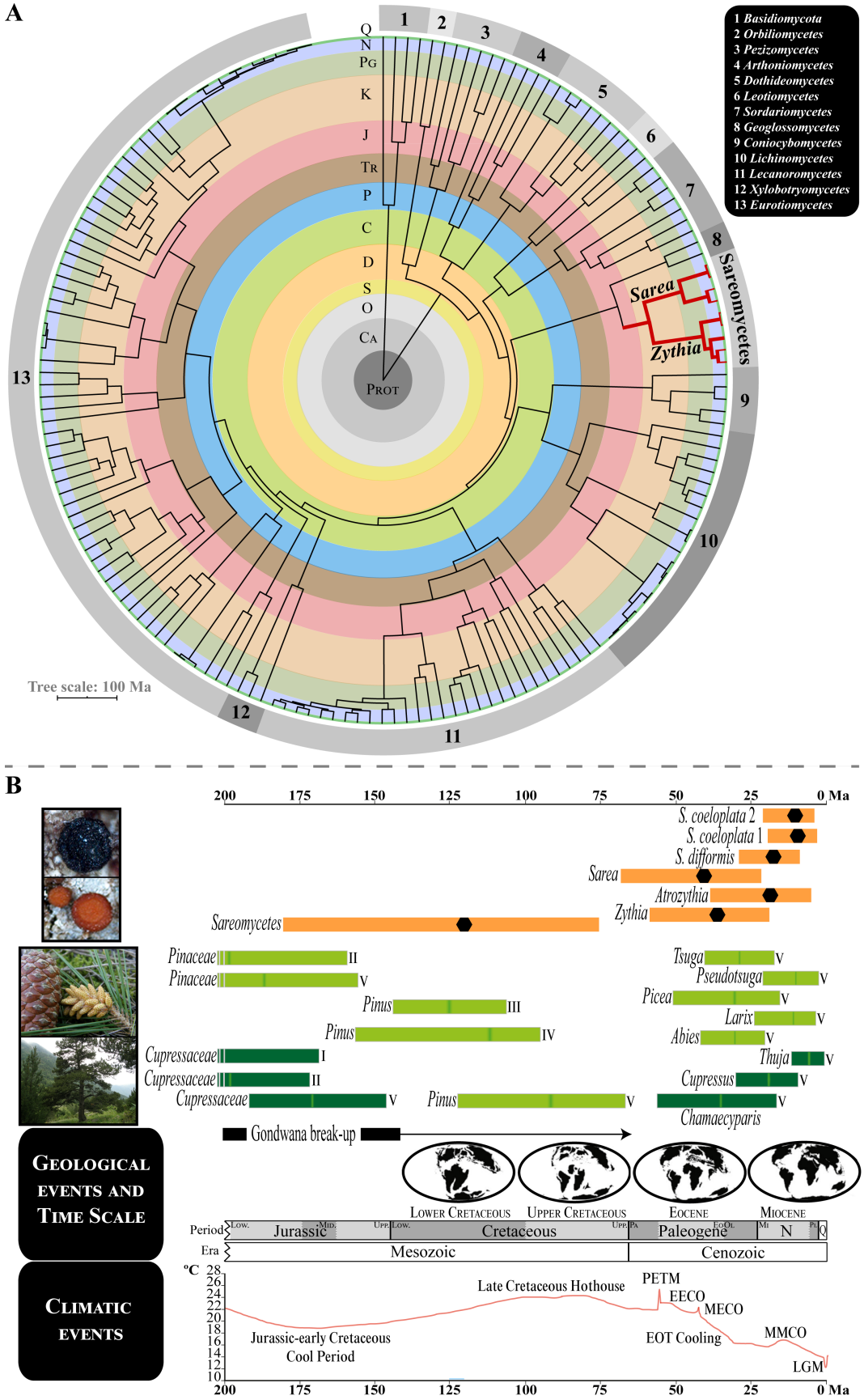
Subsection 4.4.5

Age Estimates for the Crown Nodes of *Sareomycetes* and Main Lineages Within

The maximum clade credibility (MCC) tree with 169 fungal taxa and divergence estimates obtained with BEAST showed posterior probabilities (PP) of 1.0 for all inner nodes except for the sister relationship between the clades allocating *Coniocybomycetes*+*Lichinomycetes* and *Lecanoromycetes*+*Xylobotryomycetes*+*Eurotiomycetes* that received a support of PP= 0.96 (Fig. 4.S6). The *Orbiliomycetes* and *Pezizomycetes* formed a clade at the base of *Pezizomycotina* which was dated back to 412.59 Ma (453–400 Ma, 95% HPD). This result is in agreement with the previous dating studies of Beimforde et al. (2014) and Pérez-Ortega et al. (2016). The class *Sareomycetes* was revealed to be sister to *Geoglossomycetes* with high support (PP= 1.0). The split between these two lineages might have occurred during the Middle Jurassic (*ca.* 168.20 Ma; 327.24–109.14 Ma, 95% HPD). The crown node of class *Sareomycetes* was dated to the Lower Cretaceous, *ca.* 120.88 Ma (181.35–75.76

Ma, 95% HPD) according to our six-locus dating using several fossils as calibration points; however, the use of alternative dating methods in our second step (see section "Inferring a Time Frame for The Diversification of *Sareomycetes*" in Materials and Methods above), which was based on a three-locus dataset, provided different time intervals for such an event (Fig. 4.6; Fig. 4.S7; Table 4.S5). Hence, median age estimates obtained with secondary calibrations drawn from our first, six-locus dating analysis generated similar time intervals as expected (*ca.* 149.37 to 114.81 Ma, Upper Jurassic-Lower Cretaceous), whereas the use of the *Erysiphales* and *Melanohalea* nuITS substitution rates shifted this temporal window towards more recent geological times (Upper Cretaceous-Eocene, *ca*. 72.87–53.1 Ma). We then drew the corresponding rate of evolution of the *Sareomycetes* nuITS from the posterior distribution of our three-locus analysis (first analysis in section "Inferring a Time Frame for The Diversification of *Sareomycetes*" in Material and Methods above) using the parameter *.rate* as reported in FigTree. The value was 1.269×10^{-3} s/s/Ma (minimum and maximum 95% HPD values: 8.528×10^{-5} and 3.075×10^{-3} s/s/Ma) which implies a slower rate of evolution for this region compared to estimates in the *Erysiphales* (2.52×10^{-3} s/s/Ma) and *Melanohalea* (3.41×10^{-3} s/s/Ma).

The five chronograms inferred for estimating a time frame for the diversification of *Sareomycetes* showed high posterior probabilities supporting relationships among the main lineages except for the sister relationship between *Sarea difformis* and *S. coeloplata* 1 (PP= 0.93–0.94). Similar to previous results, divergence ages obtained with *Erysiphales* and *Melanohalea* nuITS substitution rates generated much more recent time estimates (Table 4.S5). All in all, the origin and diversification of *Zythia*, *Atrozythia* and *Sarea* occurred during the Tertiary (Table 4.S5). Thus, the crown nodes of *Zythia* and *Sarea* were estimated in the Eocene-Miocene, whereas that of *Atrozythia* in the Oligocene-Miocene (Fig. 4.6). The split between the


A
1 Basidiomycota
2 Orbiliomycetes
3 Pezizomycetes
4 Arthoniomycetes
5 Dothideomycetes
6 Leotiomycetes
7 Sordariomycetes
8 Geoglossomycetes
9 Coniocybomycetes
10 Lichinomycetes
11 Lecanoromycetes
12 Xylobotryomycetes
13 Eurotiomycetes
Q
N
PG
K
J
TR
P
C
D
S
O
CA
PROT
Sarea
Zythia
Sareomycetes
Tree scale: 100 Ma
B
200 175 150 125 100 75 50 25 0 Ma
S. coeloplata 2
S. coeloplata 1
S. difformis
Sarea
Atrozythia
Zythia
Sareomycetes
Pinaceae II
Pinaceae V
Pinus III
Pinus IV
Cupressaceae I
Cupressaceae II
Cupressaceae V
Pinus V
Tsuga V
Pseudotsuga V
Picea V
Larix V
Abies V
Thuja V
Cupressus V
Chamaecyparis V
Gondwana break-up
GEOLOGICAL EVENTS AND TIME SCALE
LOWER CRETACEOUS
UPPER CRETACEOUS
EOCENE
MIOCENE
Period
Jurassic
Cretaceous
Paleogene
N
Era
Mesozoic
Cenozoic
CLIMATIC EVENTS
°C
Late Cretaceous Hothouse
PETM
EECO
MECO
EOT Cooling
MMCO
LGM
Jurassic-early Cretaceous Cool Period

←**Figure 4.6.** Dating analyses for *Sareomycetes*. **A** Circular time-calibrated MCC tree constructed in BEAST using a six-locus dataset and 169 fungal taxa, including representatives of main *Ascomycota* lineages and *Basidiomycota* (outgroup). The class *Sareomycetes*, comprising *Zythia* and *Sarea* in this analysis, is highlighted in red. Numbers on the chronogram perimeter designate different classes in *Ascomycota* (see legend on the upper-right corner). **B** The 95% HPD age intervals obtained in BEAST to frame in time the crowns of *Sareomycetes* and the three included genera and species; black hexagons represent median ages. Dating results were those obtained using the three-locus dataset and calibrating the crown node of *Sareomycetes* with a time estimate of 120.88 Ma (181.35–75.76 Ma, 95 % HPD) based on results of our six-locus dating analysis. 95% HPD age intervals for the crowns of different gymnosperm plant families and species are represented in boxes coloured with different shades of green (light green, *Pinaceae*; dark green, *Cupressaceae*). These were obtained from different studies: I (Mao et al. 2012), II (Lu et al. 2014), III (Saladin et al. 2017, FBDI approach), IV (Saladin et al. 2017, NDbl approach), and V (Leslie et al. 2018). Paleogeographic maps and climatic graph were drawn after Scotese (2002, 2016). Geological time periods in A and B are shaded and abbreviated as: Quaternary (Q), Neogene (N), Paleogene (PG), Cretaceous (K), Jurassic (J), Triassic (TR), Permian (P), Carboniferous (C), Devonian (D), Silurian (S), Ordovician (O), Cambrian (CA), and Proterozoic (PROT); epochs are abbreviated as PL (Pliocene), MI (Miocene), OL (Oligocene), and PA (Paleocene). PETM: Paleocene-Eocene Thermal Maximum (55.8 Ma), EECO: Early Eocene Climatic Optimum (54–46 Ma), MECO: Mid-Eocene Climatic Optimum (42 Ma), EOT: Eocene-Oligocene Transition (40–33 Ma), MMCO: Mid-Miocene Climatic Optimum (15–13 Ma), and LGM: Last Glacial Maximum (21,000 years ago).

two *Atrozythia* species (*A. klamathica* and *A. lignicola*) probably occurred during the Miocene. The crown nodes of the three *Sarea* species were placed in the Oligocene-Miocene. Finally, the different dating strategies estimated that intraspecific diversification in the three studied genera occurred < 10 Ma, in the Neogene and Pleistocene (Figs. 4.S8-4.S12).

Section 4.5

Taxonomy

Although the terms "holotype" and "lectotype" as defined in Article 9 of the *International Code of Nomenclature for algae, fungi, and plants* (ICN) (Turland et al. 2018) do not apply to names at ranks higher than species, they are used by analogy here to indicate type species of monotypic genera or type species selected by their authors and type species selected by later

authors, respectively (Art. 10, Note 1). All specimens have been identified by us unless otherwise indicated. Colour coding refers to Inter-Society Color Council (1976). Full data on additional specimens examined are given in Appendix B.

Sareomycetes Beimforde *et al.*, *Fungal Syst. Evol.* **6**: 29 (2020).

Sareales Beimforde *et al.*, *Fungal Syst. Evol.* **6**: 29 (2020).

Zythiaceae Clem., *Gen. Fung.*: 128 (1909).

= *Sareaceae* Beimforde *et al.*, *Fungal Syst. Evol.* **6**: 29 (2020).

Atrozythia J.K. Mitch., Quijada, Garrido-Ben. & Pfister, ***gen. nov.*** (MB838699).

Etymology: from the Latin for black (*ater*) and the genus name "*Zythia*," referring to the macroscopic resemblance to *Zythia* species, but with a dark coloration.

Diagnosis: Apothecia of *Atrozythia* differ from *Zythia* in their colour (black *vs*. orange) and from *Sarea* because of their white to light blue grey pruina. Paraphyses in *Atrozythia* are unbranched whereas those in *Sarea* are always branched or anastomose, at least in the basal cells. *Zythia* can have unbranched paraphyses but differs from *Atrozythia* in the amount and colour of lipid guttules, orange and abundant *vs*. yellowish and sparse, respectively. *Atrozythia* has a hyaline ectal and medullary excipulum that are sharply delimited by a narrow dark brown pigmented layer; in *Zythia* there is no brown pigmented layer between these layers. In *Sarea* the medullary excipulum is always differentiated by its dark brown colour.

Holotype species: *Atrozythia klamathica* J.K. Mitch. & Quijada 2021

Description: *Sexual morph*: see description for *Atrozythia klamathica* below. *Asexual morph*: see description of *Arthrographis lignicola* in Sigler & Carmichael, *Mycotaxon* **18**: 502-505 (1983). *Notes*: This genus currently encompasses two species, both apparently uncommon or under-collected, with one known only in an apothecial morph and the other only in a hyphomycetous asexual morph. Both are found on dead or living conifers; there are some indications of a resinicolous habit in the type species, *A. klamathica*, but additional information is needed to elucidate the ecology of these fungi. In our phylogenetic analyses, the affinities of this group apparently lie closer to *Zythia* than to *Sarea*, but *Atrozythia* species are located on a relatively long branch compared to these two genera. There are apparently no closely matching, unnamed environmental sequences on GenBank assignable to this genus, possibly suggesting rarity rather than merely being overlooked.

Atrozythia klamathica J.K. Mitch. & Quijada ***sp. nov.*** (MB838700).

Etymology: Named after the collection locality of the holotype, Klamath National Forest.

Diagnosis: See generic diagnosis above.

Type: **USA**: *California*: Siskiyou County, Klamath National Forest, southwest side of Forest Route 17N11, 41°50'03.6" N 123°25'42.1" W, 566 m a.s.l., apothecia on resinous wounds of living young *Chamaecyparis lawsoniana*, 12 Dec. 2017, *J.K. Mitchell JM0068* (FH 00965406 – holotype).

Description: *Sexual morph* apothecial. *Apothecia* discoid to cupulate, scattered, erumpent from the resin, consistency coriaceous and ascomata slightly shrunken when dry, but expanding and fleshy when moist, 0.7–1.2 mm diam, to 1 mm high, subsessile to short-stipitate (0.1–0.3 × 0.2–0.3 mm), stipe narrower toward the base. *Disc* concave to plane, round or somewhat irregular by

internal growing pressure, smooth or slightly wrinkled, black (267.black) to dark greyish brown (62.d.gy.Br), with or without light white (263.White) to light blue grey (190.l.bGray) coating pruina; margin distinct, raised when immature but not protruding beyond the hymenium when mature, 0.5–1 mm thick, entire and smooth or radially cracked, concolourous with hymenium and usually pruinose. *Receptacle* concolourous with hymenium and margin, strongly roughened, more heavily pruinose, pruina extending downward on the stipe, anchoring hyphae surrounding the receptacle from base of stipe to lower flank and rarely at margin; pruina can be lost during development and is usually more frequent in immature apothecia. *Asci* (103–)131–158(–166) × (27.5–)29.5–36.5(–40.5) µm, cylindric-clavate, multispored, mature asci 35–50 µm below the hymenial surface prior to spore discharge, ascus dehiscence rostrate, inner wall material expanding, protruding *c*. 40–50 µm, reaching the hymenial surface at spore discharge; apex hemispherical, thick-walled, strongly staining in CR, apex with an apical chamber, apical wall 3–5 µm thick, chamber later disappearing and apical tip thickening, becoming 10–15.5 µm thick, projecting into the ascus, becoming dome-like, with intermediate morphologies also observed, inner wall not or faintly amyloid, outer wall intensely amyloid; lateral walls 1–3.5 µm thick, asci covered with an amyloid gel layer; base arising from a perforated crozier. *Ascospores* 1.8–2.3 µm diam, globose to subglobose, hyaline, inamyloid, aseptate, wall slightly thick and with one eccentric medium grey (265.med.Gy) lipid guttule. *Paraphyses* embedded in a thick, hyaline layer of gel, cylindrical, uninflated to medium clavate, straight or slightly wavy, terminal cell (5.5–)6.5–9(–11.5) × 2–3.3(–4.5) µm, covered by a strong yellowish brown (74.syBr) to deep yellowish brown (78.d.yBr) amorphous exudate, lower cells (6.5–)8.5–11 × 2–3 µm, basal cells (12.5–)14.5–18(–20.5) × 1.5–2 µm, simple, unbranched, hyaline, septate, septa strongly staining in CR, basal cells ± equidistantly septate, terminal and lower cells shorter, walls smooth, sparse

tiny yellow grey (93.yGray) lipid guttules throughout, from the basal to terminal cells. *Excipulum* composed of two differentiated layers sharply delimited, *ectal excipulum* strongly gelatinised, (111–)127–165(–192) µm thick at lower flank and base, (32–)48–124(–132) µm thick at margin and upper flank, constituted of three layers; *innermost layer* of moderately packed *textura intricata* immersed in a pigmented gel, strong brown (55.s.Br) to dark brown (59.d.Br), with sparse dark greyish yellow (91.d.gy.Y) refractive amorphous lumps; *middle layer* with loosely packed hyaline cells, strongly gelatinised, parallel to each other (sometimes interwoven) and oriented perpendicular to the outer surface, *outermost layer* with shorter, parallel and very tightly packed cells without intercellular spaces, walls pigmented and surrounded by a strong brown (55.s.Br) to dark brown (59.d.Br) amorphous exudate, cortical layer irregular and black (267.Black). *Individual cells* at middle layer of ectal excipulum (5–)6.5–9(–10) × 2–3.5 µm at margin, (6.5–)8.5–12(–15.5) × 2–3 µm at lower flank and base, cell walls 0.5–1.5(–3.5) µm thick. *Medullary excipulum* of slightly gelatinised *textura intricata*, tightly packed, cells neither with intercellular spaces nor particular orientation, (10–)12.5–16.5(–19) × 2–3(–3.5) µm. *Asexual morph* unknown.

Notes: This species is known from two specimens (of which the holotype was sequenced twice) and is illustrated in Fig. 4.3. It was probably also observed once in Alaska (Goff 2020), but no specimen was collected. Little is known about its ecology or possible asexual morphs. Sequence and morphological data are sufficient to separate it from *Sarea* and *Zythia*, and it shows a closer affinity to the latter. Although apparently collected only twice, it is possible (given the rarity with which *Sarea difformis* is found on cupressaceous hosts) that *A. klamathica* is the fungus which was isolated as an endophyte of cupressaceous plants in central Oregon and reported as *S. difformis* (Petrini and Carroll 1981) but due to the lack of detailed data in the report, that

supposition can neither be confirmed nor refuted. Culture work with fresh material should be done.

Additional material studied: see Appendix B.

Atrozythia lignicola (Sigler) J.K. Mitch., Garrido-Ben. & Pfister ***comb. nov.*** (MB838701).

≡ *Arthrographis lignicola* Sigler, *Mycotaxon* **18**: 502 (1983).

Holotype: UAMH 4095, Canada: Alberta: Division No. 13, Westlock, dried culture isolated from conifer wood chips and bark from a logging truck, Feb. 1978, leg. L. Sigler [isol. 14 Feb. 1978] (not seen); Ex-type cultures: ATCC 52699, CBS 689.83, IFM 52650, IMI 282334, UAMH 4095.

Description: *Sexual morph* unknown. *Asexual morph* fully described in the protologue (Sigler and Carmichael 1983).

Notes: Although hyphomycetes producing arthroconidia are thus far unknown as asexual morphs among members of the *Sareomycetes*, sequence data generated independently on four separate occasions from ex-type strains place this species as congeneric with *Atrozythia klamathica* (Murata et al. 2005; Kang et al. 2010; Giraldo et al. 2014; Saar 2018). This relationship with *Sareomycetes* has also been suggested in previous phylogenetic analyses (Giraldo et al. 2014). The species has been found both in North America (Sigler and Carmichael 1983; Wang and Zabel 1990; Lumley et al. 2001) and in Europe (Metzler 1997; Arhipova et al. 2011, as '*Arthrographis pinicola*'). No sexual morph is known, and as with its congener, *A. lignicola* appears to be rarely found and recognised.

Sarea Fr., *Syst. orb. veg.* **1**: 86 (1825), *nom. sanct.* (Fries, *Elench. fung.* **2**: 14, 1828).

Lectotype species: *Peziza difformis* Fr., *nom. sanct.* (designated by Hawksworth & Sherwood 1981: 358).

= *Coniothyrium* subgen. *Epithyrium* Sacc., *Syll. fung.* **10**: 268 (1892).

Lectotype species: *Coniothyrium resinae* Sacc. & Berl. (designated by Sutton 1980: 625).

≡ *Epithyrium* (Sacc.) Trotter, *Syll. fung.* **25**: 249 (1931).

= *Biatoridina* Schczedr. *nom. inval.* (Art. 40.1), *Bot. Zhurn. (Moscow & Leningrad)* **49**: 1315 (1964).

Description: *Sexual morph* apothecial. *Apothecia* black, erumpent from the resin, discoid, roundish to ellipsoid, coriaceous to fleshy, sessile with broad attachment; hymenium and tissues in section purple or brown, turning blue or without change in KOH. *Asci* clavate, multispored, dehiscence rostrate, apex hemispherical, thick-walled, ascus apex staining strongly in CR, with an apical chamber and thin apical wall, chamber later disappearing and apical tip thickening, projecting into the ascus, becoming dome-like, inner wall not or faintly amyloid, outer wall intensely amyloid and covered with an amyloid gel, base short-stipitate with a crozier. *Ascospores* globose to subglobose, hyaline, inamyloid, aseptate, wall slightly thick and with one lipid guttule. *Paraphyses* embedded in gel, cylindrical, uninflated to slightly clavate, straight or slightly bent at the apex, terminal cell covered by a dark brownish amorphous exudate, lower cells and basal cells hyaline and containing tiny yellowish lipid guttules; branched, usually bifurcate, septa strongly staining in CR, basal cells ± equidistantly septate, but lower and terminal cells shorter, walls smooth. *Excipulum* at margin and upper (-lower) flank composed of two well-delimited layers, ectal and medullary excipulum at lower flank to base not always differentiated, tissues strongly gelatinised. Ectal excipulum with loosely packed cells running

parallel to each other and surrounded by hyaline or brownish gel, frequently bifurcated and oriented perpendicular to the outer surface, cortical layer of shorter, parallel, and very tightly packed cells covered by a dark brown to black amorphous exudate. Medullary excipulum of moderately packed *textura intricata*, cells gelatinised, gel dark brown, becoming lighter in the subhymenium. *Asexual morph* pycnidial; see descriptions of *Epithyrium* and *E. resinae* in Sutton (1980: 625-626) and *Sarea difformis* in Hawksworth & Sherwood (1981: 361-362).

Notes: The genus *Sarea* here is restricted to the group of species resembling the type, *S. difformis*. The two remaining species detected are morphologically indistinct but see notes under *Sarea coeloplata*.

No obvious morphological differences were detected among the (infrequently encountered) asexual morph of sequenced *Sarea* specimens; as a result, we retain all previously synonymised names with asexual type species as synonyms of *S. difformis*.

Sarea difformis (Fr.) Fr., *Elench. fung.* **2**: 14 (1828).

≡ *Peziza difformis* Fr., *Syst. Mycol.* **2**(1): 151 (1822), *nom. sanct.* (Fries, *l.c.*).

Neotype: K(M), Germany: Bavaria: im Wald bei Sugenheim, an Fichten [*Picea* sp.] auf ausgeflossenem Harze, 1871, leg. H. Rehm [*Ascomyceten* no. 577] (examined and designated by Hawksworth & Sherwood 1981: 366);

Isoneotypes: FH 00995483, FH 01093951.

≡ *Patellaria difformis* (Fr.) Schwein., *Trans. Amer. Philos. Soc.,* n.s. **4**(2): 236 (1832) [1834].

≡ *Lecidea difformis* (Fr.) Nyl. *nom. inval.* (Art. 36.1), *Observ. Peziz. Fenn.*: 68 (1868).

≡ *Tromera difformis* (Fr.) Arnold, *Flora* **57**(6): 85 (1874).

≡ *Lecidea difformis* (Fr.) Nyl. ex Vain. *nom. illegit.* (Art. 53.1), *Meddeland. Soc. Fauna Fl. Fenn.* **2**: 65 (1878).

≡ *Biatorella difformis* (Fr.) Vain., *Meddeland. Soc. Fauna Fl. Fenn.* **10**: 143 (1883).

≡ *Biatora difformis* (Fr.) Willey, in Tuckerman, *Syn. N. Amer. Lich.* **2**: 130 (1888).

≡ *Biatorella difformis* (Fr.) H. Olivier *comb. superfl.* (Art. 6.3), *Mem. Real Acad. Ci. Barcelona,* [n.s.] **11**(15): 264 (1914).

≡ *Biatorina difformis* (Fr.) Kirschst., *Ann. Mycol.* **36**(5/6): 378 (1938).

= *Tromera sarcogynoides* A. Massal. *nom. inval.* (Art. 35.1), *Flora* **41**(31): 507 (1858).

≡ *Tromera myriospora* var. *sarcogynoides* (A. Massal.) Kremp. *nom. inval.* (Art. 35.1), *Denkschr. Königl.-Baier. Bot. Ges. Regensburg* **4**(2): 228 (1859).

≡ *Tromera myriospora* f. *sarcogynoides* (A. Massal.) Anzi *nom. inval.* (Art. 35.1), *Lich. Rar. Langob. Exs.* **7**: 267B (1862).

= *Lecidea resinae* f. *minor-denigrata* Nyl., *Lich. Lapp. Orient.*: 185 (1866).

= *Coniothyrium resinae* Sacc. & Berl., *Atti Reale Ist. Veneto Sci. Lett. Arti,* ser. 6 **3**(4): 739 (1885) [1884-1885].

Holotype: PAD, Hb. Saccardo, Italy: Veneto: horto Patavino, in resina dejecta uda, leg. D. Saccardo (examined by Hawksworth, *Persoonia* **9**(2): 194 (1977)).

≡ *Clisosporium resinae* (Sacc. & Berl.) Kuntze, *Revis. gen. pl.* **3**(3): 458 (1898).

≡ *Lichenoconium resinae* (Sacc. & Berl.) Petr. & Syd., *Repert. Spec. Nov. Regni Veg. Beih.* **42**(3): 436 (1927).

≡ *Epithyrium resinae* (Sacc. & Berl.) Trotter, *Syll. fung.* **25**: 250 (1931).

= *Biatoridina pinastri* Schczedr. *nom. inval.* (Art. 40.1), *Bot. Zhurn. (Moscow & Leningrad)* **49**(9): 1315 (1964).

Description: *Apothecia* discoid, roundish to ellipsoid, scattered, or gregarious, erumpent from the resin, consistency coriaceous and apothecia slightly to moderately contracted when dry, expanding and fleshy when moist, 0.2–1.3 mm diam, to 0.5 mm high, sessile, entirely black (267.Black). *Disc and receptacle* rough; margin distinct, slightly raised when immature or dry but not protruding from the hymenium after rehydration, 0.5–1 mm thick, rough or radially cracked, concolourous with hymenium and receptacle. *Hymenium* and tissues in section light purple (222.l.P) to deep purple (219.deepP), pigments turning brilliant blue (177.brill.B) to deep blue (179.deepB) in KOH. *Asci* (34–)46.5–53.5(–78) × (9.5–)12.5–14.5(–18.5) µm, clavate, multispored, mature asci 10–30 µm below the hymenial surface prior to spore discharge, ascus dehiscence rostrate, inner wall material expanding, protruding *c*. 9–15 µm, reaching the hymenial surface at spore discharge; apex hemispherical, thick-walled, strongly staining in CR, apex with an apical chamber, apical wall 2-3.5 µm thick, chamber later disappearing and apical tip thickening, becoming 7-11 µm thick, projecting into the ascus, becoming dome-like, inner wall not or faintly amyloid, outer wall intensely amyloid; lateral walls 0.5–1.5 µm thick, asci covered with an amyloid gel layer; base short-stipitate and arising from a crozier. *Ascospores* (1.7–)2.1–2.3(–3) µm diam, globose to subglobose, hyaline, inamyloid, aseptate, wall slightly thick and with one eccentric medium grey (265.med.Gy) lipid guttule. *Paraphyses* embedded in gel, cylindrical, uninflated to slightly clavate, straight or slightly curved at the apex, terminal cell (4–)6–7.5(–11.5) × 1.5–2.5(–3) µm, covered with a deep brown (59.d.Br) to brown black (65.brBlack) amorphous exudate, lower cells (4.5–)7.5–8.5(–11.5) × 1.5–2.5 µm, basal cells (6.5–)9–10(–12) × 1.5–2.5 µm, bifurcate in lower cells, hyaline, septate, septa strongly staining

in CR, basal cells ± equidistantly septate, but lower and terminal cells shorter, walls smooth, sparse tiny yellow grey (93.yGray) lipid guttules in all cells. *Excipulum* at margin and upper (-lower) flank composed of two well differentiated layers, lower flank to base not always differentiated into two types of tissues. *Ectal excipulum* strongly gelatinised, (41–)57–67(–92) µm thick at lower flank and base, (28–)49–60(–86) µm thick at margin and upper flank, cells loosely packed and surrounded by a light greyish brown (60.l.gy.Br) to medium brown (58.m.Br) gel, running parallel each other (sometimes interwoven), frequently bifurcated and oriented perpendicular to the outer surface, cortical layer with shorter, parallel and very tightly packed cells without intercellular spaces, walls strongly pigmented and surrounded by a dark brown (59.d.Br) to brown black (65.br.Black) amorphous exudate. *Ectal cells* (6.5–)10–12.5(–18.5) × 1.5–3 µm at upper flank and margin, (7–)11–13.5(–25.5) × 1–2.5 µm at lower flank and base, cell walls 0.5–1.5(–2) thick. *Medullary excipulum* of textura intricata, cells moderately packed and gelatinised, gel dark brown (59.d.Br.) to brown black (65.brBlack), becoming lighter in the subhymenium, cells (6.5–)10–12(–20.5) × (1.5–)2.5–4 µm.

Notes: The concept of *Sarea difformis* is here restricted to those specimens presenting a purple pigment in the hymenium which turns blue when a strong base is applied, a character clearly visible in one isoneotype (FH 00995483) and illustrated in Fig. 4.1. The other isoneotype housed in FH (FH 01093951) is quite poor, with only 2-3 intact apothecia; as a result, only a macromorphological examination was conducted of that specimen.

Additional material studied: see Appendix B.

Sarea coeloplata (Norman) J.K. Mitch., Garrido-Ben. & Quijada, ***comb. nov.*** (MB838702).

≡ *Biatorella coeloplata* Norman, *Öfvers. Kongl. Vetensk.-Akad. Förh.* **41**(8): 32 (1884).

Lectotype: TROM L-565247, Norway: Buskerud: prope Drammen ad Gulskoven [= Gulskogen], leg. J.M. Norman (**designated here**, MBT 395923); Isolectotype: MICH 62597 (MBT 395924).

?= *Tympanis abietis* P. Crouan & H. Crouan, *Fl. Finistère*: 43 (1867).

Holotype: CO, Hb. Crouan, France: Finistère, sur la partie rugueuse de l'écorce d'un sapin [*Abies* sp.] abattu, à la base des ergots, leg. P.M. Crouan & H.M. Crouan (examined by Le Gal 1953: 131).

≡ *Retinocyclus abietis* (P. Crouan & H. Crouan) J. W. Groves & D. E. Wells, *Mycologia* **48**: 869 (1957) [1956].

= *Biatorella coeloplata* f. *carbonata* Norman, *Öfvers. Kongl. Vetensk.-Akad. Förh.* **41**(8): 32 (1884).

Lectotype: TROM L-565247, Norway: Buskerud: prope Drammen ad Gulskoven [= Gulskogen], leg. J.M. Norman (**designated here**, MBT 395927).

Description: *Apothecia* macroscopically like *Sarea difformis*, sometimes larger, to 1.5 mm diam. Hymenium and excipulum in section light greyish brown (60.l.gy.Br) to dark greyish brown (62.d.gy.Br) and not changing to blue in KOH. *Asci* (30.5–)42.5–45.5(–62.5) × (11.5–)16–17.5(–22.5) µm. *Ascospores* 1.7–2.5 µm diam, morphology indistinguishable from *S. difformis*. *Paraphyses* cylindrical, uninflated to slightly clavate, straight or slightly bent in upper cells, terminal cell (4–)5.5–6(–8.5) × 1–3 µm, covered by a greyish brown (61.gy.Br) to deep brown (59.d.Br) amorphous exudate, terminal cell of lower cells (4–)5.5–6.5(–9.5) × 1–3 µm, terminal cell of basal cells (4.5–)7–8.5(–11.5) × 1–2.5 µm, branched, usually dichotomously and with

connections close to terminal cell, but also below, in lower cells and basal cells; all other morphological features like *S. difformis*. *Ectal and medullary excipulum* morphology like *S. difformis*, but differing in colour, light greyish brown (60.l.gy.Br) to dark greyish brown (62.d.gy.Br), ectal excipulum (23.5–)51.5–60(–78) µm thick at lower flank and base, (12.5–)34–44.5(–71) µm thick at margin and upper flank, mostly with strong differentiation in the colour of ectal and medullary cells, being hyaline and surrounding by a colourless gel unlike *S. difformis* which is brownish. *Ectal cells* (5–)7–10.5(–20) × 2–3.5 µm at upper flank and margin, (5–)7–9(–12.5) × 1.5–3.5 µm at lower flank and base, cell walls 0.5–1(1.5) µm thick. *Medullary cells* (3.5–)8–11.5(–19.5) × 1.5–3.5 µm.

Notes: A specimen collected by Norman at the type locality and stored under the name *Biatorella coeloplata* in TROM is here designated the lectotype. Norman (1884) described a form, *Biatorella coeloplata* f. *carbonata*, for older apothecia; we use a single specimen to lectotypify this form as well as the species. Since it is clear that even Norman considered the two forms merely different developmental stages of the same fungus, we see no reason to consider this form a separate taxon.

The holotype of *Tympanis abietis* was not available for examination from CO. Its true affinities are unclear, but Le Gal's (1953) statement "L'hyménium est plongé dans une matière brunâtre qui en agglutine les éléments" in her description of the holotype likely place it in one of the two clades we assign to *S. coeloplata s. lat.*; morphological re-examination of the type should be conducted to verify this placement.

The description above applies to both *Sarea coeloplata* 1 and *Sarea coeloplata* 2 as presented in our phylogenetic analyses. We have been unable to separate the two morphologically, and thus we cannot assign the examined type to one clade or the other. We

have observed morphological variations among collections (Fig. 4.1) and are confident that the difficulty of characterizing the members of these two clades may be overcome by careful analyses involving DNA and morphological examination of single apothecia. This will avoid the problem of mixed collections. For more information, see our discussion of mixed collections below.

Additional material studied: see Appendix B.

Zythia Fr., *Syst. orb. veg.* **1**: 118 (1825).

Lectotype species: *Sphaeria resinae* Fr. (designated by Clements & Shear 1931: 372).

= *Tromera* A. Massal. *nom. inval.* (Art. 38.1), *Flora* **41**(31): 507 (1858).

= *Tromera* A. Massal. ex Körb., *Parerga lichenol*: 453 (1865).

Holotype species: *Lecidea resinae* Fr.

≡ *Retinocyclus* Fuckel, *Jahrb. Nassauischen Vereins Naturk.* **25-26**: 332 (1871) [1871-2].

Lectotype species: *Lecidea resinae* Fr. (designated by Hawksworth & Sherwood 1981: 358).

= *Pycnidiella* Höhn., *Sitzungber. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Cl., Abt. 1* **124**(1-2): 91 (1915).

Lectotype species: *Cytospora resinae* Ehrenb. (designated by Clements & Shear 1931: 372).

Description: *Sexual morph* apothecial. *Apothecia* brilliant orange-yellow (67.brill.OY) to deep orange (51.deepO), erumpent from the resin, discoid to cupulate, roundish or slightly ellipsoid, coriaceous and darker when dry, fleshy and lighter after rehydration, hymenium and receptacle

concolourous, margin usually differentiated and protruding slightly beyond the hymenium; sessile with broad attachment, sub-stipitate to prominently stipitate. Hymenium and tissue colours not changing in KOH. *Asci* and *ascospores* exhibiting morphology and reactions as in *Sarea*. *Paraphyses* cylindrical, uninflated to slightly or moderately clavate, straight or bent at the apex, completely surrounded by gel that contains hyaline or grey yellow (90.gy.Y) amorphous lumps, all cells with a high amount of brilliant orange-yellow (67.brill.OY) to vivid orange-yellow (66.v.OY) lipid guttules; terminal cell and 1–2 cells below covered by medium yellow (87.m.Y) rough amorphous exudate; usually branched at apical cells or cells below, rarely unbranched, frequently with anastomoses, septa frequently constricted and equidistantly septate with terminal and lower cells shorter (moniliform). *Excipulum and medulla* not well differentiated in section, although two layers can be noted mostly from the margin to the flanks because of the arrangement of cells and amount of pigments. *Ectal excipulum* in lower flank to margin strongly gelatinised, pigmented due to a high amount of brilliant orange-yellow (67.brill.OY) to vivid orange-yellow (66.v.OY) lipid guttules or not pigmented, cells moderately packed and running parallel to each other and surrounded by hyaline gel sometimes including hyaline or grey yellow (90.gy.Y) amorphous lumps, cortical layer with shorter, parallel or unoriented, tightly packed cells without intercellular spaces, amorphous rough exudate covering the cortical cells, hyaline or coloured between deep orange-yellow (72.d.OY) to brown orange (54.brO), usually more abundant at the margin, sometimes even appearing as glassy processes. Amyloid reaction present mostly in the ectal excipulum at the margin and flanks, or absent. *Medullary excipulum* composed of *textura intricata*, cells changing from ectal excipulum to medulla progressively, hyaline, less spaced and gelatinised; subhymenium somewhat similar or differentiated from medulla because of the presence of pigmented lipid guttules, cells without

intercellular spaces and without gel. *Asexual morph* pycnidial; see descriptions of *Pycnidiella* and *P. resinae* (Ehrenb.) Höhn. in Sutton (1980: 544) and *Sarea resinae* in Hawksworth & Sherwood (1981: 365).

Notes: The history of typification in the genus *Zythia* is somewhat complicated. This is due both to the sparse protologue and apparent confusion among some authors as to whether or not Fries' *Sphaeria resinae* had been a combination of Ehrenberg's *Cytospora resinae*. This has been discussed at length in a recent publication on the matter (Mitchell and Quijada 2020).

Zythia resinae (Ehrenb.) P. Karst., *Meddeland. Soc. Fauna Fl. Fenn.* **14**: 104 (1887) [1888].

≡ *Cytospora resinae* Ehrenb., *Sylv. mycol. berol.*: 28 (1818); *nom. cons. prop.*

Syntypes: B 700016297 & HAL 3029 F, [Germany: Berlin], Hasenheide & Grunewald, leg. C.G. Ehrenberg (seen by Braun, *Schlechtendalia* **30**: 19 (2016), but see Mitchell & Quijada 2020).

≡ *Tubercularia resinae* (Ehrenb.) Thüm., *Oesterr. Bot. Z.* **30**(10): 313 (1880).

≡ *Knyaria resinae* (Ehrenb.) Kuntze, *Revis. gen. pl.* **2**: 856 (1891).

≡ *Pycnidiella resinae* (Ehrenb.) Höhn., *Sitzungber. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Cl., Abt. 1* **124**(1-2): 91 (1915).

= *Sphaeria resinae* Fr., *Observ. mycol.* **1**: 180 (1815), *nom. sanct.* (Fries, *Syst. mycol.* **2**(2): 453, 1823).

Lectotype: UPS F-541757, Sweden: leg. E.M. Fries, *Scleromyceti Sueciae* 37 (examined and designated by Hawksworth & Sherwood 1981: 366; *typ. cons. prop.* for *Cytospora resinae* (proposed by Mitchell & Quijada, 2020)); Isolectotype: FH 00964792.

≡ *Nectria resinae* (Fr.) Fr., *Summa veg. Scand.* **2**: 388 (1849).

≡ *Nectriella resinae* (Fr.) Sacc., *Syll. fung.* **2**: 451 (1883).

≡ *Dialonectria resinae* (Fr.) Cooke, *Grevillea* **12**(64): 109 (1884).

= *Lecidea resinae* Fr., *Observ. mycol.* **1**: 180 (1815).

Lectotype: H 951143/H-ACH 431 B, Sweden, leg. E.M. Fries (examined and designated by Hawksworth & Sherwood 1981: 366).

≡ *Peziza resinae* (Fr.) Fr., *Syst. mycol.* **2**(1): 149 (1822); *nom. sanct.* (Fries, *l.c.*).

≡ *Lecidea resinae* (Fr.) Nyl. *comb. superfl.* (Art. 6.3), *Mém. Soc. Imp. Sci. Nat. Cherbourg* **3**: 183 (1855).

≡ *Biatorella resinae* (Fr.) Th. Fr., *Lich. arct.*: 199 (1860).

≡ *Biatorella resinae* (Fr.) Mudd *comb. superfl.* (Art. 6.3), *Man. Brit. lich.*: 191 (1861).

≡ *Biatoridium resinae* (Fr.) Uloth, *Ber. Oberhess. Ges. Natur-Heilk.* **11**(4): 95 (1865).

≡ *Tromera resinae* (Fr.) Körb., *Parerga lichenol.*: 453 (1865).

≡ *Pezicula resinae* (Fr.) Fuckel, *Jahrb. Nassauischen Vereins Naturk.* **23-24**: 279 (1870) [1869-70].

≡ *Biatora resinae* (Fr.) Tuck., *Gen. lich.*: 169 (1872).

≡ *Sarea resinae* (Fr.) Kuntze, *Revis. gen. pl.* **3**(3): 515 (1898).

≡ *Peziza myriospora* Hepp *nom. illegit.* (Art. 52.1), *Die Flechten Europas* **6**: 332 (1857).

≡ *Tromera myriospora* (Hepp) Anzi *comb. inval.* (Art. 35.1), *Cat. lich. Sondr.*: 117 (1860).

≡ *Peziza myriosperma* Hepp *nom. illegit.* (Art. 52.1), *Abbild. beschr. spor., Synonymen-Register I-XII*: 13 (1860).

≡ *Retinocyclus flavus* Fuckel *nom. illegit.* (Art. 52.1), *Jahrb. Nassauischen Vereins Naturk.* **25-26**: 332 (1871) [1871-2].

= *Tromera xanthostigma* A. Massal. *nom. inval.* (Art. 35.1), *Flora* **41**(31): 507 (1858).

≡ *Tromera myriospora* var. *xanthostigma* (A. Massal.) Kremp. *nom. inval.* (Art. 35.1), *Denkschr. Königl.-Baier. Bot. Ges. Regensburg* **4**(2): 228 (1859).

≡ *Tromera myriospora* f. *xanthostigma* (A. Massal.) Anzi *nom. inval.* (Art. 35.1), *Lich. Rar. Langob. Exs.* **7**: 267A (1862).

= *Peziza resinae* var. *stipitulata* P. Karst. *nom. inval.* (Art. 38.1), *Fungi Fenniae Exsiccati* **4**: 324 (1866).

= *Tromera resinae* var. *stipitulata* P. Karst., *Acta Soc. Fauna Fl. Fenn.* **2**(6): 154 (1885).

Lectotype: FH 01093952, [Finland: Kanta-Häme:] Mustiala, Dec., leg. P.A. Karsten, *Fungi Fenniae Exsiccati 324* (**designated here**, MBT 395925).

≡ *Biatorella resinae* var. *stipitulata* (P. Karst.) Boud., *Hist. classific. discomyc. Europe*: 157 (1907).

Description: See description above for *Zythia* and notes below.

Notes: The status of the basionym of *Zythia resinae* is somewhat confused, with authors treating *Cytospora resinae* either as a new name or as a new combination of Fries' *Sphaeria resinae*. Examination of the protologue (Ehrenberg 1818) shows no references, direct or indirect, to Fries' earlier name, and Ehrenberg explicitly includes his species in the index of new species and

attributes it to himself ("mihi"); we thus accept this as having been a *species novum*. It is desirable to conserve *Cytospora resinae* with the same type as *Sphaeria resinae* (UPS F-541747) because these names are: (1) almost always treated as synonyms, (2) share the same epithet (and thus will demand a replacement name for one if they are taken out of synonymy and included in the same genus), and (3) are likely indistinguishable based on morphological features. This conservation has been formally proposed by Mitchell and Quijada (2020).

We do not provide an additional description for *Z. resinae* here since at present it is the only accepted species in this genus, and our description of the genus serves as a description of this broadly-defined species. It has been noted, however, that collections in our phylogenetic analyses do exhibit morphological variation, some visible in Fig. 4.2. Examples of this variation were found in the excipular tissues, *i.e.*, a slightly amyloid reaction in the excipulum of specimens in clade 8 (Fig. 4.2, j2), specimens with sessile apothecia in clades 3, 6 and 9 (Fig. 4.2, e1, i1, m1) *vs*. stipitate apothecia in clades 5 and 12 (Fig. 4.2, h1, k1), specimens with a strongly pigmented cortical layer in clades 2 and 3 (Fig. 4.2, f2, e2), an almost hyaline ectal excipulum in clades 1, 6 and 12 (Fig. 4.2, g2, i2, k2), ectal excipulum with high content of pigments in clades 9 and 13 (Fig. 4.2, m2, l2) and margin with glassy processes in clade 12 (Fig. 4.2, k2) (clade names are from Fig. 4.S1). We also found examples of variation in the hymenium, *i.e.*, the presence of an additional thick amyloid gel layer in specimens in clade 3 (Fig. 4.2, e5), and paraphyses simple and not branched in the apical or lower cells in clades 6, 8 and 9 (Fig. 4.2, i9, j9, m9) *vs*. bifurcate or branched at apical cell in clades 2, 3, 6 and 12 (Fig. 4.2, f9, e9, l9, k9). We have not separated species within what is almost certainly a complex of many species because of questions of the prevalence of mixed collections and our inability to examine type

material of *Lecidea resinae*. For additional information, see our discussion of mixed collections and species diversity below.

Additional material studied: see Appendix B.

Subsection 4.5.1

Excluded Species: *Lecidea tantilla* and Isonyms

The invalid (Art. 35.2) names "*Lecidea tantilla* Nyl." and "*Lecidea resinae var. tantilla* Nyl.", which are, paradoxically, cited with the same protologue (Nylander 1857a), have historically been considered synonyms of *Sarea difformis*. Two specimens matching the original description were found in H (H-NYL 19509/H9510278 and H-NYL 21581/H9510242) and examined; both proved to be typical *Strangospora pinicola*. The name was accepted and validly published at species level by Leighton in 1871; four of the nine specimens he cites were found in K (Leighton 1871). Of these, the authors were able to examine three prior to herbarium closures due to the ongoing global pandemic (K(M)263364, K(M)263365, and K(M)263366). Two of these were *S. pinicola*, and one specimen was *Strangospora moriformis*. Based on these studies, we propose the following synonymies:

Strangospora pinicola (A. Massal.) Körb., *Parerga lichenol.*: 173 (1860).

= *Lecidea tantilla* Nyl. *nom. inval.* (Art. 35.2), *Actes Soc. Linn. Bordeaux, sér. 3* **21**: 363 (1857) [1856].

= *Lecidea resinae* var. *tantilla* Nyl. *nom. inval.* (Art. 35.2), *Actes Soc. Linn. Bordeaux, sér. 3* **21**: 363 (1857) [1856].

= *Lecidea tantilla* Nyl. ex Leight., *Lich. Fl. Gr. Brit.*: 354 (1871).

Lectotype: K(M)263366, [United Kingdom: England: West Midlands,] Shropshire, Wilcot[t], 12 May 1871, leg. W.A. Leighton (**designated here**, MBT 395926).

≡ *Biatorella tantilla* (Nyl. ex Leight.) H. Olivier, *Mem. Real Acad. Ci. Barcelona,* [n.s.] **11**(5): 8 (264) (1914).

Subsection 4.5.2

Misapplied Names

The specimen issued as "*Lecidea resinae* Fr." under number 277 of Leighton's *Lichenes Britannici Exsiccati* (FH 00964658) is *Biatoridium monasteriense*, which had not been described at the time of issue (Leighton 1858). Mudd (1861), citing this and other specimens, described *Z. resinae* as having a green thallus, brown apothecia, a thin margin, ellipsoid spores, and having been collected on elms (*Ulmus* sp.). None of these traits characterise any species in *Sareomycetes*. That his conception of *Z. resinae* was incorrect and at least partly based on *B. monasteriense* is confirmed by Magnusson's examination and reidentification of one of Mudd's specimens in the Rehm herbarium (Magnusson 1935). Mudd (1861) also described the new variety *Biatorella resinae* var. *rubicundula*, which has been accepted as being an synonym of a *Strangospora* species (Fries 1874; Rehm 1889); unfortunately, type material could not be located at K or BM for examination (Angela Bond & Gothamie Weerakoon, pers. comm.). Many subsequent authors refer to specimens cited or issued by Mudd and Leighton (Crombie 1870; Leighton 1872, 1879; Smith 1926), perpetuating this error.

A similar case to the preceding arose in Southern California around the turn of the twentieth century. Hasse reported *Z. resinae* from the area three times, first in a publication by McClatchie (1897), then in two of his own (Hasse 1898, 1908). He describes the substrate of the specimens as bark, and in the last publication describes the species with black apothecia turning brown when moist, and without margins. These features are all uncharacteristic of species in *Sareomycetes*. Examination of a specimen labelled "*Lecidea (Biatora) resinae* Fr." (*i.e.*, *Zythia resinae*) sent by Hasse to George Knox Merrill (FH 00964657) revealed that it was a specimen of *Strangospora moriformis*. Additionally, the collecting information matches that given in his 1898 publication, suggesting that this is the specimen he based that report on. An additional Farlow Herbarium specimen (FH 00480746) matches the collecting information and description of the 1908 publication and was originally determined by Hasse as "*Biatorella resinae* (Fr.)" (*i.e.*, *Zythia resinae*) but later changed by him to "*Biatorella moriformis* (Ach.) Th. Fr." (*i.e.*, *Strangospora moriformis*) with the later identification confirmed by an annotation by Magnusson. These specimens, along with his description, suggest that his concept of *Z. resinae* was at the time partly or completely based on *S. moriformis*, but that he later realised his error. By 1913, Hasse removed *Zythia resinae* from his list of Southern California lichens entirely (Hasse 1913).

Section 4.6

Discussion

Subsection 4.6.1

Species Diversity

The number of species in *Sarea s.lat.* (*i.e.*, *Sareomycetes*) has long been a matter of discussion. Hawksworth and Sherwood (1981) traced the idea of there being only a single species for both black and orange fungi to Johann Hepp's (1857b: Tab. 37 Fig. 1) superfluous name *Peziza myriospora*, noting that he designated two forms ("a" being orange and "b" being black); in the printed *Synonymen-Register* (p. 13) to vols. I–XII, however, he used the name "*Peziza myriosperma* Hepp" which may have been a *lapsus*, but similarly must be treated as validly published but superfluous as it refers back to no. 332 (Hepp 1860); this name is missing from *Index Fungorum*. If this was a mistake, the mistake was repeated with the publication of the printed *Synonymen-Register* (p. 16) to vols. I-XVI (Hepp 1867). Hepp's designation of these two forms is presumably in the boxed set of the exsiccata (Sayre 1969) as we could not find them in either an example of the unbound exsiccata (FH 00964656), the specimen from the Patouillard Herbarium (FH 00964655), or those Lee Davies (pers. comm.) examined in K(M); each contains a single specimen, and the labels make no mention of colour or forms. A *Sarea* species dominates in both specimens in FH, and Hepp cited "*Synon. Peziza et Lecid. Resinae Fries*" (*i.e. Zythia resinae*) as a synonym of his proposed new name; it is likely that he considered both orange and black fungi to be a single species (Hepp 1857a, b). Consideration of the orange and black apothecia as representing a single species carried into the 20th century (Nylander 1857b, 1866; Koerber 1865; Leighton 1872; Fink 1935). As stated by Hawksworth and Sherwood (1981), the orange and black fungi, each treated as a single species, rested in separate genera (for *Z. resinae*, *Biatorella*; for *S. difformis*, *Retinocyclus*) for much of the 20th century. Based on morphological similarities, they were then united in a single genus, *Sarea*, where they stood as two separate species, easily differentiated by colour, although they noted that the differences in

iodine reactions and the different asexual morphs "might be considered possible grounds for separation at the generic level" (Hawksworth and Sherwood 1981).

The current study employed integrative taxonomy (Goulding and Dayrat 2016; Haelewaters et al. 2018; Lücking et al. 2020) to assess the number of species in *Sareomycetes*. In addition to two species in the new genus *Atrozythia*, one previously undescribed and one not previously recognised as a relative of this group, it was determined that the black and orange fungi deserve to each be treated in separate genera. However, species concepts in *Zythia* and *Sarea* cannot be assessed straightforwardly. The phylogenetic structure combined with the distribution of the internal clades in Fig. 4.4 strongly suggests that cryptic speciation is occurring in both genera, with at least five and four species in *Sarea* and *Zythia*, respectively. The black fungi are recognised as the core genus *Sarea* and are conservatively interpreted here as three phylospecies and two morphospecies based on tree topology and the combined ABGD-BFD species delimitation approach. *Sarea difformis*, the type species of the genus, is quite distinctive and specimens are easily identifiable based on the purple pigment in the hymenium and (sometimes) stipe that turns blue in application of strong base (*e.g.*, Fig. 4.1, g1-5). The remaining morphospecies and two phylospecies represent *Biatorella coeloplata*, here combined as *Sarea coeloplata*; the type could not be assigned to a single phylospecies due to issues addressed in our discussion of mixed collections. The existence of cryptic speciation is even more evident in the orange fungi, which are recognised in the genus *Zythia* and are provisionally retained as a single species, *Zythia resinae*. The results of morphological and ABGD analyses together with the phylogenetic structure observed in Fig. 4.4 indicate, however, that there are likely many species. The least conservative estimates in our ABGD analyses suggested the existence of up to 24 or 52 putative species, which in our opinion represent inflated estimates, as

is often the case when non-distance based methods for species delimitation are used, such as those that use tree branch lengths or the coalescent (*e.g.* Bayesian Poisson Tree Processes (bPTP) and Generalized Mixed Yule Coalescent (GMYC) models; Pons et al. 2006; Zhang et al. 2013). In contrast, the ABGD solutions involving 6 or 10 species are more in accordance with the phylogenetic structure represented in Fig. 4.4. Given the contradictions between the different approaches, and due to inability to examine the type specimen of *Lecidea resinae* and the issues caused by mixed collections, we refrain from formally proposing and naming any new species in *Zythia*. Our adoption of this much more conservative vision of species diversity in *Zythia* aims at avoiding falsely circumscribing entities that do not represent actual species, even if it implies failing to recognise clearly delimited entities (Miralles and Vences 2013; Carstens et al. 2013).

Furthermore, it may happen that the well supported clades observed in Figs. 4.4 and 4.S1 merely represent geographic structure of the *Sarea* and *Zythia* datasets. Both genera are widely distributed in Europe, North America, Asia, and Africa, with *Z. resinae* also present in Australasia (Hawksworth and Sherwood 1981; Gadgil and Dick 1999; Beimforde et al. 2020). Records from the Southern Hemisphere almost certainly represent anthropogenic introductions, but the Northern Hemisphere distribution is still broad. Similar broad distributions are known in other taxa, and although they can suggest cryptic speciation (Zhong and Pfister 2004; Stadler et al. 2014; Lücking et al. 2014, 2017; Skrede et al. 2017; Tanney and Seifert 2019), it is not always the case (Pringle et al. 2005; Quijada et al. 2016; Liu et al. 2017; Baral et al. 2018). In addition to the broad geographic range, *Sareomycetes* species are found on the resin of a wide variety of host species. *Sarea* species are found on the resin of seven genera in *Pinaceae* and *Z. resinae* is found on twelve or thirteen genera in *Cupressaceae* and *Pinaceae* (see Table 4.S6).

This broad host range is again not necessarily indicative of cryptic diversity (Johnston and Park 2005; Baral et al. 2018), but is suggestive (Herrera et al. 2015; Martinović et al. 2016; Pärtel et al. 2017). Finally, published nuITS sequences assignable to the *Sareomycetes* are variable at levels greater than the standard 3% threshold for species delimitation in fungi (Izzo et al. 2005; Ciardo et al. 2006; Blaalid et al. 2013; Geml et al. 2014; Gweon et al. 2015), and greater than even the genus threshold (5.7% difference) suggested for filamentous fungi in a recent study (Vu et al. 2019). While such thresholds are known to not be constant across kingdom Fungi and thresholding is not an ideal way to delimit species (Nilsson et al. 2008; Kõljalg et al. 2013; Lücking et al. 2020), this is also suggestive of cryptic diversity.

Subsection 4.6.2

Biogeography and Host Specificity

Little to no phylogeographic pattern in the studied *Sareomycetes* species is recovered in our analyses. This may be due to the fact that conifers in *Pinaceae* and *Cupressaceae* have been widely introduced around the world for ornamental and commercial purposes (Farjon 2017). We hypothesise that a number of *Sareomycetes* strains have been distributed worldwide, travelling on the resin of hosts or as endophytes. The most obvious example is the introduction of *S. coeloplata* 1 to Antarctica reported in a study of the wood decay fungi on huts dating from the early 20th century (Held et al. 2003; Arenz et al. 2006). This fungus presumably was inhabiting the pinaceous timber brought to build the Discovery Hut on Ross Island (77° S), during the Discovery Expedition (1901–04). Our haplotype network suggests that the origin of that strain was in Northern or Central Europe, where the countries supplying materials for these expeditions

are located. The persistence of this species over the course of a century is perhaps an indication of how easy it would be to accidentally introduce these fungi to a new area. Another clear and relatively recent introduction is that of both *Zythia resinae* and *S. coeloplata* 1 to Cape Verde (reported in this study). Since no conifers are native to Cape Verde, we can again be sure that this is a case of human introduction (Hansen and Sunding 1993; Arechavaleta Hernández et al. 2005; Farjon 2017); *Pinus* spp. and *Cupressus* spp. have been widely introduced to Cape Verde (Frahm et al. 1996). At least two haplotypes of *Zythia resinae* and *Sarea coeloplata* 1 from Macaronesia (Cape Verde and the Canary Islands) are identical, or closely related, to haplotypes from the Iberian Peninsula. This makes sense since these archipelagos have close historical relationships with Spain and Portugal. The reports of *Zythia resinae* from New Zealand almost certainly represent a third instance of anthropogenic introduction. *Pinaceae* and *Cupressaceae* are the only families known to host fungi in *Sareomycetes*; of these families, only two species in *Cupressaceae* are native to New Zealand (De Lange and Rolfe 2010), but all reports of *Zythia* are from *Abies*, *Pinus*, and *Pseudotsuga*, in *Pinaceae* (Gadgil and Dick 1999; Beimforde et al. 2020). A final apparent indicator of ease of transmission through wood projects are a series of seven nuITS sequences uploaded to GenBank and misidentified as '*Hormococcus conorum*' and '*Zythia pinastri*' (NCBI, NLM, Bethesda (MD) 2020a, b, c, d, e, f, g). Since these are part of a project titled "Imported wood products to United States as vectors for potential invasive fungal species," it may be surmised that these were generated from imported wood products. On the other hand, the almost complete lack of genetic structure in the geographic distributions of species and the extensive geographic distribution in the Northern Hemisphere of some genetic lineages may be also due to long-distance dispersal of minute spores by wind, or even migratory birds, which use coniferous trees as perches in their migration routes (Hallenberg and Küffer

2001; Muñoz et al. 2004; Wilkinson et al. 2012; Viana et al. 2016). Based on age estimates for the divergence among closely related haplotypes in all *Sareomycetes* species, intercontinental dispersal of lineages could have occurred during the Quaternary (< 2.59 Ma), and this could have been concomitant with events of population expansion, as suggested by neutrality test results in the nuITS and nuLSU markers. Larger datasets assembled with a population-genetics scope are needed to evaluate these hypotheses. Nevertheless, there are exceptions to this general pattern, since seven clades in total contain only specimens from relatively restricted, and sometimes sympatric, ranges: one from the eastern USA (*Zythia resinae* clade 13 in Fig. 4.S1), one from New England (*Z. resinae* clade 5 in Fig. 4.S1), one from the Pacific Slope (*Atrozythia klamathica*), and three from Japan (*Z. resinae* clades 2, 4, & 7 in Fig. 4.S1). Without broader sampling, particularly in Asia and Africa, and considering all available environmental sequences, it is difficult to determine if these are truly lineages of limited range, or a sampling artifact.

Likewise, there is little overall pattern of host specificity, except perhaps at the host family level. This might be expected, since resin composition is broadly similar within each conifer family (Langenheim 2003; Lambert et al. 2005) but still varies among species (Lambert et al. 2007) and even varies within a single species (Tappert et al. 2011). If there is a pattern of specificity even at family level, it appears not to hold for all species. For example, *Sarea coeloplata* 1 was found growing on *Thuja occidentalis* (ACD0147) in addition to a number of species in *Pinaceae*. Similarly, *Zythia resinae* clade 8 (in Fig. 4.S1) encompasses primarily specimens on *Pinaceae*, but also a specimen found growing on *Cupressus forbesii* (JM0077), and the two known specimens of *Atrozythia klamathica* are from hosts in different families. Although this could be explained by a complete lack of host specificity, an alternative explanation is that different strains/species in *Sareomycetes* in some way selectively grow on

resin containing or lacking certain components. Production of specific resin components need not mirror evolutionary relationships (Tappert et al. 2011), so what currently appears random may still contain a hidden pattern. Nonetheless, there are clades suggestive of host specificity at the host generic or specific level, even if most clades are found on mixed hosts. *Zythia resinae* clade 4 (in Fig. 4.S1) contains only samples found associated with *Chamaecyparis obtusa*. *Zythia resinae* clade 5 (in Fig. 4.S1) and an unnumbered clade appearing only in our three-gene and mtSSU analyses appear to be found only on *Chamaecyparis* spp. and *Cupressus* spp., respectively. Perhaps significantly, each of these clades also shows a fairly restricted geographic pattern, noted above, and each of these clades is among the least well-sampled, supported groups in our phylogeny. Wider, more robust sampling could change the pattern seen. Ultimately, a more detailed understanding of the specific ecology of species in *Sareomycetes* is needed to generate and test hypotheses regarding host specificity.

Our dating analyses provide additional insight into host specificity in *Sareomycetes* at the temporal scale (Fig. 4.6). The results of our dating analyses match well with estimates of the diversification of the tree host genera of these fungi. Our estimate of 120.88 Ma (181.35–75.76 Ma, 95 % HPD) for the crown node of *Sareomycetes* places the origin of this group concurrent with or after the origins of *Cupressaceae* and *Pinaceae* in the Cretaceous Period (Mao et al. 2012; Lu et al. 2014; Leslie et al. 2018), and roughly concurrent with the origin of the genus *Pinus* in the Jurassic Period (Saladin et al. 2017; Leslie et al. 2018). This suggests that the *Sareomycetes* evolved to exploit the new niche of resin provided by *Pinus* or another, now extinct taxon (Smith et al. 2017; Leslie et al. 2018). The origins of the genera *Atrozythia*, *Sarea*, and *Zythia* and subsequent diversification in *Sarea* (specific estimates given in Table 4.S5) also correspond well with a later period of diversification of host genera in *Cupressaceae* and

Pinaceae of these fungi in the Cenozoic Era (Leslie et al. 2018). This occurred during and following a period of global cooling (Scotese 2016) together with some of the last important geological events, including Cenozoic orogenies, which influenced the worldwide distribution of conifers. Close evolutionary histories among fungi and their hosts are well known in several parasitic and ectomycorrhizal fungal clades (Takamatsu 2013; Sánchez-Ramírez et al. 2017; Looney et al. 2020)

Subsection 4.6.3

Mixed Collections

An unexpected complicating problem was uncovered during these investigations. Prior to this study, authors have noted that both *Sarea* and *Zythia* species can be found growing on the same piece of resin (Hawksworth and Sherwood 1981; Spier and Aptroot 2000; Yatsyna 2017). This was noted in our study of specimens: *Atrozythia klamathica* was found growing alongside *Zythia resinae* (JM0068), and *Z. resinae* was found growing with *Sarea difformis* (*e.g.*, PV-D863), *S. coeloplata* 1 (*e.g.*, ACD0147), and *S. coeloplata* 2 (*e.g.*, IGB316). Less obviously, it was discovered that multiple clades of *Z. resinae* or species of *Sarea* can be found mixed in a single collection. This was first seen when sequencing multiple loci for specimen BHI-F779. An initial DNA extraction, PCR, and sequencing yielded sequences matching *Z. resinae* clade 1; a subsequent round of sequencing from the same collection yielded sequences matching *Z. resinae* clade 13. Later, *S. difformis* was detected living alongside *S. coeloplata* 1 (*e.g.*, JM0072) and *S. coeloplata* 2 (*e.g.*, JM0011). This ability to share substrate with closely related species, while ecologically interesting, poses serious challenges to the identification of morphological

synapomorphies and matching them with the corresponding phylogenetic clade. Given the frequency with which we have found mixed collections, it cannot be excluded that some of the specimens we sequenced and examined morphologically contain mixes of *S. coeloplata* 1 and 2 or mixes of multiple *Z. resinae* clades. This could account for the lack of consistent morphology observed during our investigations of these species and informs our decision to not name these clades.

Based on our experience, future investigation of this family should be conducted by extracting DNA, examining micromorphology, and performing culture work from single apothecia. While this can be a challenge, given that apothecia are typically <1 mm in diameter, we feel that this is the only reliable way of accurately characterizing this group of fungi.

Subsection 4.6.4

Morphological Observations

Colour changes in sections

We observed that microtome cut sections of *Zythia resinae* stored out of light in dried gum arabic solution on glass slides for a period of several months showed a marked degradation of pigment. Only the high concentration of pigments in the ectal excipulum and in the epithecium remained evident. A similar pattern was observed in sections permanently mounted in glycerine. In addition to colour loss, the encrusting layer over the ectal excipulum and the epithecium was found to dissolve, further altering morphological characters of the fungus.

Such changes posed a challenge to morphological examination, since they create artificial morphological patterns that differ from those seen in recent or fresh material, or even in

fungarium material. For these reasons, to accurately assess pigment-related and other morphological characters, we recommend that any morphological examination of *Zythia* species be done on newly sectioned material rather than material sectioned by previous investigators and stored on glass slides or mounted.

Ascus dehiscence

Previous authors have reported the asci of *Sareomycetes* as “lecanoralean” (*i.e.*, “rostrate") and “not functionally bitunicate" (Hawksworth and Sherwood 1981; Nash et al. 2008) or of the broadly defined "archaeascé" type (Letrouit-Galinou 1973). Our observations indicate that all three genera, and *Atrozythia* in particular, have ascus dehiscence characterised by a rupture of the outer layer at the tip of the ascus and protrusion of an inner wall. The inner wall extends some distance beyond the outer wall, varying among species. This agrees with the electron microscopic examination of a *Sarea* species performed by Bellemère (1994). It is not clear in our observations whether there is any zone of full wall separation between the inner and outer layers; we thus agree with the view that this is the "rostrate" type of ascus dehiscence (Eriksson 1981; Bellemère 1994a).

Subsection 4.6.5

Ecology

Are fungi in Sareomycetes *lichenised?*

The controversy regarding the ecology of species in *Sarea* and *Zythia* is long-standing; they have often been thought of as lichens. This is reflected in the taxonomy of the synonymous

names. This idea goes back to Fries' original publication, in which he placed *Zythia resinae* in the lichen genus *Lecidea* and included the phrase "*crusta tenuissima membranacea contigua cinerascenti*" apparently describing a lichen thallus (Fries 1815). Hawksworth and Sherwood (1981) provided evidence that he had corresponded regarding its possible lichen nature with his colleague, the eminent lichenologist Erik Acharius whom he much respected as the last student to defend his thesis before Linnaeus. Since Fries' time, various authors have included *Sarea* and *Zythia* species among the lichenised fungi (Arnold 1858; Tulasne and Tulasne 1861; von Krempelhuber 1861; Nylander 1866; Vainio 1883; Fink 1935; Tucker and Jordan 1979; Etayo 1996; Purahong et al. 2017). A number of other authors were vaguer. Hepp (1857a) included an unnumbered, mixed specimen of *Zythia resinae* and a *Sarea* sp. in his exsiccata, *Die Flechten Europas*. His opinion of whether it was a lichen or fungus, however, is obscured by the fact that the specimen was provided as an example of something easily confused with the black-apothecial lichen he included as number 332 ('*Calicium inquinans γ. sessile*'). Other authors referred to species in *Sareomycetes* as intermediate between lichens and fungi, sometimes placing them in named groups (*e.g.,* "Lichenes ambigua," "Lichenes parasitici," "Pseudolichenes," "Hybridolichenes," and "Fungilli lichenoides") (Anzi 1860; Fries 1860; Koerber 1865; Ohlert 1870; Lettau 1912). One of the more unusual cases is that of Cappelletti (1924), who stated that *S. difformis* could be found both lichenised and non-lichenised in different samples. This situation is known in some fungi (Wedin et al. 2004, 2006), but that Cappelletti reported this relationship in several resinicolous fungi casts doubt on his observations. Additionally, the concepts of some authors accepting species in *Sareomycetes* as lichens have been based on incorrectly identified material; (see sections “Excluded Names" and "Misapplied Names" above). Other mycologists and lichenologists, including the majority of

modern authors, treat species in *Sareomycetes* as non-lichenised. We accept them as non-lichenised fungi.

Are fungi in Sareomycetes *parasitic?*

The occurrence of these fungi on resinous wounds has inevitably raised the question of whether they are parasitic (Kujala 1950; Groves and Wells 1956; Malençon 1979; Hawksworth 1981; Suto and Kanamori 1990). This question has been investigated by attempting to satisfy Koch's postulates, with varying results. The first of these was conducted by Ayers (1941), who used one of his cultures of *Z. resinae* to attempt to infect *Pinus strobus*; he saw no effect. Researchers in the then-north-western-USSR used inoculation studies to investigate a disease of pines. They called the fungus they identified as the causal agent "*Biatoridina pinastri*," which they proved was the asexual morph of a *Sarea* species (Shchedrova 1964, 1965). In a broad study of conifer associated discomycetes, Smerlis (1973) concluded that *Z. resinae* was mildly pathogenic, producing cankers on every pinaceous host tested. An inoculation study conducted in the 1980s to determine the cause of a disease of *Pinus koraiensis* in north-eastern China also found no evidence of infection by *Z. resinae* and identified the true causal agent, *Tympanis confusa* (Sūn et al. 1983; Cuī et al. 1984; Xiang et al. 1985; Xiang and Song 1988; Kobayashi et al. 1990). A similar study in Japan on a disease of *Pinus thunbergii* gave the same results; inoculations with *Z. resinae* produced no symptoms, but inoculations with a species of *Ascocalyx* did (Kobayashi and Kusunoki 1985; Kobayashi and Zhao 1989). Additional studies to determine the causal agent of the resinous stem canker of *Chamaecyparis obtusa* determined that *Z. resinae* did not cause symptoms on hosts in *Pinaceae* or *Cupressaceae*, and identified the causal agent as *Cistella japonica* (Hayashi and Kobayashi 1985; Yokozawa et al. 1986, 1989; Suto 1987, 1992,

1997, 1998; Kobayashi et al. 1990). The varying results and generality of these tests leave unresolved the question of pathogenicity of species in *Sareomycetes*; some authors assume pathogenicity and others accept a saprobic lifestyle, as summarised by Beimforde et al. (2020).

Fungi in Sareomycetes *as endosymbionts of photosynthetic organisms*

Other aspects of the ecology of species in *Sareomycetes* have been established with more certainty. These fungi have frequently been isolated as endophytes of conifers in *Pinaceae* (Petrini and Fisher 1988; Kowalski and Kehr 1992; Giordano et al. 2009; Koukol et al. 2012; Arhipova et al. 2015; Sanz-Ros et al. 2015; U'Ren and Arnold 2016; Marmolejo Monciváis 2018) and *Cupressaceae* (Petrini and Carroll 1981; Suto and Ougi 1999; Sieber 2007). This pattern is consistent with previous studies that have shown both saprobes and parasites living within their potential hosts (Fisher and Petrini 1992; Kogel et al. 2006; Oses et al. 2008). Somewhat more unusually, species in *Sareomycetes* have also been isolated as endophytes of grasses (Sánchez Márquez et al. 2008), mistletoes (Peršoh 2013), and possibly deciduous woody plants (Novas and Carmarán 2008). Apart from the *Pinus*-dwelling mistletoe, which presumably allows the fungus close access to the resin seeping from any wounds created by the mistletoe, the occurrence of these fungi in these various hosts is difficult to explain. A closer look at the cupressaceous endophytisms reveals a similarly difficult-to-explain pattern: a *Sarea* species was isolated (Petrini and Carroll 1981), but the current work represents the first report of a *Sarea* species sporulating on a cupressaceous host. Several studies have found *Sarea* and *Zythia* species living within thalli of foliose and fruticose lichens in Europe and Asia (Peršoh and Rambold 2012; NCBI, NLM, Bethesda (MD) 2018a, b; Masumoto and Degawa 2019; Yang et al. 2020). One group of researchers has apparently even recovered *Sarea coeloplata* 1 (identified as

Hormococcus conorum) associated with a marine alga, *Fucus vesiculosus*, in the Venetian Lagoon (NCBI, NLM, Bethesda (MD) 2013). Many questions about the ecology of this family remain.

The ecology of Atrozythia *species*

This uncertainty extends to our new genus, *Atrozythia.* Some cellulolytic capacity has been reported for *A. lignicola* (Sigler and Carmichael 1983), and the fungus has been recovered from both diseased (Sigler and Carmichael 1983) and dead/rotting wood (Sigler and Carmichael 1983; Wang and Zabel 1990; Metzler 1997; Lumley et al. 2001; Arhipova et al. 2011) of *Pinus* and *Picea* (although the possibility of isolation from *Populus tremuloides* by Lumley et al. (2001) cannot be excluded entirely). Additional study is needed to determine if *A. lignicola* is resinicolous, since all other members of *Sareomycetes* seem to be, or if it has some other lifestyle. *Atrozythia klamathica*, known thus far from only two specimens, was found fruiting directly on the resin of *Chamaecyparis lawsoniana* and *Tsuga heterophylla*; it presumably shares a similar ecology with other members of *Sareomycetes*.

Subsection 4.6.6

Taxonomic Placement

The placement of species in *Sareomycetes* in the fungal tree of life has had a long and confused history, which we attempt to elucidate here with more details than Beimforde et al. (2020). In the late nineteenth century authors grouped species generally among the fleshy discomycetes (Crouan and Crouan 1867; Cooke 1871; Saccardo 1889) and more specifically

with *Dermateaceae* (Karsten 1885; Saccardo 1889) or *Patellariaceae* (Fuckel 1871), or among the lichenised fungi in *Lecideaceae*, allied with *Biatora* (Tuckerman 1872; Stein 1879). A number of mycologists between 1889 and 1934 (starting with Rehm) placed species among the *Patellariaceae* (see Table 4.S7). Researchers later placed species variously in *Lecanorales* and *Helotiales*, or declined to place them; for instance, the first (and several subsequent) edition(s) of the *Dictionary of the Fungi, Retinocyclus* is listed as belonging with the lichen fungi or in *Helotiales*, and *Sarea* as being of uncertain placement (Ainsworth and Bisby 1943, 1950). Placement was stabilised in 1981, when Hawksworth and Sherwood, based on morphological similarities with *Agyrium rufum*, placed *Sarea* and *Zythia* in *Agyriaceae* (*Lecanorales*) (Hawksworth and Sherwood 1981). Subsequent molecular evidence indicated that *A. rufum* was unrelated to the remainder of *Agyriaceae* (Lumbsch et al. 2007; Lumbsch and Huhndorf 2010) and resulted in the move of *Sarea* and *Zythia* to *Trapeliaceae* (Hodkinson and Lendemer 2011). Not all authors followed these placements. In the course of an electron microscopical study of asci, Bellemère stated that the placement of both *S. difformis* and *Z. resinae* based on ascus ultrastructure was uncertain, and noted that the two species differed in their method of ascus dehiscence (Bellemère 1994b). This study must be considered with some caution, since the substrate of the *Z. resinae* specimen used was said to be stone, indicating that the specimen was likely misidentified. Schultheis et al. (2001) placed *Sarea difformis* under the heading "*Ascomycetes Incertae Sedis*". The application of molecular techniques was needed to properly place these taxa.

The history of the multiple publications attempting to elucidate the taxonomic position of these fungi using molecular data is outlined by Beimforde, et al. (2020). Reliance on these publications is likely the reason for uncertain placements or placements in *Leotiomycetes* by

several subsequent authors (Lumbsch et al. 2007; Kirk et al. 2008; Eriksson 2014; Hüseyin and Selçuk 2014; Miadlikowska et al. 2014; Garrido-Benavent 2015). Recently, use of information from six genes and sampling taxa throughout *Pezizomycotina* resulted in the erection of the new class *Sareomycetes* to accomodate *Sarea* and *Zythia* (Beimforde et al. 2020). This placement explains over two centuries of confusion and uncertainty.

Section 4.7

Conclusion

Our studies of species in *Sareomycetes* have revealed the existence of three genera, one described as new. *Sarea* is restricted to the group of species traditionally identified as *Sarea difformis*, but shown to be at least three phylospecies, *Sarea difformis s. str.*, with a purple hymenial pigment, and two cryptic species lacking such a pigment and identifiable morphologically with the type of *Biatorella coeloplata*, combined here as *Sarea coeloplata*. *Zythia* is resurrected for *Z. resinae* (syn. *Sarea resinae*), which is retained provisionally as a single, highly diverse species. *Atrozythia* and the new species *A. klamathica* are described, and a combination is made for *Arthrographis lignicola*. The family name *Zythiaceae* is resurrected as an earlier name for *Sareaceae*. This family displays few biogeographic patterns and little evidence of host specificity. It is shown to have arisen in the late Jurassic or Cretaceous; subsequent diversification occurred roughly concurrently with the diversification of *Cupressaceae* and *Pinaceae*. Further work on this family is recommended, including type studies on *Lecidea resinae* and *Tympanis abietis,* use of precise methodologies to study the two

phylospecies assignable to *S. coeloplata* and to split the *Zythia resinae* complex, and collection of the data required to do population genetic analyses at least for *Zythia*.

Section 4.8

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Section 4.9

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Chapter 5

Bisporella no more: species of a common genus of discomycetes belong in at least four genera in three families of *Leotiomycetes*

This chapter is coauthored by myself and Drs. Luis Quijada, Peter R. Johnston, and Donald H. Pfister.

Section 5.1

Abstract

Bisporella as typically conceived is a genus of noticeable, bright yellow inoperculate discomycetes. This interpretation of the genus, however, is at odds with *Bisporella pallescens*, the type species; furthermore, the genus has been interpreted as including the unusual species *Bisporella resinicola*. By comparing morphological and molecular traits of species traditionally included in *Bisporella*, we show that the genus is polyphyletic, with many "typical" members of the genus belonging instead in *Calycina*. *Bisporella pallescens* is conclusively linked with its anamorph, *Bispora antennata*, and the genus *Bisporella* is abandoned as a later synonym of the monotypic genus *Bispora* (*Helotiaceae*), previously applied only to anamorphic fungi. *Bisporella resinicola* is shown to represent an independent monotypic genus, *Eustilbum*, which so far is unplaced in Helotiales. '*Bisporella*' *subpallida* belongs in an unnamed genus in *Helotiaceae*, possibly related to '*Phaeohelotium*' *epiphyllum*.

Section 5.2

Introduction

In an ongoing review of resinicolous discomycetes, the authors came upon fungarium specimens and collected fresh material of the asexual and sexual states of an unusual fungus known only from conifer resin. This fungus is typically known by the names *Bisporella resinicola* or *Eustilbum aureum* (applied to the sexual and asexual states, respectively), but has a number of additional synonyms (Seifert and Carpenter 1987). The two states of this fungus have been conclusively linked through culture studies (Baranyay and Funk 1969; Seifert and Carpenter 1987), and it was noted that the morphology of both the sexual and asexual states of the fungus present unusual features for a species of *Bisporella*. To place this species taxonomically, we provide a review of the genus *Bisporella*.

Prior to its reinstatement almost half a century ago, the genus *Bisporella* included only the type species, *Bisporella monilifera* (= *Bisporella pallescens*) (Korf and Carpenter 1974); since its restoration, thirty-seven species have been placed in the genus (Korf and Carpenter 1974; Carpenter 1975, 1981; Svrček 1977; Dennis 1978; Beaton and Weste 1978; Carpenter and Dumont 1978; Stadelmann 1979; Korf 1982; Sharma and Korf 1982; Arendholz and Sharma 1983; Kirk and Spooner 1984; Raitviir and Sharma 1984; Korf and Bujakiewicz 1985; Seifert and Carpenter 1987; Holm and Nannfeldt 1990; Galán 1993; Lizoň and Korf 1995; Gamundí and Romero 1998; Zhuang et al. 2017). There are no published molecular data for the type species (*B. monilifera*/*pallescens*, www.ncbi.nlm.nih.gov/genbank/, accessed 27.ii.2020), and all of the species added to the genus have been combined or described based on perceived morphological similarities among species or due to genetic similarity to the other, sequenced species currently placed in the genus. The genus was considered easily recognized in the past because of its bright

or pallid yellow-orange, turbinate apothecia with a tough consistency that grow mostly on wood, the smooth receptacle concolorous with or slightly lighter than the hymenium. The genus was characterized microscopically by an outer ectal excipulum composed of thick-walled, *textura prismatica-angularis* to *oblita*, the hyphae of which are embedded in a gelatinous matrix, undulate, and run more or less parallel at an angle almost perpendicular to the outer surface; a medullary excipulum, usually composed of *textura intricata*; a cortical layer with or without protruding cells; 4-8-spored asci that are amyloid or not; aseptate or multiseptate ascospore with shapes that range from ellipsoid to fusoid; and cylindrical paraphyses (Korf and Carpenter 1974; Dennis 1978; Zhuang et al. 2017). The most recognizable and reported species is *Bisporella citrina*, with 10,677 records on GBIF (https://www.gbif.org/, accessed 19.viii.2020) and 1,843 observations on iNaturalist (https://www.inaturalist.org/, accessed 19.viii.2020); in contrast, the next most reported species (*Bisporella sulfurina*) has 1,708 records on GBIF and only 254 observations on iNaturalist (figures include synonyms). After these two, the next most reported species have 293 reports on GBIF (*B. subpallida*) and 20 observations on iNaturalist (*B. resinicola*); the type species of the genus has only 194 records on GBIF and 3 observations on iNaturalist. The frequencies with which these fungi have been encountered no doubt has colored the perception and circumscription of the genus, with most people basing their concept more on *B. citrina* and *B. sulfurina* rather than the type species *Bisporella monilifera* (= *Bisporella pallescens*). Furthermore, it is debated whether *B. citrina* and *B. sulfurina* belong in *Bisporella* at all. Baral et al. (2013) determined that, based on morphological and molecular data, several of the common species placed in *Bisporella*, including *Bisporella citrina*, *B. sulfurina*, *B. claroflava*, *B. discedens*, *B. drosodes*, *B. lactea*, and *B. scolochloae* were similar to the type of *Calycina*, *C. herbarum*, and thus were more appropriately treated in that genus. Both genera can

possess similar gelatinized ectal excipula but can be distinguished as follows: *Bisporella* spp. possess *Hymenoscyphus*-type apical rings and multiguttulate paraphyses, and *Calycina* spp. possess *Calycina*-type apical rings and paraphyses with elongate vacuolar bodies (Baral 1987). These placements were supported also by a later analysis (Baral and Rämä 2015). Accordingly Baral, in a later classification of *Leotiomycetes*, included only two species in *Bisporella,* treating the genus in *Helotiaceae* (Jaklitsch et al. 2016), and included *Calycina* in *Pezizellaceae*, a view that was maintained and further supported in a later expansion based on Baral's classification (Johnston et al. 2019). Many subsequent authors (Zheng and Zhuang 2015; Zhuang et al. 2017) and competing classifications (Wijayawardene et al. 2017; Ekanayaka et al. 2019) have apparently rejected this interpretation, and maintained *Bisporella* in the broad sense of Korf and Carpenter, placing it either in *Helotiaceae* or *Pezizellaceae*. A recent classification follows Johnston et al. (2019), but also includes the classification of Ekanayaka et al. (2019) "to encourage positive dialogue" (Wijayawardene et al. 2020).

Prior placements of *Bisporella resinicola* have been based entirely on morphological characters, with taxonomic conclusions being reached based on the morphology of the sexual state and the asexual state, *Eustilbum aureum*. *Bisporella resinicola* was originally placed in *Helotium*, with the anamorph tentatively placed in *Stilbella*, the former already at that point an abandoned generic name and the latter a fairly uninformative form-genus (Dennis 1963; Baranyay and Funk 1969; Seifert 1985). Seifert and Carpenter (1987) placed *B. resinicola* in *Bisporella* based primarily on analogy with the common, yellow species now placed in *Calycina*. These authors rely on features this taxon shares with other species placed in *Bisporella*: it is bright yellow, a feature not exhibited by the type species of *Bisporella* (Korf & Carpenter 1974); an association with dematiaceous hyphomycetes, a character shared by most, if not all,

resinicolous fungi (pers. obs.); ectal excipulum of a compact *textura intricata*; refractive hyphae; and a poorly differentiated medullary excipulum. In addition, the authors made comparisons between *B. resinicola* and species in the genus *Proliferodiscus*—currently accepted in *Lachnaceae* (Johnston et al. 2019)—due to some additional morphological features (ascospore shape, apothecia with hairs arising from branching stalks, and asci without a visible apical pore). The uncertainty regarding the affinities of the sexual state were not mirrored in these authors' assessment of the asexual state. Based on the morphology of the synnemata, it was accepted that this species could not be accommodated in any extant genus, and so it was kept in the monotypic genus *Eustilbum*. It may be noted that this moniliaceous, synnematous asexual state differs greatly from the dematiaceous, arthroconidial or phialidic asexual states placed in the genera *Bispora*, *Bloxamia*, *Chalara*, *Cystodendron*, and *Phialophora* known or suspected to be associated with other species of *Bisporella* (Korf and Carpenter 1974; Carpenter 1975, 1981; Johnston 1988; Sánchez Márquez et al. 2007). Later, the species was uncritically placed in *Hymenoscyphus* (Sharma 1988), likely because most species of *Helotium* were transferred to *Hymenoscyphus* when *Helotium* was abandoned (Dennis 1963). Weber & Baral referred a German specimen of *B. resinicola* to the genus *Cistella* in the family *Hyaloscyphaceae* based on the blunt, granular, hyaline hairs and the thin-walled excipular cells of the sexual morph; they also noted that although the asci had previously been reported as inamyloid, the ascus pore reaction was of the hemiamyloid type (Weber 1992). These authors did not publish a new combination, and this placement did not garner much attention.

The object of the current work is to clarify the placement of *Bisporella resinicola* in *Leotiomycetes* and to determine whether it is related to *Bisporella* (*Helotiaceae*), *Hymenoscyphus* (*Helotiaceae*), *Cistella* (*Helotiales incertae sedis*), *Hyaloscyphaceae*, or

Calycina (*Pezizellaceae*). To this end, fresh material from Europe and North America of the asexual and sexual states of *Bisporella resinicola* were studied. Fresh material of the type species of *Bisporella*, *Bisporella pallescens*, and the hyphomycete it is found in association with, *Bispora antennata*, as well as a member of the group of species recently treated in *Calycina*, *C. cf. confluens*, were also collected and studied. In addition to morphological examination, DNA was extracted and nuITS, nuLSU, *TEF*, *MCM7*, and *RPB2* amplified and sequenced for phylogenetic analysis and comparison with published sequences.

Section 5.3

Materials and Methods

Subsection 5.3.1

Specimens Examined

Six fresh specimens of *Bisporella resinicola* were examined by the authors. The host range was limited, with most specimens originating on species of *Picea.* The geographical distribution of these specimens was broad despite their low number, with specimens coming from Alaska, Maine, and Switzerland. One of the collections from Maine was made by the last author and one by Alejandro Huereca while at the Eagle Hill Institute. Further specimens were collected by and borrowed from Elizabeth Kneiper (Maine, also on the campus of the Eagle Hill Institute), Connor Goff (Alaska), and the Universalmuseum Joanneum (GJO) (Switzerland, collected by Erich Zimmermann and Silvia Feusi). An nuITS sequence of an unexamined specimen from New Brunswick was also provided by Joey Tanney.

Two fresh, mixed specimens of *Bisporella pallescens* and *Bispora antennata* were also examined by the authors. As is typical of this species, they were both collected on *Fagus*. The specimens were collected on the island of Zealand, in Denmark, by Frede Scheye and lent by Thomas Læssøe.

For purposes of comparison, a specimen of *Calycina cf. confluens* was also examined. This specimen was collected by the second and first authors in Massachusetts on unidentified rotten wood. The second author also examined several collections of *Calycina* spp. from the Canary Islands and Chile.

Subsection 5.3.2

Molecular Methods

DNA extractions were performed from ¼-3 apothecia, 1-3 synnemata or an approximately rice-grain-sized area of loose conidia. Where there was ample material the DNeasy Plant Mini Kit (QIAGEN) was employed following the manufacturer's recommendations. Older or scantier material was extracted with the QIAamp DNA Micro Kit (QIAGEN), again following the manufacturer's recommendations.

Up to five gene regions (including two rDNA and three protein-coding genes) were amplified: the internal transcribed spacer regions plus 5.8S gene (nuITS), the nuclear large subunit ribosomal RNA gene (nuLSU), the minichromosome maintenance complex component 7 gene (*MCM7*), the translation replication factor 1-α gene (*TEF*), and the second largest subunit of RNA polymerase II gene (*RPB2*). The nuITS region was amplified using the primer pair ITS1-F (Gardes and Bruns 1993) + LR3 (Vilgalys and Hester 1990). The nuLSU region was

amplified using the primer pair LR0R (Rehner and Samuels 1994) + LR5 (Vilgalys and Hester 1990). The *MCM7* gene was amplified with either the primer pair Mcm7-709for + Mcm7-1348rev (Schmitt et al. 2009) or Mcm7-CalicF + Mcm7-CalicR (Prieto et al. 2013). The *TEF* gene was amplified with the primer pair EF1-983F + EF1-2218R (Rehner and Buckley 2005). The *RPB2* gene was amplified employing the primer pair fRPB2-5F + fRPB2-7cR (Liu et al. 1999), but this primer pair was highly nonspecific, and some preliminary and published sequences were used to design the following primer pairs: RPB2-5FCal (5'-TTCCGAAGACTTACACAAGATG-3') + RPB2-7RCal (5'-GGAAAAGGGATGATACTGGCG-3') and RPB2-5FEus (5'-ATATCTGAAGAGCTGCGTCG-3') + RPB2-7REus (5'-GGAAAGGGAATAATGCTTGCG-3'), used to amplify *Calycina cf. confluens* and *Bisporella resinicola*, respectively.

When amplifying nuITS, nuLSU, and *MCM7*, EconoTaq DNA Polymerase (Lucigen) was used. When amplifying *TEF*, REDExtract-N-Amp PCR ReadyMix (Sigma-Aldrich) was used. When amplifying *RPB2*, Q5 High-Fidelity DNA Polymerase (New England BioLabs) was used. All PCR reactions were performed using 5 µL of full strength, 1/10 dilution, or 1/100 dilutions of the DNA extracts as templates in a total reaction volume of 25 µL and utilized either a Mastercycler ep gradient (Eppendorf) or a C1000 Touch Thermal Cycler (Bio-rad). All PCR recipes and cycling parameters are included in Appendix C.

When PCR products contained multiple bands, the band of interest was excised from a 2% agarose gel and purified using either a QIAquick Gel Extraction Kit (QIAGEN) or a Monarch DNA Gel Extraction Kit (New England BioLabs, Inc.). Otherwise, single-band PCR Products were purified with a QIAquick PCR Purification Kit (QIAGEN) or a Monarch PCR & DNA Cleanup Kit (New England BioLabs, Inc.). In the case of faint PCR products,

reamplification was performed using 5 µL of a 1/100 dilution of the previous PCR product as template in a total reaction volume of 25 µL. The same polymerase, primers, reaction recipe, and cycling parameters as previously were used, except in the case of *MCM7*, where the internal primer pair Mcm7-CalicF + Mcm7-CalicR was sometimes used after an initial amplification with Mcm7-709for + Mcm7-1348rev.

In preparation for sequencing, all purified products were run on a 1% agarose gel with 0.0001% GelRed Nucleic Acid Stain, 10,000× in Water (Biotium) added for DNA visualization and using Gel Loading Dye Purple (6×), no SDS (New England BioLabs) to avoid a UV shadow interfering with image analysis of the gel. UV photographs of gels were taken with an AlphaImager EP (Alpha Innotech), and band fluorescence was estimated using the AlphaView software (Alpha Innotech). Purified PCR product concentration was assessed by comparison with the fluorescence of the bands in Low DNA Mass Ladder (Invitrogen) run on the same gel. All PCR products of all genes were sent to GeneWiz Inc. sequencing facilities (Cambridge, MA) for Sanger Sequencing. The forward and reverse sequences from each PCR product were edited and a consensus sequence generated using Sequencher v. 5.1 (GeneCodes). All sequences were submitted to GenBank (NCBI Resource Coordinators 2016), with accession numbers listed in Table 5.1.

Subsection 5.3.3

Phylogenetic Analysis Methods

Newly generated sequences (Table 5.1) were incorporated into the 15-gene DNA sequence alignment from Johnston et al. (2019; data available from doi.org/10.7931/T5YV-

Table 5.1. Sequences newly generated in this study.

Species	Asexual or Sexual State	Isolate/Identifier	Herbarium	GenBank Accession Numbers				
				ITS	LSU	*MCM7*	*TEF*	*RPB2*
Bispora pallescens	A	DMS-10075832A	hb. DMS	MW203179	MW203179	—	—	—
	S	DMS-10075832T	hb. DMS	MW203180	MW203180	MW244566	MW244573	MW244581
	A	DMS-10078235A	hb. DMS	MW203181	MW203181	—	MW244574	—
	S	DMS-10078235T	hb. DMS	MW203182	MW203182	MW244567	MW244575	MW244582
Calycina cf. *confluens*	S	LQH-9a	FH	MW203183	MW115642	MW244568	MW244576	MW244583
Eustilbum aureum	S	JM-CG-01a	FH	MW203184	MW115643	MW244569	MW244577	—
	A	JMEK.1a	FH	MW203185	MW115644	MW244570	MW244578	—
	A	SF298a	GJO	MW203186	MW203186	MW244571	MW244579	MW244584
	A	SF299a	GJO	MW203187	MW203187	MW244572	MW244580	—
	A	NB2	—	MW113716	—	—	—	—

BE95) together with sequences extracted from the *Calycina marina* genome, generated by Teppo Rämä (The Arctic University of Norway) and Joseph Spatafora (Oregon State University), sequences extracted from the *Xylogone sp.* PMI_703 genome generated by Francis Martin (MycorWeb) and Alejandro Rojas (University of Arkansas), both as part of the JGI 1000 Fungal Genomes project, and additional sequences of taxa in *Hyaloscyphaceae* and basal *Helotiales* from a recent study (Kosonen et al. 2020). The sequences available for each gene were aligned using MAFFT (Katoh and Standley 2013) as implemented in Geneious. The ends were manually trimmed, and introns were removed manually; all remaining data were then concatenated. Maximum likelihood (ML) analyses were run with IQ-TREE v. 1.6.6 (Nguyen et al. 2015; Chernomor et al. 2016), using models selected by ModelFinder (Kalyaanamoorthy et al. 2017) for each partitioned gene; ultrafast bootstrap (BS) analysis with 1,000 replicates estimated branch support in the ML tree (Hoang et al. 2018). *Xylaria hypoxylon* (AFTOL-ID 51, isolate OSC 100004, JGI genome Xylhyp) and *Neurospora crassa* (isolate OR74A, JGI genome Neucr2) were used as outgroups.

For the ITS phylogeny, our newly generated ITS sequences (Table 5.1) were aligned with representative *Pezizellaceae* and *Helotiaceae* sequences downloaded from GenBank, aligned and analyzed using the same methods as the multigene analysis, using the TIM2e+I+G4 model.

Subsection 5.3.4

Morphological Methods

Microscopic examination was conducted on free-hand sections cut under a dissecting microscope (Wild M5) and also sections cut on a freezing microtome. Microtome sections were

prepared by stabilizing water-hydrated apothecia on a freezing stage (Physitemp BFS-MP) with a diluted gum arabic solution and cutting sections at approximately 25 µm with a sliding microtome (Bausch & Lomb Optical Co.). The resulting sections were applied serially to a clean glass slide and allowed to dry. Using freshly cut sections, slides were prepared under a dissecting microscope (Olympus SZX9) and studied with a compound microscope (Olympus BX40). Microphotographs were taken with an Olympus XC50 USB camera. Hand sections were pre-treated in 3% potassium hydroxide (KOH) and stained with Congo Red (CR) or Melzer's reagent (MLZ). Micro-photographs were taken using a Motic B1 compound light microscope (MoticEurope S.L.U., Spain) with a USB Moticam 2500 camera. Photographic figures were assembled using Illustrator CC (Adobe Systems, San José, CA).

Section 5.4

Results

Subsection 5.4.1

Phylogenetic Analyses

The results of our analyses largely support the conclusions of Baral et al. (2013) and the overall topology of the ML phylogeny (Fig. 5.1) agrees with Johnston et al. (2019). *Bisporella s.l.* (Korf & Carpenter 1974) is constituted by four different groups: *Bispora* (including *Bisporella s.s.*)*, Calycina*, *Eustilbum* and an unnamed clade (Figs. 5.1 & 5.2). *Bisporella s. str.*, represented by the type species of the genus (*B. monilifera = B. pallescens*), and *Bispora*, represented by the type species *Bispora antennata*, are synonymous and placed in *Helotiaceae*

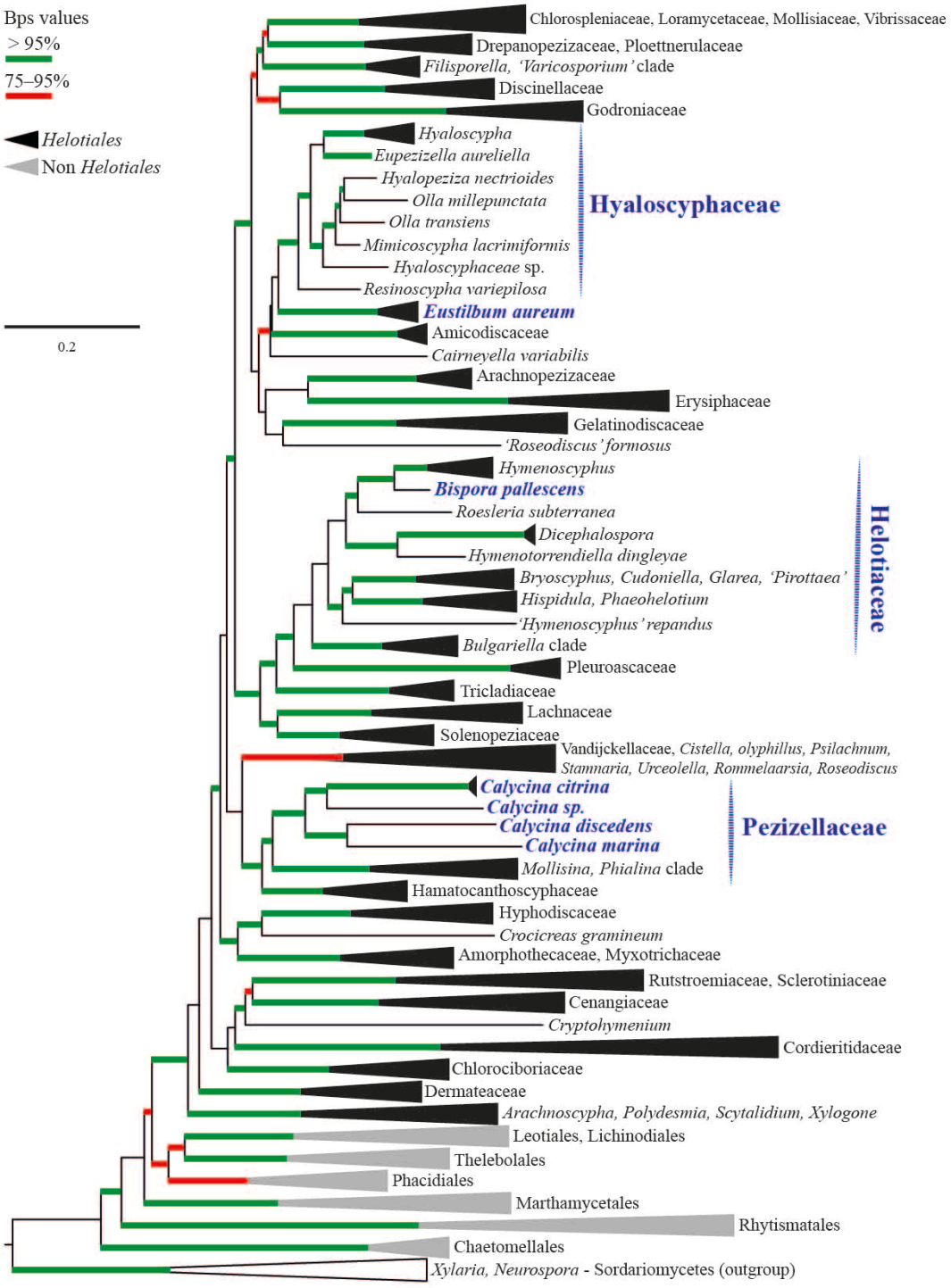

Figure 5.1. ML tree based on concatenated DNA sequences including *Bispora* and *Bisporella s.l.* (*Bisporella*, '*Bisporella*' *subpallida*, *Eustilbum* and *Calycina*) plus taxa treated by Johnston et al. (2019). Families of *Helotiales* not related to *Bisporella s.l.* are collapsed (black clades). Orders for all *Leotiomycetes* except *Helotiales* are collapsed (grey clades). Thick branches have bootstrap support values above 75%.

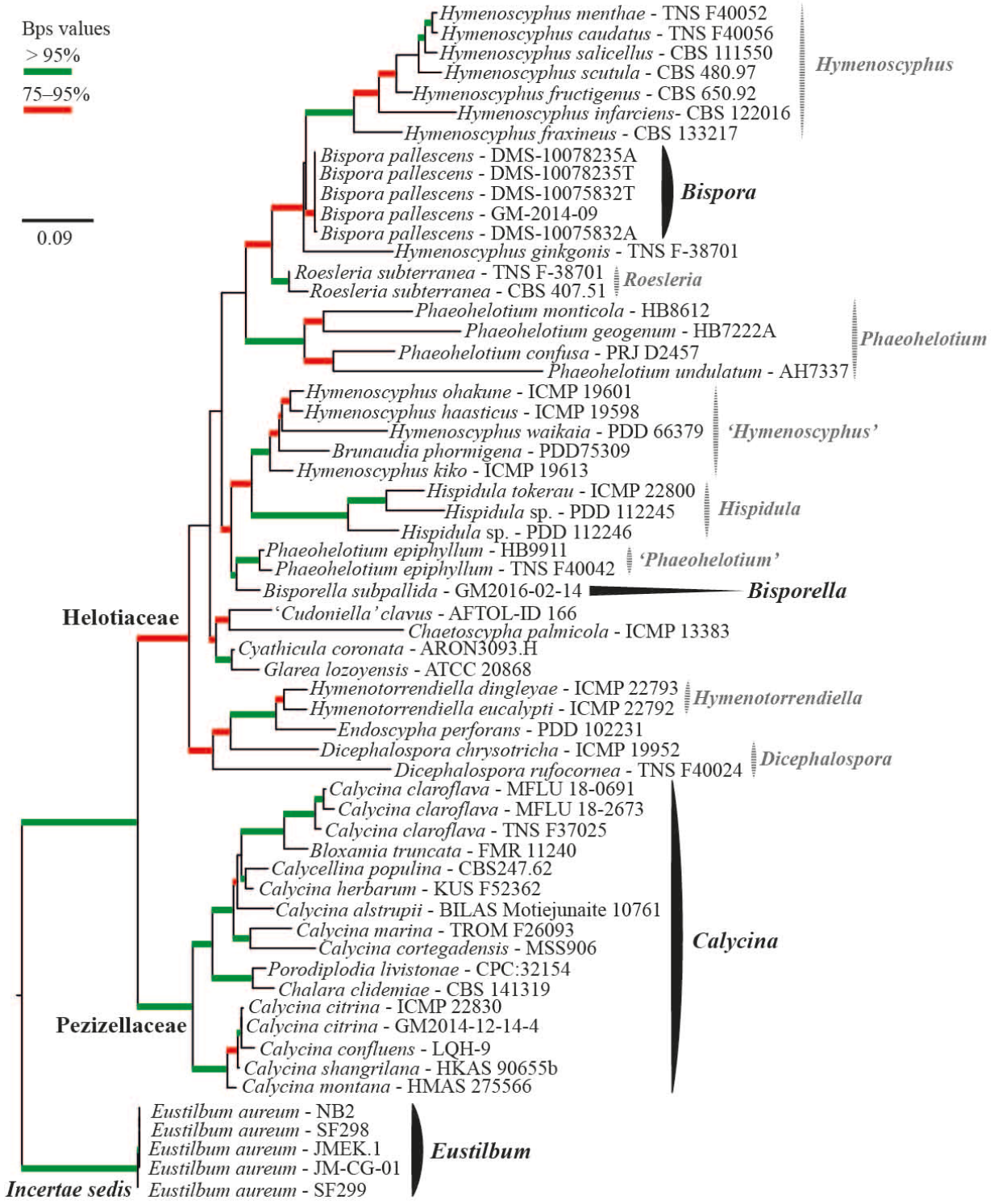

Figure 5.2. ITS ML tree based including *Bispora*, *Bisporella*, *Eustilbum* and *Calycina* plus taxa treated by Johnston et al. (2019) in the families *Helotiacaeae* and *Pezizellaceae*. Thick branches have bootstrap support values above 75%.

(Fig. 5.1), sister to *Hymenoscyphus* and *Roesleria subterranea* (Figs. 5.1 & 5.2). *Eustilbum aureum* (= *Bisporella resinicola*) is not related to *Helotiaceae* or *Pezizellaceae* for which sequences are available and clusters in a moderately supported clade with *Hyaloscyphaceae*, *Amicodiscaceae* and *Cairneyella* (Fig. 5.1). Almost all other sequenced species of *Bisporella s.l.* are in *Calycina* sensu Baral et al. (2013) in *Pezizellaceae* (Figs. 5.1 & 5.2). It may be noted, however, that *Calycina citrina, Calycina* cf. *confluens*, *Calycina montana comb. nov.*, and *Calycina shangrilana comb. nov.* form a supported clade within *Calycina*, separate to that containing the type species *C. herbarum* (Fig. 5.2). '*Bisporella*' *subpallida* is an exception to the placement of most remaining species in *Calycina*; our analyses place it in a separate '*Bisporella*' clade in *Helotiaceae*, closely related to '*Phaeohelotium*' *epiphyllum* (Fig. 5.2).

Subsection 5.4.2

Morphological Analyses

In Figs. 5.3 & 5.4 the genera included in *Bisporella s.l.* have been compared each other.

Based on the results of our morphological analyses of specimens of the sexual morph of *E. aureum* having inamyloid asci, we conclude that the specimens examined by Weber and Baral with hemiamyloid asci were misidentified (Weber 1992). The incorrect concept used by those authors possibly extends to a few other publications involving the same authors from that period (Krieglsteiner 1991; Tholl et al. 1994).

Subsection 5.4.3

Taxonomy and Nomenclature

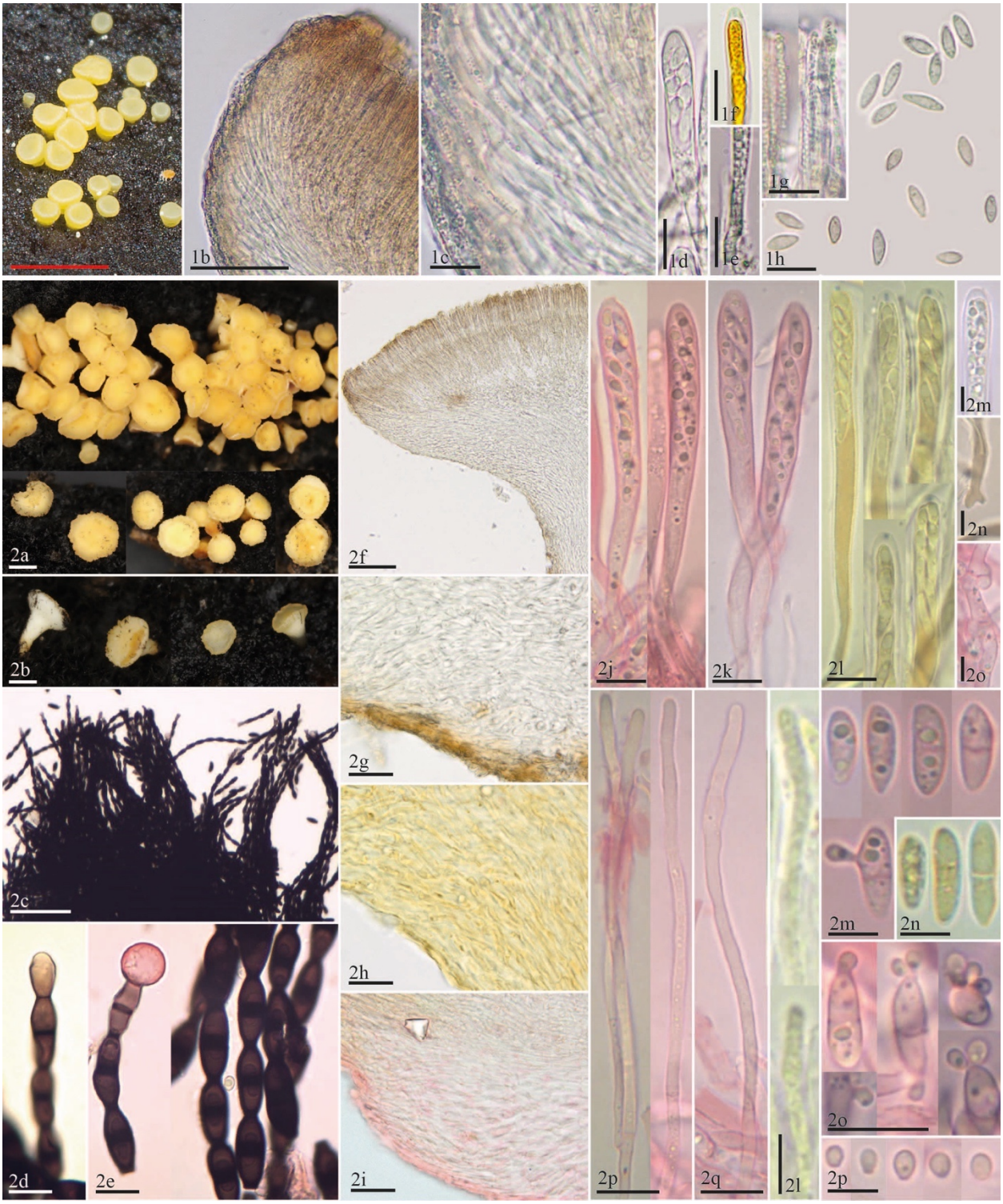

Figure 5.3. Morphological features of '*Bisporella*' *subpallida* and *Bispora pallescens*. **1** '*Bisporella*' *subpallida*. **1a** Living apothecia in situ. **1b-c** Medial section of apothecium: 1b. Margin and excipulum, 1c. Detail of excipulum. **1d-g** Details of hymenial elements: 1d. Mature ascus, 1e. Ascus base, 1f. Immature ascus apex, 1g. Paraphyses. **1h** Mature ascospores. **2** *Bispora pallescens*. **2a,b** Dried apothecia in situ. **2c-e** Asexual state: 2c. Chains of conidia, 2d-e.

Details of conidia and conidiogenesis. **2f-i** Medial sections of apothecia: 2f. Dection overview, 2g. Flank, 2h. Excipulum, 2i. Margin. **2j-r** Details of hymenial elements: 2j-l. Mature asci, 2m. Immature ascus apex, 2n-o. Ascus bases with croziers, 2p-r. Paraphyses. **2s-v** Ascospores and conidia: 2s-t. Mature ascospores, 2u. Budding ascospores, 2v. Conidia budded from ascospores. Reagents: H_2O = 1b-e, 1g-h; MLZ = 1f, 2h; KOH = 1c, 2f-g, 2m; CR = 2i; KOH+MLZ = 2d, 2l, 2n, 2t-u; KOH+CR = 2e, 2j-k, 2o-q, 2s, 2v. Scale bars: 500 µm = 2a-b; 100 µm = 2c, 2f; 50µm = 1b; 20 µm = 2g-i; 10 µm = 1c-e, 1g-h, 2d-e, 2j-l, 2p-q, 2u; 5 µm = 1f, 2m-o, 2r-t, 2v. Collections: hb. Enrique Rubio s.n. = 1a-1h; DMS-10075832 = 2b, 2f, 2h-v; DMS-10078235 = 2a, 2c-e, 2g.

Although the terms "holotype" and "lectotype" as defined in Article 9 do not apply to names at ranks higher than species, they will be used by analogy here to indicate type species of monotypic genera or type species selected by their authors and type species selected by later authors, respectively (Art. 10, Note 1; Turland et al. 2018). Exclamation points after a specimen identifier indicate that it was examined by the authors.

Eustilbum Rabenh., Hedwigia 2(10): 59 (1862).

Holotype species: *Eustilbum rehmianum* Rabenh.

Classification: *Incertae sedis*, *Helotiales*, *Leotiomycetes*, *Pezizomycotina*, *Ascomycota*.

Eustilbum aureum (Pers.) Seifert & S.E.Carp., *Canad. J. Bot.* **65**(6): 1263 (1987).

≡ *Helotium aureum* Pers., *Syn. Meth. Fung.* **2**: 678 (1801).

Holotype: L 0111002 (910.256-1303), Germany: Saxony: Meissen, leg. C.F.(?) Ludwig (examined by Dennis, *Kew Bull.* **7**(3): 301 (1952)) (MBT 390348).

≡ *Peziza aurea* (Pers.) Fr., *Syst. Mycol.* **2**(1): 156 (1822), *nom. sanct.* (Fries, *l.c.*).

≡ *Sarea aurea* (Pers.) Schwein., *Trans. Amer. Philos. Soc. n.s.* **4**: 178 (1832).

≡ *Hymenoscyphus aureus* (Pers.) W.Phillips, *Man. Brit. Discomyc. Ed. 1*: 139 (1887).

≡ *Calycina persoonii* Kuntze, *Revis. Gen. Pl.* **3**(3): 448 (1898).

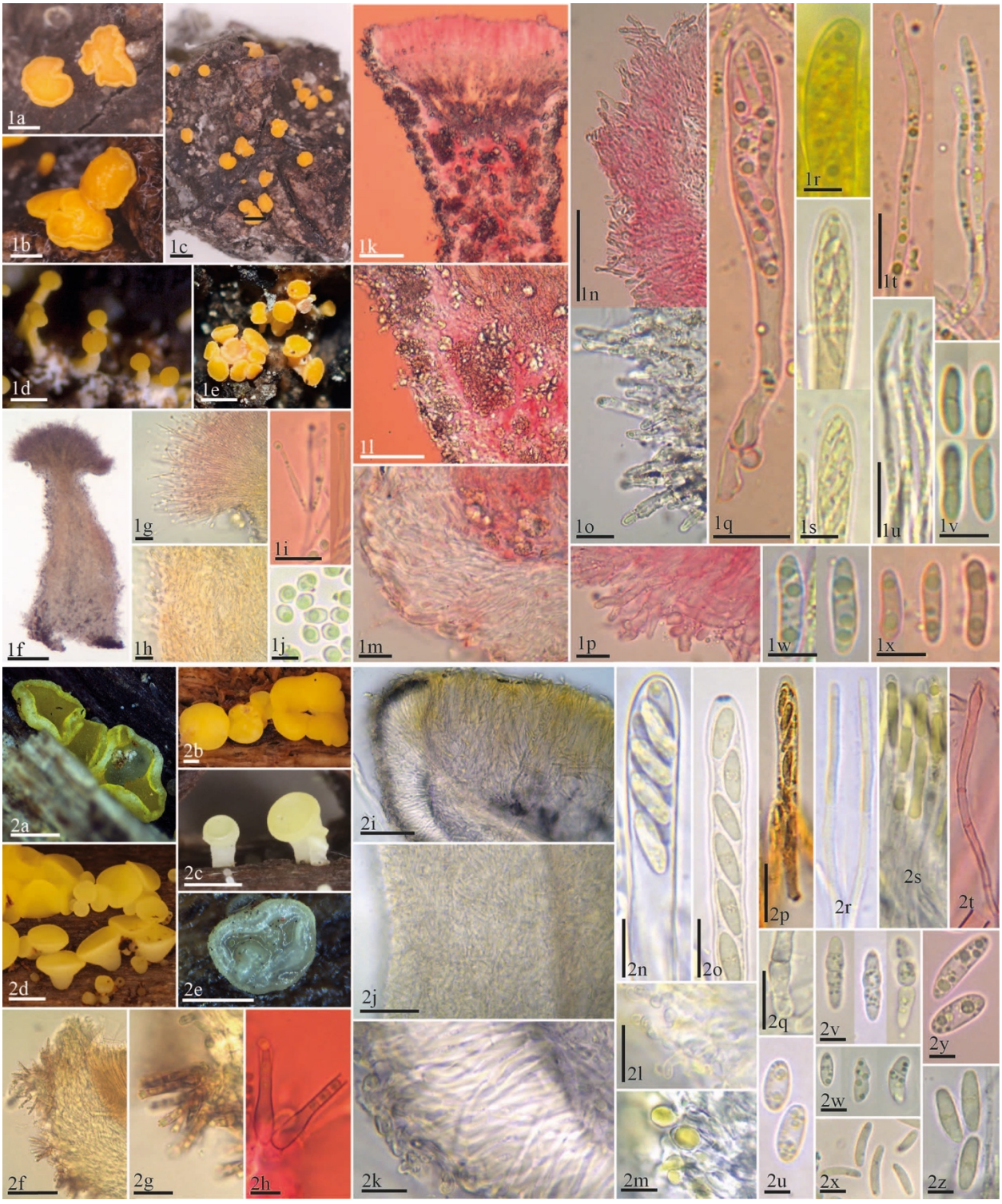

Figure 5.4. Morphological features of *Eustilbum aureum* and *Calycina* spp. **1** *Eustilbum aureum*. **1a-e** Fungus in situ: 1a-c, e. Apothecia, 1d. Synnemata. **1f-j** Microscopic details of the asexual state: 1f. Medial section of a synnema, 1g. Details of the capitulum of a synnema, 1h. Details of the stipe of a synnema, 1i. Conidiogenous cells, 1j. Conidia. **1k-p** Medial sections of apothecia: 1k. Overview of section, 1l. Details of flank, 1m. Details of margin, 1n-p. Details of excipular

hairs. **1q-t** Details of hymenial elements: 1q. Mature ascus with croziers, 1r-s. Ascus apices, 1t. Paraphyses. **1v-x** Mature ascospores. **2** *Calycina* spp.: *Calycina citrina* = 2c-d, 2n, 2r, 2u; *C. claroflava* = 2a, 2j, 2l-m, 2s, 2w; *C.* cf. *confluens* = 2b, 2o, 2y-z; *C. scholochloae* = 2e, 2i, 2k, 2q, 2v; *C. vulgaris* = 2p, 2t, 2x; *Calycina* sp. = 2f-h. **2a-e** Apothecia in situ. **2f-m** Medial sections of apothecia: 2f. Excipulum with dematiaceous, phialidic hyphomycete typical of many *Calycina* species, 2g-h. Details of conidiogenous cells and conidia, 2i. Overview of apothecium section, 2j-k. Detail of layering in the excipular tissues, 2l-m. surface cells of the excipulum. **2n-q** Detail of hymenial elements: 2n-p. Ascus apices, 2q. Ascus base, 2r-t. Paraphyses. **2u-z** Mature ascospores. Reagents: H_2O = 1o, 1w, 2i-n, 2q-s, 2u-x; MLZ = 2z; IKI = 1r; CR = 1k-l, 2y; KOH = 1f-h, 1j; KOH+MLZ = 1s, 1u-v, 2o-p; KOH+CR = 1i, 1m-n, 1p-q, 1t, 1x, 2t. Scale bars: 1 mm = 1c-e, 2b-d; 500 µm = 1a-b, 2a, 2e; 100 µm = 1f, 1k; 50 µm = 1l, 1n, 2f, 2i-j; 10 µm = 1g-i, 1m, 1o-q, 1s-u, 2g, 2k-t, 2x; 5 µm = 1r, 1v-x; 2h, 2u-w, 2y-z. Collections: JM-CG-01 = 1a-c, 1f-i, 1n-q, 1s-x; Zi M299 = 1k-m; hb. Elisabeth Stöckli s.n. = 1d-e, 1j, 1r; LQH-9 = 2b, 2o, 2y-z; TFC 23415 = 2a, 2i, 2k-m, 2s; TFC 23431 = 2e, 2q, 2v; TFC 23551 = 2w; TFC 23924 = 2p, 2t, 2x; CH-228 = 2d; CH-262 = 2c, 2j, 2n, 2r, 2u; QCNEM 3192 = 2f-h.

= *Coniocybe baeomycioides* A.Massal., *Lotos* **6**: 83 (1856).

Holotype: VER Bel. no. 576, Italy: Ajrag(?), on trunk of *Abies* sp. (examined by Seifert & Carpenter, *Canad. J. Bot.* **65**(6): 1265 (1987)) (MBT 390349).

≡ *Fulgia baeomycioides* (A.Massal.) Trevis., *Flora* **45**(1): 7 (1862).

≡ *Eustilbum baeomycioides* (A.Massal.) Arnold, *Flora* **68**(11): 226 (1885).

≡ *Dendrostilbella baeomycioides* (A.Massal.) Lindau, *Raben. Krypt.-Fl. Ed. 2* **Band 1, Abth. 9**(110): 305 (1908) [1910].

≡ *Stilbum baeomycioides* (A.Massal.) Sacc., *Syll. Fung.* **22**(2): 1439 (1913).

= *Eustilbum rehmianum* Rabenh., *Hedwigia* **2**(10): 59 (1862).

Lectotype: *Hedwigia* 2, Tab. X, fig. III. 2!, designated here.

≡ *Stilbum rehmianum* (Rabenh.) Sacc., *Syll. Fung.* **4**: 565 (1886).

≡ *Botryonipha rehmiana* (Rabenh.) Kuntze, *Revis. Gen. Pl.* **2**: 845 (1891).

≡ *Stilbella rehmiana* (Rabenh.) Lindau, *Raben. Krypt.-Fl. Ed. 2* **Band 1, Abth. 9**(109): 294 (1908) [1910].

= *Coniocybe crocata* Körb., *Parerga Lichenol.*: 300 (1863) [1865].

Holotype: W 19769, in herb. Körber (examined by Seifert & Carpenter, *Canad. J. Bot.* **65**(6): 1265 (1987)) (MBT 390361).

≡ *Roesleria crocata* (Körb.) Sacc., *Syll. Fung.* **8**: 828 (1889).

≡ *Pilacre crocata* (Körb.) Boud., *Hist. Classific. Discomyc. Europe*: 91 (1907).

= *Stilbum resinae* Bres. & Sacc., *Ann. Mycol.* **1**(1): 28 (1903).

Holotype: S F45470, in herb. Bresadola, Italy: Trentino: Cavelonte, on resin and branches of *Abies pectinata*, leg. G. Bresadola (examined by Seifert & Carpenter, *Canad. J. Bot.* **65**(6): 1265 (1987)) (MBT 390362).

≡ *Eustilbum resinae* (Bres. & Sacc.) Magnus in Dalla Torre & Sarntheim, *Fl. Tirol* **3**: 562 (1905).

≡ *Stilbella resinae* (Bres. & Sacc.) Lindau, *Raben. Krypt.-Fl. Ed. 2* **Band 1, Abth. 9**(109): 297 (1908) [1910].

= *Stilbum resinarium* Peck, *Bull. New York State Mus. Nat. Hist.* **67**: 30 (1903).

Holotype: NYSf2578, USA: New York: Adirondack Mountains, on gum spots of balsam fir (*Abies balsamea*), leg. C. H. Peck (examined by Seifert & Carpenter, *Canad. J. Bot.* **65**(6): 1265 (1987)) (MBT 390363).

= *Helotium resinicola* Baranyay & A.Funk, *Canad. J. Bot.* **47**(6): 1011 (1969).

Holotype: DAVFP 18350, Canada: British Columbia: Lake Cowichan, on resin of *Tsuga heterophylla*, 10 Dec. 1963, leg. A. Funk (examined by Seifert & Carpenter, *Canad. J. Bot.* **65**(6): 1265 (1987)) (MBT 390364).

≡ *Bisporella resinicola* (Baranyay & A.Funk) S.E.Carp. & Seifert, *Canad. J. Bot.* **65**(6): 1263 (1987).

≡ *Hymenoscyphus resinicola* (Baranyay & A.Funk) M.P.Sharma, *Trends Tree Sci.*: 137 (1988).

Additional Material: **Austria**: *Lower Austria*: in silva "Wiener Wald" prope Tullnerbach, in resina *Abietis excelsae* DC. [*Picea abies*], *C. de Keißler*, *Kryptogamae exsiccatae editae a Museo Palatino Vindobonensi* 1838 (FH 00965359!); – **Canada**: *British Columbia*: Calvert Island, 51°39'18.04"N 128°08'16.76"W, 50 m a.s.l., on resin, 18 Jun. 2018, *R.T. McMullin* 19800 (CANL 132188!); *Quebec*: Lac Clair near Quebec, on spruce [*Picea* sp.], Sep. 1888, *W.G. Farlow* (FH 00995487!); – **France**: in sylvis abiegnis, ad ligna decorticata, corticemque putridam, *Mougeot & Nestler Stirpes Cryptogamae Vogeso-Rhenanae* 782 (FH 00965360!); ibid. (FH 00965350!); *Jura*: ad Pinus abietis [*Picea abies*] corticem vetustum, *P. Morthier*, *Fuckel Fungi Rhenani* 1162 (FH 00965357!); – **Germany**: *Bavaria*: Sugenheim, ad Pini [*Pinus* sp.] cortices, *H. Rehm*, *Rabenhorst Fungi Europaei Exsiccati* 677 (FH 00965358!); – **Italy**: *Vercelli*: [Valsesia], Riva, nelle anfrattuosita e cicatrici resinose della corteccia delle Conifere, 1863, *A. Carestia*, *Rabenhorst Lichenes Europaei* 736 (FH 00995484!); ibid., *Erbario Crittogamico Italiano* 1166 (FH 00965351!); ibid. (FH 00965352!); – **Switzerland**: *Bern*: Grindelwald, Itramenwald, 46°36'28.211"N 7°59'31.611"E, 1500 m a.s.l., on resin on trunk 1m50 above ground, 23 Aug. 2019, *S. Feusi & E. Zimmerman* Zi M298 (GJO 0093990!); ibid., 46°36'38.614"N 7°59'47.987"E, 1368 m a.s.l., on resin on trunk 1m50 above ground, 23 Aug. 2019, *S. Feusi & E. Zimmerman* Zi M299 (GJO 0093991!); – **USA**: *Alaska*: Sitka, Sitka National Historical Park, 57°02'53.6"N 135°19'00.9"W, on resin, 4 Mar. 2019, *C. Goff* JM-CG-01 (FH!); *Maine*: Washington County, Machiasport, on living tree (fir [*Abies* sp.]), 26 Aug. 1898, *M.A. Barker* 44 (FH 00995486!); ibid., Steuben, Eagle Hill Institute, 44°27'35.03"N 67°55'53.01"W, 5 m a.s.l., on *Picea rubens* resin, 22 May 2017, *E. Kneiper* JMEK (FH!); ibid., 44°27'38.35"N

67°56'03.21"W, on resin of *Picea rubens*, 17 Jun. 2019, *A. Huereca* (FH!); ibid., on resin of *Picea* (?) sp., 18 Jun. 2019, *D.H. Pfister* (FH!); York County, York, on spruce [*Picea* sp.] resin, 12 Aug. 1897, *R. Thaxter* (FH 00995492!); ibid., on resin of *Picea* sp., *R. Thaxter*, *Reliquiae Farlowianae* 669 (FH 00995493!); ibid. (FH 00965349!); ibid., on spruce [*Picea* sp.] resin, *R. Thaxter* 3760 (FH 00995496!); *New Hampshire*: Carroll County, Jackson, Jun. 1898, *W.G. Farlow* (FH 00995489!); ibid., Tamworth, Chocorua, Sep. 1907, *W.G. Farlow* (FH 00995494!); ibid., 1910, *W.G. Farlow* (FH 00995495!); Coos County, Shelburne, on spruce [*Picea* sp.], *W.G. Farlow* (FH 00995488!); ibid., Sep. 1891, *W.G. Farlow* (FH 00995490!); *New York*: Adirondacks, Essex County, Keene Valley, Sep. 1902, *W.G. Farlow* (FH 00995485!); Catskills, on spruce [*Picea* sp.] gum, 1868, *C.H. Peck* 246 (FH 00995491!); *North Carolina*: Swain County, Great Smoky Mountains National Park, 35°32'25"-33'17"N 83°29'36"-44"W, 1768-1859 m a.s.l., on *Abies* sap, 10 Oct. 2011, *E.A. Tripp & J.C. Lendemer* 2261 (NY 01685454!); *Tennessee*: Sevier County, Great Smoky Mountains National Park, Appalachian Trail, 35°38'45"N 83°21'36"W, 1615 m a.s.l., on *Abies* sap, 12 Oct. 2011, *E.A. Tripp, K. Deregibus, M. Smith & M. Stevens* 2347 (NY 01685326!); ibid., Boulevard Trail, 35°38'03"N 83°24'50"W, 1814 m a.s.l., on *Abies* sap, 7 Aug. 2012, *E.A. Tripp & J.C. Lendemer* 3446 (NY 01685081!); ibid., Sugarland Mountain Trail, resinicolous on *Picea*, 26 Oct. 2017, *R.T. McMullin* 19017 (NY 03303142!).

Notes: The extensive synonymy presented here follows Seifert & Carpenter (1987), with some additions and corrections. Seifert and Carpenter designated a lectotype for *Helotium aureum*, but this cannot be accepted, since the location and collector data of the specimen is in conflict with the protologue, and there is no other compelling information indicating that this is original material. Furthermore, Dennis (1952) and the Naturalis BioPortal indicate that the holotype

exists, though in poor condition. Thus, there is no need for a lectotype, though an epitype might be selected. Similarly, a holotype was listed by Seifert & Carpenter (1987) for *Eustilbum rehmianum*. There is doubt about whether this is in fact original material; the protologue is extremely sparse, consisting of a name, an illustration, and a suggestion that Rabenhorst planned to issue specimens in century 6 of his Fungi Europaei Exsiccati (Rabenhorst 1862). The specimen listed by Seifert & Carpenter as holotype is Fungi Europaei Exsiccati no. 677 from Rehm's herbarium at S, presumably based on the assumption that, as the species was named for Rehm, it was he who originally sent material to Rabenhorst. Given the sparse information in the protologue and the notorious irregularities in Rabenhorst's collecting practices for this exsiccata (Stevenson 1967), it is difficult to know what should be considered original material; the only element that is unambiguously to be considered original material is the illustration included in the protologue. Thus, we designate this the lectotype.

Helotiaceae Rehm, *Raben. Krypt.-Fl. Ed. 2* **Band 1, Abth. 3**(37): 647 (1892) [1896], *nom. cons.*

= *Bisporaceae* (Sacc.) Nann., *Repert. Mic. Uomo*: 497 (1934).

≡ *Bisporeae* Sacc., *Syll. Fung.* **4**: 341 (1886).

= [*Hymenoscyphaceae* Bellem. *nom. inval.* (Art. 18.4), in Lanier et al., *Mycol. Forest.*: 219 (1978)].

= *Roesleriaceae* Y.J.Yao & Spooner, *Kew Bull.* **54**(3): 684 (1999).

Classification: *Helotiales*, *Leotiomycetes*, *Pezizomycotina*, *Ascomycota*.

Bispora Corda, *Icon. Fung.* **1**: 9 (1837).

Lectotype species: *Monilia antennata* Pers., designated in Clements & Shear, *Gen. Fung. Ed. 2*: 395 (1931).

≡ *Torula* subg. *Bispora* (Corda) P.Crouan & H.Crouan, *Fl. Finistère*: 10 (1867).

= [*Bispora* Fuckel *nom. illegit.* (Art. 53.1), *Jahrb. Nassauischen Vereins Naturk.* **23-24**: 310 (1870) [1869-70]].

Holotype species: *Bispora monilifera* Fuckel.

= *Bisporella* Fuckel ex. Sacc., *Bot. Centralbl.* **18**: 218 (1884).

Holotype species: *Bispora monilifera* Fuckel.

≡ *Helotium* subg. *Bisporella* (Fuckel ex. Sacc.) Lindau in Engler & Prantl, *Nat. Pflanzenfam.* **1**(1): 207 (1896) [1897].

= [*Calycella* Quél. *nom. illegit.* (Art. 53.1), *Enchir. Fung.*: 305 (1886)].

Lectotype species: *Peziza pallescens* Pers., designated in Korf & Carpenter, *Mycotaxon* **1**(1): 57 (1974).

Bispora pallescens (Pers.) J.K.Mitch. & Quijada *comb. nov.*

≡ [*Peziza lenticularis* Hoffm. *nom. illegit.* (Art. 53.1), *Deutschl. Fl. Zweiter Theil*: T. 13 (1796) [1795]].

≡ *Peziza pallescens* Pers., *Observ. Mycol.* **2**: 85 (1800) [1799], *nom. sanct.* [Fries, *Syst. Mycol.* **2**(1): 132 (1822)].

Neotype: L 0111686 (910.256-842.90), Germany, leg. F.W. Junghuhn, examined and designated by Korf & Carpenter, *Mycotaxon* **1**(1): 56 (1974) (MBT 391042).

≡ *Calycina pallescens* (Pers.) Gray, *Nat. Arr. Brit. Pl.* **1**: 670 (1821).

≡ *Helotium pallescens* (Pers.) Fr., *Summa Veg. Scand.* **Sectio Posterior**: 355 (1849).

≡ *Niptera pallescens* (Pers.) Fuckel, *Jahrb. Nassauischen Vereins Naturk.* **25-26**: 334 (1871).

≡ *Phialea pallescens* (Pers.) Gillet, *Champ. France Discomyc.* **4**: 109 (1881) [1879].

≡ *Calycella pallescens* (Pers.) Quél., *Enchir. Fung.*: 306 (1886).

≡ *Helotium citrinum* var. *pallescens* (Pers.) Massee, *Brit. Fung.-Fl.* **4**: 239 (1895).

≡ *Bisporella pallescens* (Pers.) S.E.Carp. & Korf, *Mycotaxon* **1**(1): 58 (1974).

= *Dematium antennaeforme* Hoffm., *Deutschl. Fl. Zweiter Theil*: T. 13 (1796) [1795] [*fide* Hughes, *Canad. J. Bot.* **31**(5): 741 (1958)].

≡ *Monilia antennaeformis* (Hoffm.) Gray, *Nat. Arr. Brit. Pl.* **1**: 557 (1821).

= *Monilia antennata* Pers., *Syn. Meth. Fung.* **2**: 694 (1801).

≡ *Torula antennata* (Pers.) Pers., *Traité Champ. Comest.*: 59 (1818), *nom. sanct.* (Fries, *Syst. Mycol.* **3**: 501 (1832)).

≡ [*Bispora monilioides* Corda *nom. illegit.* (Art. 52.1), *Icon. Fung.* **1**: 9 (1837)].

≡ *Hormiscium antennatum* (Pers.) Bonord., *Handb. Mykol.*: 34 (1851).

≡ *Bispora antennata* (Pers.) E.W.Mason in Hughes, *Canad. J. Bot.* **31**(5): 582 (1953).

≡ ["*Bispora antennata* (Pers.) G.Arnaud" later isonym (Art. 6.3), *Bull. Trimestriel Soc. Mycol. France* **69**(3): 282 (1954) [1953]].

?= *Torula monilioides* Corda in Sturm, *Deutschl. Fl. Abtheilung III,* **Band 2, Heft 8**: 83 (1829).

= *Bispora catenulata* Corda, *Icon. Fung.* **1**: 9 (1837) [*fide* Hughes, *Canad. J. Bot.* **31**(5): 741 (1958)].

= *Bispora intermedia* Corda, *Icon. Fung.* **1**: 9 (1837) [*fide* Hughes, *Canad. J. Bot.* **31**(5): 741 (1958)].

= *Bispora menzelii* Corda, *Icon. Fung.* **1**: 9 (1837) [*fide* Hughes, *Canad. J. Bot.* **31**(5): 741 (1958)].

≡ *Torula menzelii* (Corda) Fr., *Summa Veg. Scand.* **Sectio Posterior**: 505 (1849).

= *Bispora monilifera* Fuckel, *Jahrb. Nassauischen Vereins Naturk.* **23-24**: 310 (1870) [1869-70].

Lectotype: **G**00127695 (n° SIB 321906/1), [Germany: Hesse: Rheingau]: in sylva Hostrichiensi [Oestrich], ad *Carpini* et *Fagi* truncos putridos [on rotting wood of *Carpinus* and *Fagus*], leg. K.W.G.L. Fuckel *Fungi Rhenani Exsiccati* 2387 (examined by Korf & Carpenter, Mycotaxon 1(1): 56 (1974), designated here); Isolectotype: FH 00964998!.

≡ [*Peziza monilifera* (Fuckel) Cooke *nom. illegit.* (Art. 53.1), *Grevillea* **4**(31): 111 (1876)].

≡ *Bisporella monilifera* (Fuckel) Sacc., *Bot. Centralbl.* **18**: 218 (1884).

≡ *Hymenoscyphus moniliferus* (Fuckel) W.Phillips, *Man. Brit. Discomyc. Ed. 1*: 130 (1887).

≡ *Helotium moniliferum* (Fuckel) Rehm, *Raben. Krypt.-Fl. Ed. 2* **Band 1, Abth. 3**(39): 790 (1893) [1896].

≡ *Calycella monilifera* (Fuckel) Dennis, *Mycol. Pap. Commonw. Mycol. Inst.* **62**: 44 (1956).

Additional Material: **Denmark**: *Region Zealand*: Hesede Skov, 55°16'31.1"N 11°57'22.7"E, dead wood (including bark) of bøg (*Fagus*), 8 Jan. 2020, *F. Scheye* (DMS-10075832!); ibid., Kastrup Dyrehave (Gunderslev Holm), 55°19'45.3"N 11°35'09.7"E, dead wood (including bark) of bøg (*Fagus*), 21 Jan. 2020, *F. Scheye* (DMS-10078235!).

Notes: The synonymy above follows Hughes (1958) and Korf and Carpenter (1974). Korf and Carpenter's work relied on type studies, and we accept their conclusions. A lectotype for *Bispora monilifera* is designated based on their studies. Hughes' (1958) work was based on authentic and type material for which he did not provide specific specimen references, merely citing the herbaria from which he examined material. He examined specimens of Corda's species (held at PR), specimens of Persoon's *Monilia antennata* (at L and UPS) and Hoffman's *Dematium antennaeforme* (at B). We accept his conclusions, but more complete documentation of type materials should be undertaken, as well as investigation of Corda's *Torula monilioides*. Corda evidently considered this fungus a close relative of *Monilia antennata* (Corda 1829), and it could be that he intended to base his later *Bispora monilioides* on *Torula monilioides*; there is no concrete evidence of this, however, and he only explicitly cited Persoon's *Torula antennata* as a synonym in the protologue of *B. monilioides*. Hughes treated *Torula monilioides* as originating with Fries, and as a combination based on *B. monilioides*, an error. It is thus unclear whether he examined original material under this name in Corda's herbarium. As a result, we list it here as a tentative synonym.

Pezizellaceae Velen., *Monogr. Discomyc. Bohem.* **1**: 154 (1934).

?= *Chalaraceae* (Sacc.) Nann., *Repert. Mic. Uomo*: 433 (1934).

≡ *Chalareae* Sacc., *Syll. Fung.* **4**: 238 (1886).

?= *Triposporiaceae* (Ferraris) Nann., *Repert. Mic. Uomo*: 507 (1934).

≡ *Triposporeae* Ferraris, *Fl. Ital. Crypt., Hyphales* [**2**]: 529 (1912).

= *Bloxamiaceae* Locq. ex Hern.-Restr., Gené, R.F. Castañeda, J. Mena, Crous & Guarro, *Stud. Mycol.* **86**: 81 (2017).

= *Porodiplodiaceae* Crous, in Crous et al., *Persoonia* **40**: 363 (2018).

Classification: *Helotiales*, *Leotiomycetes*, *Pezizomycotina*, *Ascomycota*.

Calycina Nees ex Gray, *Nat. Arr. Brit. Pl.* **1**: 669 (1821).

Lectotype species: *Peziza herbarum* Pers., designated in Dumont, *Mycologia* **64**(4): 913 (1972).

A large yellow cup fungus matching Korf & Bujakiewicz's (1985) description of *Bisporella confluens* (Sacc.) Korf & Bujak. was collected by the first two authors and was sequenced. *Calycina confluens* (≡ *Bisporella confluens*) is reported as having larger apothecia and somewhat longer spores than *Calycina citrina* (Læssøe and Petersen 2019), but there is no thorough description or detailed comparison of these species. Baral et al. (2013) treated *B. confluens* as a tentative synonym of *Calycina citrina* and did not combine it in *Calycina*. We note, however, that a new combination is unnecessary since the combination was published 122 years ago:

Calycina confluens (Sacc.) Kuntze, *Revis. Gen. Pl.* **3**(3): 448 (1898).

≡ [*Peziza confluens* Schwein. *nom. illegit.* (Art. 53.1), *Trans. Amer. Philos. Soc. n.s.* **4**: 176 (1832)].

≡ *Helotium confluens* Sacc., *Syll. Fung.* **8**: 222 (1889).

≡ *Helotium citrinum* var. *confluens* (Sacc.) Rehm ex Magnus in Dalla Torre & Sarntheim, *Fl. Tirol* **3**: 388 (1905).

≡ *Bisporella confluens* (Sacc.) Korf & Bujak., *Agarica* **6**(12): 306 (1985).

Comparable material: **USA**: *Massachusetts*: Barnstable County, Cape Cod National Seashore, Marconi Beach, on a rotting deciduous tree trunk, 5 Nov. 2017, *L. Quijada & J.K. Mitchell* LQH-9 (FH!).

Notes: We are not certain of the identity of this taxon and its distinction from *Calycina citrina*. We thus refer to our sequenced material as "*Calycina* cf. *confluens*" in this publication.

Two species included in *Bisporella s.l.* have published molecular data from holotype material, and these sequences nest well in *Calycina* in our analyses (Fig. 5.2) and those of Zhuang et al. (2017) and Ekanayaka et al. (2019). We thus propose the following combinations:

Calycina montana (W.Y.Zhuang & H.D.Zheng) J.K.Mitch., Quijada, P.R.Johnst. & Pfister *comb. nov.*

≡ *Bisporella montana* W.Y.Zhuang & H.D.Zheng in Zhuang, Zheng & Ren, *Mycosystema* **36**(4): 407 (2017).

Holotype: HMAS 275566, China: Yunnan: Pingbian: Daweishan, alt. 1900 m, on rotten wood, 5 Nov. 1999, leg. W.Y. Zhuang & Z.H. Yu 3325 (MBT 378760).

Calycina shangrilana (W.Y.Zhuang & H.D.Zheng) J.K.Mitch., Quijada, P.R.Johnst. & Pfister *comb. nov.*

≡ *Bisporella shangrilana* W.Y.Zhuang & H.D.Zheng in Zhuang, Zheng & Ren, *Mycosystema* **36**(4): 409 (2017).

Holotype: HMAS 275568, China: Yunnan: Shangrila: Bitahai, alt. 3800 m, on rotten wood, 12 Aug. 2008, leg. X.Q. Zhang & D.Z. Ren 7345 (MBT 378758).

Section 5.5

Discussion

Subsection 5.5.1

Taxonomy and Systematics

As previously proposed, our analyses indicate that *Bisporella s.s.* and *Bispora* belong in *Helotiaceae* (Jaklitsch et al. 2016). We synonymize the type species of both genera, *Peziza pallescens* and *Monilia antennata,* noting the close association of the two fungi and sequence data from two specimens indicating that the asexual and sexual states are identical (Tab. 5.1, Fig. 5.2). Culture experiments were not conducted since the authors did not have access to living material. *Bisporella s.s.* becomes a later synonym of *Bispora*, which we take up as the correct generic name. We see no reason to propose the name *Bisporella* for conservation or protection with the current type. Maintaining the current type would considerably alter the concept of the genus as it is now used, which is contrary to the intended purpose of the process of conservation.

Rather than indicating a relationship to any species previously placed in *Bisporella*, our analyses indicate that *Eustilbum aureum* is not placed in any currently recognized family-level lineage in *Helotiales* and should be treated as an independent genus. Most gene regions sequenced were identical, but significant differences were found among sequences of *MCM7* from North America and Europe. This may indicate that these populations are undergoing or have undergone speciation but given the scant material and lack of morphological differences observed between these two populations, we choose not to recognize these as independent taxa, maintaining *Eustilbum* as monotypic. Should they prove to be distinct in the future, two names are available upon which to base combinations for North American material (*Stilbum resinarium* and *Helotium resinicola*). We also note that despite the statement by Weber & Baral that the asci are hemiamyloid, we have observed them to be inamyloid both in European and North American material (Weber 1992).

The results of our phylogenetic analyses agree with previously published work indicating that several species included in *Bisporella* belong instead to *Calycina* in *Pezizellaceae* (Baral et al. 2013; Baral and Rämä 2015), and we agree with Baral's combinations of those species. A number of other species remain in *Bisporella*, however: *Bisporella aesculi*, *B. allantospora*, *B. calycellinoides*, *B. filiformis*, *B. fuegiana*, *B. fuscocincta*, *B. hubeiensis*, *B. hypostroma*, *B. iodocyanescens*, *B. macra*, *B. magnispora*, *B. maireana*, *B. montana*, *B. nannfeldtii*, *B. ochracea*, *B. oritis*, *B. polygoni*, *B. pteridicola*, *B. rubescens*, *B. schusteri*, *B. shangrilana*, *B. sinica*, *B. strumosa*, *B. subpallida*, *B. tetraspora*, and *B. triseptata*. Of these, molecular data are available for three species, *B. montana*, *B. shangrilana*, and *B. subpallida* and these are treated here. The remaining species should be reviewed and, if possible, sequenced to determine their true affiliations.

Though Baral et al. (2013) assumed '*Bisporella*' *subpallida* to be closely related to *Bisporella s. str.*, our analyses show that although in the same family (*Helotiaceae*), '*B.*' *subpallida* is only distantly related, being instead closely related to '*Phaeohelotium*' *epiphyllum*. The ITS sequence for '*B.*' *subpallida* included by Baral et al. (2013) (KC411998) was excluded from our analyses, since Baral stated that it was an accidental sequence of a species of *Olla* (Hans-Otto Baral, pers. comm.). We instead used a more reliable sequence generated by Guy Marson. We have not recombined '*B.*' *subpallida* in *Phaeohelotium* since our analyses, as did Baral et al.'s (2013), also indicate that '*P.*' *epiphyllum* is not a true *Phaeohelotium*, being only distantly related to the type species.

The available sequences of the remaining two species are from holotypes. They nest well in *Calycina*, and we combine them as *Calycina shangrilana* and *Calycina montana*. We do note, however, that *Calycina* in our analyses contains at least two well-supported internal clades. If the concept of *Calycina* were to be restricted in the future, it may be of value to propose *Bisporella* for conservation with *B. citrina* as conserved type, thus allowing the name to be applied to the clade containing *Calycina citrina, C. montana, C. shangrilana*, and what we have tentatively identified as *C.* cf. *confluens*. This would largely be congruent with the previous conception of the genus *Bisporella*, though we also note that there is a fairly high diversity among sequences identified as *C. citrina*, and this confusion should be resolved prior to any such proposals. For the time being, however, we believe it is better for the name to fall into disuse.

Subsection 5.5.2

Distribution

Although originally described from Europe, *Eustilbum aureum* has also been reported from North America but the range of its distribution on each continent differs radically. In Europe it has only been reported from high-elevations in central and southern Europe, primarily in Austria and Germany (Stein 1879; Arnold 1885; Lindau 1908; Zahlbruckner 1911; von Keißler 1917; Cappelletti 1924; Dennis 1952; Jülich 1974; Seifert and Carpenter 1987; Krieglsteiner 1991; Weber 1992; Tholl et al. 1994; Baral and Matheis 2000; Müller et al. 2011). The sexual state has been reliably reported in Europe only once; as mentioned earlier, several recent reports seem to be misidentifications (Krieglsteiner 1991; Weber 1992; Tholl et al. 1994). In contrast to the limited range in Europe, in North America the range of this fungus is much broader, including the Northeastern United States and Southeastern Canada as well as the Pacific Northwest (Baranyay and Funk 1969; Ginns 1986; Seifert and Carpenter 1987; Fernando et al. 1999; Martínez-Iñigo et al. 2000; Tanney 2020; Crous et al. 2019). We further extend the range with reports of one specimen from Alaska and four specimens from the southern Appalachian Mountains. This range likely extends as well through central Canada where the host trees are found. In addition, the sexual state is frequently found in association with the asexual state in North America, especially in the Pacific Northwest (Baranyay and Funk 1969; Seifert and Carpenter 1987). *Eustilbum aureum* has not been reported in Asia but it seems likely that it is also present and should be sought there.

Subsection 5.5.3

Host

Eustilbum aureum does not exhibit a pattern of host specificity beyond being found only on members of *Pinaceae*. It has been reported from *Abies* (Baranyay and Funk 1969; Ginns 1986; Seifert and Carpenter 1987; Martínez-Iñigo et al. 2000), *Larix* (Seifert and Carpenter 1987), *Picea* (Baranyay and Funk 1969; Ginns 1986; Seifert and Carpenter 1987), *Pseudotsuga* (Baranyay and Funk 1969; Ginns 1986), and *Tsuga* (Baranyay and Funk 1969; Ginns 1986). Its absence from the extremely resinous genus *Pinus* was previously noted by Baranyay and Funk (1969), who hypothesized that there may be some component in the resin of *Pinus* that has a particularly inhibitory effect on *E. aureum.* This hypothesis remains to be tested, but no other obvious explanation for observation has presented itself.

Subsection 5.5.4

Asexual States

Additional evidence for the distant relationships of species of *Bispora*, *Calycina* and *Eustilbum* previously included in *Bisporella* is the difference in their known asexual states (we have found no reports of an asexual state for '*Bisporella*' *subpallida*). As shown here, the asexual state of *Bispora pallescens* is a dematiaceous hyphomycete (formerly called *B. antennata*) that produces two-celled arthroconidia. It has long been suspected that these different states were the same fungus; many authors have noted their close association (Hoffmann 1796; Persoon 1800; Fuckel 1870; Dennis 1978; Breitenbach and Kränzlin 1984; Vesterholt 2000). To our knowledge these two states have never been previously shown to be genetically identical. This asexual state differs significantly from that known from culture work (Baranyay and Funk 1969) to be the asexual state of *Bisporella resinicola* (= *Eustilbum aureum*). *Eustilbum aureum* produces

moniliaceous hyphae and yellow-orange synnemata with solitary, hyaline, single-celled conidia produced from phialides. Both of these asexual states differ from those reported for species of *Calycina*. Although apparently less frequently reported, several *Calycina* species have been reported with mutually similar sexual states (phialidic, dematiaceous hyphomycetes). *Calycina herbarum* (the type species of that genus) has been shown to be genetically similar or identical to a *Phialophora*-like anamorphic fungus (Sánchez Márquez et al. 2007). '*Bisporella*' *tetraspora*, *Calycina drosodes*, and *Calycina vulgaris* have been described as having or growing in close association with a *Chalara*-like anamorph; '*Bisporella*' *polygoni* is also found with a species of *Cystodendron* (Carpenter 1981; Morozova 2014). '*Bisporella*' *maireana* has been described as bearing brown phialides on the ectal excipulum (Galán 1993). The most commonly reported anamorph, however, is that of *Calycina claroflava*. It has been described as belonging to the genera *Cystodendron* (Carpenter 1975) or *Bloxamia* (Berthet 1964; Johnston 1988; Lizoň and Korf 1995; Gamundí and Giaiotti 1998). It has also been noted that a number of species of *Chalara* nest phylogenetically within *Calycina* (Baral and Rämä 2015; Guatimosim et al. 2016). Even though these fungi have been assigned to several different asexual-typified genera, the descriptions of these phialidic, dematiaceous asexual states are similar. Thus, it appears that asexual states assigned to *Bisporella s.l.* fall into three distinct groups corresponding to three distinct genera supported by phylogenetic analyses (*Bispora*, *Calycina*, and *Eustilbum*). These differences in asexual states bolster the finding that their sexual states fall into different groups, further supporting the hypothesis that these should be considered in at least three genera.

Section 5.6

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Section 5.7

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Appendix A

Chapter 4 PCR Protocols Used

PCR recipes (including specific components) and cycling parameters used for amplification of sequences used in this study. Protocols are listed under the primer pair they apply to.

NS1-NS4:

PCR Solution

Component	Concentration	Volume (µL)
EconoTaq	5 U/µL	0.125
dNTPs	10 mM each	0.5
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	10×	2.5
DNA Template	1×	5
ddH_2O	—	14.375
Total	—	25

PCR Program:

1. 95°C, 5 minutes
2. 95°C, 1 minute
3. 53°C, 30 seconds
4. 72°C, 2 minutes
5. Go to 2, repeat 2-4, 35 times
6. 72°C, 10 minutes
7. 4°C, ∞

ITS1F-5.8S:

PCR Solution

Component	Concentration	Volume (µL)
EconoTaq	5 U/µL	0.125
dNTPs	10 mM each	0.5
BSA	1% in H_2O	1
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	10×	2.5
DNA Template	.01-1×	5
ddH_2O	—	13.375

Total	—	25

PCR Program:

8. 95°C, 4 minutes
9. 95°C, 1 minute
10. 53°C, 1 minute
11. 72°C, 45 seconds
12. Go to 2, repeat 2-4, 40 times
13. 72°C, 7 minutes
14. 4°C, ∞

5.8SR-ITS4:

PCR Solution

Component	Concentration	Volume (µL)
EconoTaq	5 U/µL	0.125
dNTPs	10 mM each	0.5
BSA	1% in H_2O	1
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	10×	2.5
DNA Template	.01-1×	5
ddH_2O	—	13.375
Total	—	25

PCR Program:

1. 95°C, 4 minutes
2. 95°C, 1 minute
3. 55°C, 1 minute
4. 72°C, 45 seconds
5. Go to 2, repeat 2-4, 40 times
6. 72°C, 7 minutes
7. 4°C, ∞

ITS1F-ITS4:

PCR Solution

Component	Concentration	Volume (µL)
EconoTaq	5 U/µL	0.125
dNTPs	10 mM each	0.5
BSA	1% in H_2O	1
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	10×	2.5
DNA Template	.01-1×	5
ddH_2O	—	13.375

Total	—	25

PCR Program:

1. 95°C, 4 minutes
2. 95°C, 1 minute
3. 53°C, 1 minute
4. 72°C, 1 minute
5. Go to 2, repeat 2-4, 40 times
6. 72°C, 7 minutes
7. 4°C, ∞

ITS1F-LR3:

PCR Solution

Component	Concentration	Volume (µL)
EconoTaq	5 U/µL	0.125
dNTPs	10 mM each	0.5
BSA	1% in H_2O	1
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	10×	2.5
DNA Template	.01-1×	5
ddH_2O	—	13.375
Total	—	25

PCR Program:

1. 95°C, 5 minutes
2. 95°C, 1 minute
3. 53°C, 30 seconds
4. 72°C, 2 minutes
5. Go to 2, repeat 2-4, 35 times
6. 72°C, 10 minutes
7. 4°C, ∞

LR0R-LR5:

PCR Solution

Component	Concentration	Volume (µL)
EconoTaq	5 U/µL	0.125
dNTPs	10 mM each	0.5
BSA	1% in H_2O	1
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	10×	2.5
DNA Template	.01-1×	5
ddH_2O	—	13.375

Total	—	25

PCR Program:

1. 95°C, 4 minutes
2. 95°C, 1 minute
3. 53°C, 1 minute
4. 72°C, 1 minute 30 seconds
5. Go to 2, repeat 2-4, 40 times
6. 72°C, 7 minutes
7. 4°C, ∞

ITS1F-LR5:

PCR Solution

Component	Concentration	Volume (µL)
DNA Template	1×	1
Forward Primer	10 µM	2.5
Reverse Primer	10 µM	2.5
ddH_2O	—	5.7
REDExtract-N-Amp PCR ReadyMix	1×	13.3
Total	—	25

PCR Program:

1. 94°C, 3 minutes
2. 94°C, 1 minute
3. 50°C, 45 seconds
4. 72°C, 1 minute 30 seconds
5. Go to 2, repeat 2-4, 35 times
6. 72°C, 10 minutes
7. 4°C, ∞

mrSSU1-mrSSU3R:

PCR Solution

Component	Concentration	Volume (µL)
Q5	2 U/µL	0.25
dNTPs	10 mM each	0.5
BSA	1% in H_2O	1
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	5×	5
DNA Template	.01-1×	5
ddH_2O	—	10.75
Total	—	25

PCR Program:

1. 98°C, 30 seconds
2. 98°C, 10 seconds
3. 62°C, 30 seconds
4. 72°C, 30 seconds
5. Go to 2, repeat 2-4, 35 times
6. 72°C, 2 minutes
7. 4°C, ∞

fRPB2-5F-fRPB2-7cR:

PCR Solution

Component	Concentration	Volume (µL)
Q5	2 U/µL	0.25
dNTPs	10 mM each	0.5
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	5×	5
DNA Template	1×	5
ddH_2O	—	11.75
Total	—	25

PCR Program:

1. 98°C, 30 seconds
2. 98°C, 10 seconds
3. 67.5°C, 30 seconds, -1°C/cycle
4. 72°C, 40 seconds
5. Go to 2, repeat 2-4, 10 times
6. 98°C, 10 seconds
7. 63°C, 30 seconds
8. 72°C, 40 seconds
9. Go to 2, repeat 6-8, 35 times
10. 72°C, 2 minutes
11. 4°C, ∞

fRPB2-7cF-fRPB2-11aR:

PCR Solution

Component	Concentration	Volume (µL)
Q5	2 U/µL	0.25
dNTPs	10 mM each	0.5
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	5×	5
DNA Template	1×	5
ddH_2O	—	11.75

Total	—	25

PCR Program:

1. 98°C, 30 seconds
2. 98°C, 10 seconds
3. 72°C, 30 seconds, -1°C/cycle
4. 72°C, 40 seconds
5. Go to 2, repeat 2-4, 10 times
6. 98°C, 10 seconds
7. 67.5°C, 30 seconds
8. 72°C, 40 seconds
9. Go to 2, repeat 6-8, 35 times
10. 72°C, 2 minutes
11. 4°C, ∞

Appendix B

Chapter 4 Full Specimen Citations

Full information for specimens examined, including fine locality data, host, collection date, and collector number.

Atrozythia klamathica: **USA**: *Washington*: Whatcom County, Baker Lake, Boulder Creek Campground on Baker Lake Road, 48°42'53" N 121°41'40" W, 287 m a.s.l., apothecia on resin on bole of *Tsuga heterophylla,* 12 Mar. 2018, *M. Haldeman 2748* (hb. Haldeman).

Sarea coeloplata: **Austria**: *Styria*: Wald unter dem Schutzhaus am Stuhleck, auf Harz und Rinde auf Lärchenzweigen [*Larix* sp.], 29 Jun. 1900, *F.X.R. von Höhnel* (FH 0096533). – **Canada**: *Newfoundland and Labrador*: Newfoundland, Division No. 5, Mount Ignoble top, 48°59'55.5" N 57°45'08.7" W, 283 m a.s.l., on *Picea mariana* resin, 26 May 2018, *A. Voitk 18.05.26.AV04* (VAL); ibid., *A. Voitk 18.05.26.AV05* (VAL). *Prince Edward Island*: Kings County, Southampton Wildlife Management Area, 46°21'01.9" N 62°34'10.6" W, *Picea* resin, 3 Oct. 2014, *R.T. McMullin 14963* (CANL); Prince County, Greenpark Provincial Park, 46°35'33.6" N 63°53'33.7" W, *Picea* resin, 30 Sep. 2014, *R.T. McMullin 14565* (CANL 129898). *Quebec*: Lac Clair near Quebec [City?], on spruce [*Picea* sp.], Sep. 1888, *W.G. Farlow* (FH 00995487). *Yukon*: 60°48'13" N 137°26'03" W, 670 m a.s.l., on conifer exudate [probably *Picea* sp.], 7 Jun. 2011, *J.C. Lendemer 29136* (NY 01575087). – **Cape Verde**: *Santo Antão*: Agua das Caldeiras, 17°06'58.91" N 25°04'10.68" W, 1387 m a.s.l., on *Pinus* cf. *nigra* resin, Aug. 2017, *I. Garrido-Benavent IGB457* (VAL). – **Europe**: *J.A.P. Hepp*, *Die Flechten Europas s.n.* (FH 00964656). –

France: *Sarthe*: Bourg-le-Roi, sur la resine des pins [*Pinus* sp.], Aug. 1907, *E. Monguillon 2092* (B 600006463). – **Germany**: *Baden-Württemberg*: Donnstetten auf der Württemberger Alp, an Fichten [*Picea* sp.], 1866, *C.A. Kemmler*, *L.G. Rabenhorst Lichenes Europaei 786* (FH 00965340). *Hessen*: Bergstraße-Odenwald, Oberschönmattenwag, Ellenbachtal, 300 m a.s.l., *Picea*-Harz, 3 May 1953, *O. Behr 6699* (B 600006464). *North Rhine-Westphalia*: Münster, zwischen Lütkenbeck u. Angelmotte [und Angelmodde], auf Wurzeln von Tannen [*Abies* or *Pinus* sp.], Jul. 1861 (B 600198626). – **Italy**: *Sondrio*: ad coniferarum truncos et ramos resina illinitos, *M. Anzi Lichenes Rariores Langobardi Exsiccati 267B* (FH 00965341). *Vercelli*: Valsesia, presso Riva, nelle anfrattuosità e cicatrici resinose della corteccia delle conifere, 1863, *A. Carestia*, *Erbario Crittogamico Italiano 1166* (FH 00965351). – **Norway**: *Buskerud*: prope Drammen ad Gulskoven [= Gulskogen], *J.M. Norman* (TROM L-42692). *Hedmark*: Furuberget Quarry, 60°49'01.11" N 11°02'23.53" E, on resin of fallen *Pinus sylvestris* attacked by *Cronartium flaccidum* or *Peridermium pini*, 14 Sep. 2017, *P. Vetlesen PV-D836-B* (FH 00965387). – **Spain**: *Madrid*: San Lorenzo de el Escorial, Pinar de Abantos, 40°35'38.77" N 4°09'36.11" W, 1200 m a.s.l., on *Pinus pinaster* resin, 5 Jun. 2017, *I. Garrido-Benavent IGB454* (VAL). *Santa Cruz de Tenerife*: Tenerife, Lomo de la Jara, on *Pinus radiata* resin, 23 May 2019, *R.N. Piñero 19052301* (VAL). *Soria*: Abejar, Playa Pita, 41°50'16.42" N 2°46'43.85" W, 1090 m a.s.l., on *Pinus sylvestris* resin, 16 Mar. 2014, *I. Garrido-Benavent IGB316* (VAL). *Valencia*: Barx, Pla de la Nevereta, 38°59'52.43" N 0°18'15.35" W, 677 m a.s.l., on *Pinus halapensis* resin, 4 Jan. 2018, *I. Garrido-Benavent IGB452* (VAL); Quatretonda, Pla de Mora, 38°59'58.67" N 0°22'34.71" W, 223 m a.s.l., on *Pinus halapensis* resin, 27 Dec. 2017, *I. Garrido-Benavent IGB448* (VAL); ibid., *I. Garrido-Benavent IGB451* (VAL). – **Switzerland**: *Grisons*: Davos, Davos Lake, 46°49'07.06" N 9°51'25.33" E, 1579 m a.s.l., on *Picea abies* resin, 18 Jun. 2018, *I.*

Garrido-Benavent IGB716 (VAL); ibid., *I. Garrido-Benavent IGB717* (VAL). *Wallis*: Unter Wallis, Va. d'Herens, S. of Sion. Arbey, c. 1 km W of Evolène, c. 46°06'36.0" N 7°29'02.1" E, c. 1450 m a.s.l., 26 Jul. 1990, *H. Sipman* 30286 (B 600080177). – **USA**: *Arkansas*: Faulkner County, Cove Creek Natural Area, 35°17'24" N 92°28'48" W, on *Pinus* resin, 7 Oct. 2010, *J.C. Lendemer, D. Ladd & C.A. Morse 26230-A* (NY 01218604). *California*: Del Norte County, Jedediah Smith Redwoods State Park, 41°49'11.9" N 124°07'02.3" W, 35 m a.s.l., on *Tsuga heterophylla* resin, 13 Dec. 2017, *J.K. Mitchell JM0071* (FH); ibid., 41°48'44.3" N 124°06'32.3" W, 57 m a.s.l., on *Tsuga heterophylla* resin, 13 Dec. 2017, *J.K. Mitchell JM0072* (FH); ibid., Redwoods National Park, 41°32'05.6" N 124°04'16.0" W, 10 m a.s.l., on *Picea sitchensis* resin, 14 Dec. 2017, *J.K. Mitchell JM0073.8* (FH); El Dorado County, Eldorado National Forest, Placerville Ranger District Headquarters, 38°44'15.1" N 120°39'51.0" W, 985 m a.s.l., on *Pinus ponderosa* resin, 6 Dec. 2017, *J.K. Mitchell JM0047* (FH); ibid., *J.K. Mitchell JM0048* (FH); ibid., 38°44'10.1" N 120°39'52.1" W, 1022 m a.s.l., on *Pinus nigra* subsp. *laricio* resin, 6 Dec. 2017, *J.K. Mitchell JM0049.1* (FH); Humboldt County, Prairie Creek Redwoods State Park, 41°21'13.5" N 124°01'35.5" W, 32 m a.s.l., on *Picea sitchensis* resin, 14 Dec. 2017, *J.K. Mitchell JM0075.2* (FH); Nevada County, Tahoe National Forest, Supervisor's Office, 39°16'09.6" N 121°01'02.3" W, 784 m a.s.l., on *Pinus ponderosa* resin, 7 Dec. 2017, *J.K. Mitchell JM0055* (FH); Plumas County, Plumas National Forest, 39°42'26.7" N 121°11'39.8" W, 1060 m a.s.l., on *Pseudotsuga menziesii* var. *menziesii* resin, 8 Dec. 2017, *J.K. Mitchell JM0064.2* (FH); Sierra County, Tahoe National Forest, 39°31'10.1" N 121°00'03.1" W, 668 m a.s.l., on *Pseudotsuga menziesii* var. *menziesii* resin, 7 Dec. 2017, *J.K. Mitchell JM0060.2* (FH); ibid., 39°31'09.3" N 121°00'03.1" W, 668 m a.s.l., on *Pinus ponderosa* resin, 7 Dec. 2017, *J.K. Mitchell JM0061.2* (FH); Siskiyou County, Klamath National Forest, 41°50'04.5" N

123°25'35.0” W, 549 m, a.s.l., on *Pseudotsuga menziesii* var. *menziesii* resin, 12 Dec. 2017, *J.K. Mitchell JM0070.2* (FH 00965409); Yuba County, Tahoe National Forest, 39°24'08.0” N 121°04'46.2” W, 505 m a.s.l., on *Pseudotsuga menziesii* var. *menziesii* resin, 7 Dec. 2017, *J.K. Mitchell JM0057.2* (FH); ibid., 39°24'16.8” N 121°04'34.9” W, 524 m a.s.l., on *Pinus ponderosa* resin, 7 Dec. 2017, *J.K. Mitchell JM0058.2* (FH); ibid., 39°31'09.8” N 121°00'03.5” W, 668 m a.s.l., on *Pseudotsuga menziesii* var. *menziesii* resin, 7 Dec. 2017, *J.K. Mitchell JM0059* (FH). *Maine*: York County, York, on spruce [*Picea* sp.] roots, *R. Thaxter 1459* (FH 00965337); ibid., on spruce [*Picea* sp.] resin, 12 Aug. 1897, *R. Thaxter* (FH 00995492). *Massachusetts*: Bristol County, New Bedford, on white pine [*Pinus strobus*], 1883, *H. Willey* (FH 00979165); Essex County, Appleton Farms Grass Rides, 42°38'40.80” N 70°52'04.20” W, 21 May 2017, *E. Kneiper & J.K. Mitchell JM0003* (FH); ibid., Groveland, Aug. 1890, *W.G. Farlow* (FH 00445743); ibid., on *Pinus rigida*, Aug. 1890, *W.G. Farlow* (FH 00979164); Middlesex County, Concord, Estabrook Woods, 42°29'00.26” N 71°21'24.88” W, on *Pinus strobus* resin, 19 Sep. 2017, *J.K. Mitchell JM0017* (FH); ibid., 42°29'00.19” N 71°21'24.15” W, 67 m a.s.l., on resin of *Pinus strobus*, 25 Jan. 2020, *J.K. Mitchell & D.E.W. Adamec JM0132* (FH); Suffolk County, Arnold Arboretum, 42°17'55.34” N 71°07'33.38” W, on *Pinus tabuliformis* 16576N resin, 27 Jul. 2017, *J.K. Mitchell JM0011* (FH); ibid., 42°17'53.71” N 71°07'40.06” W, on *Picea glehnii* 16485-B resin, 8 Oct. 2017, *J.K. Mitchell & L. Quijada JM0020* (FH); ibid., Thompson Island, 42°18'44.69” N 71°00'39.81” W, on *Pinus nigra* resin, 17 May 2017, *L.A. Kappler & J.K. Mitchell BHI-F925* (FH); ibid., 42°18'44.96” N 71°00'40.93” W, on *Pinus nigra* resin, 17 May 2017, *L.A. Kappler & J.K. Mitchell BHI-F926* (FH); Worcester County, Devens Reserve Forces Training Area, 42°28'22.60” N 71°39'11.34” W, 87 m a.s.l., on hardened trunk resin of *Pinus rigida*, 10 Sep. 1998, *E. Kneiper K987694* (FH 00405294). *New Hampshire*: Carroll County,

Tamworth, Chocorua, on pine [*Pinus* sp.] resin, 23 Sep. 1909, *W.G. Farlow* (FH 00979162); Hillsborough County, Antrim, Loveren's Mill Cedar Swamp Preserve, 43°14'22.96" N 72°01'28.19" W, 336 m a.s.l., on *Abies balsamea* resin, 10 Sep. 2018, *J.K. Mitchell & Luis Quijada JM0104.2* (FH). *New York*: Adirondacks, Essex County, Keene Valley, Sep. 1902, *W.G. Farlow* (FH 00995485). *Ohio*: Morgan County, Burr Oak State Park, 39°31'44.24" N 82°01'38.14" W, on *Pinus strobus* resin, 7 Oct. 2017, *T.J. Curtis JM-TJC01* (KE 5869). *Oregon*: Lane County, Eugene, Hendricks Park, on *Pseudotsuga* resin, 5 Aug. 1978, *M.A. Sherwood* (FH 00965334); ibid., H. J. Andrews Experimental Forest, 472 m a.s.l., 16 Mar. 1979, *M.A. Sherwood* (FH 00965336). *Wisconsin*: Door County, Whitefish Dunes State Park, 44°55'22.8" N 87°11'39.8" W, 190 m a.s.l., on resin of *Thuja occidentalis*, 10 May 2019, *A.C. Dirks ACD0147* (MICH 139996). *Vermont*: Washington County, Calais, Chickering Bog Natural Area, 44°19'48.00" N 72°28'17.60" W, on *Pinus* cf. *banksiana* resin, 21 Oct. 2017, *J.K. Mitchell & L. Quijada JM0024* (FH); ibid., 44°19'43.30" N 72°28'17.50" W, on *Pinus* cf. *banksiana* resin, 21 Oct. 2017, *J.K. Mitchell & L. Quijada JM0027* (FH); ibid., 44°19'28.80" N 72°28'24.40" W, on *Abies balsamea* resin, 21 Oct. 2017, *J.K. Mitchell & L. Quijada JM0029* (FH).

Sarea difformis: **Canada**: *British Columbia*: Calvert Island, 51°39'18.0" N 128°08'16.8" W, resinicolous, 18 Jun. 2018, *R.T. McMullin 19801* (CANL 132189). *Nova Scotia*: Halifax County, Old Annapolis Road Nature Reserve, 44°45'03.9" N 63°56'33.5" W, resinicolous, 25 Jun. 2017, *R.T. McMullin 17350* (CANL). *Ontario*: Nipissing District, Algonquin Provincial Park, 45°54'08.5" N 77°53'13.1" W, *Picea* sp., 1 Sep. 2013, *R.T. McMullin 12673* (CANL 132522). *Prince Edward Island*: Kings County, Dromore Wildlife Management Area, 46°18'30.3" N 62°49'47.8" W, *Picea* resin, 7 Oct. 2014, *R.T. McMullin 14881* (CANL 129879); Queens

County, Mount Stewart Wildlife Management Area, 46°22'55.9" N 62°51'40.0" W, *Picea* resin, 1 Oct. 2014, *R.T. McMullin 14453* (CANL). – **Czechia**: *Central Bohemia*: Brdy Hills, Nepomuk, 49°40'02" N 13°49'05" E, 765 m a.s.l., on resin of *Picea abies,* 15 Aug. 2018, *J. Malíček & J. Vondrák 12001* (hb. Malíček). *Plzen*: Srby, 49°31'21" N 13°34'25" E, 550 m a.s.l., on resin of *Picea abies*, 25 Oct. 2018, *J. Malíček & J. Vondrák 12161* (hb. Malíček). – **Europe**: *J.A.P. Hepp, Die Flechten Europas s.n.* (FH 00964655). – **Italy**: *Vercelli*: Valsesia, presso Riva, nelle anfrattuosità e cicatrici resinose della corteccia delle conifere, 1863, *A. Carestia*, *Erbario Crittogamico Italiano 1166* (FH 00965351). – **Norway**: *Hedmark*: Furuberget Quarry, 60°49'01.11" N 11°02'23.53" E, on resin of fallen *Pinus sylvestris* attacked by *Cronartium flaccidum* or *Peridermium pini*, 14 Sep. 2017, *P. Vetlesen PV-D836* (FH 00965386). – **USA:** *Arkansas*: Faulkner County, Cove Creek Natural Area, 35°17'24" N 92°28'48" W, on *Pinus* resin, 7 Oct. 2010, *J.C. Lendemer, D. Ladd & C.A. Morse 26230* (NY 01218605). *California*: Del Norte County, Jedediah Smith Redwoods State Park, 41°48'44.3" N 124°06'32.3" W, 57 m a.s.l., on *Tsuga heterophylla* resin, 13 Dec. 2017, *J.K. Mitchell JM0072* (FH); ibid., Redwoods National Park, 41°32'05.6" N 124°04'16.0" W, 10 m a.s.l., on *Picea sitchensis* resin, 14 Dec. 2017, *J.K. Mitchell JM0074.1* (FH); Plumas County, Plumas National Forest, 39°42'31.9" N 121°11'40.3" W, 1056 m a.s.l., on resin of *Pinus lambertiana* resin, 8 Dec. 2017, *J.K. Mitchell JM0065.2* (FH). *Georgia*: Douglas County, Sweetwater Creek State Park, 33°45'12.86" N 84°37'44.54" W, on *Pinus* cf. *taeda* resin, 21 Jul. 2017, *J.K. Mitchell & M. Barrios JM0010.1* (FH 00965390); White County, Unicoi State Park, 34°42'43.00" N 83°43'49.60" W, on *Pinus* sp. resin, 16 Jul. 2017, *J.K. Mitchell JM0009.2* (FH 00965389). *Indiana*: Monroe County, Morgan-Monroe State Forest, 39°18'16" N 86°23'24" W, 259 m a.s.l., on *Pinus strobus* resin, 13 Apr. 2017, *J.C. Lendemer 51265* (NY 02795595); ibid., 39°17'56" N 86°23'37" W, 232 m a.s.l., on

Pinus strobus resin, 13 Apr. 2017, *J.C. Lendemer 51272* (NY 02795588). *Maine*: Washington County, Eagle Hill Institute, 44°27'35.03" N 67°55'53.01" W, 5 m a.s.l., on *Picea rubens* resin, 22 May 2017, *E. Kneiper JMEK* (FH); ibid., 44°27'23.36" N 67°55'44.11" W, 51 m a.s.l., on *Pinus banksiana* resin, 28 May 2017, *J.M. Karakehian 17052821F* (FH); ibid., 44°27'36.01" N 67°55'46.92" W, on *Picea* cf. *glauca* resin, 3 Jul. 2017, *J.K. Mitchell JM0007* (FH); ibid., 44°27'34.8" N 67°55'58.6" W, resinicolous on *Picea*, 7 Jun. 2018, *R.T. McMullin 19157* (CANL); ibid., Machiasport, on living tree (fir [*Abies* sp.]), 26 Aug. 1898, *M.A. Barker 44* (FH 00995486); York County, Kittery, Kittery Point, on resin of *Pinus strobus*, 5 Feb. 1887, *R. Thaxter* (FH 00979158); ibid., *R. Thaxter 2886* (FH 00995497); ibid., York, on spruce [*Picea* sp.] roots, *R. Thaxter 1459* (FH 00965337); ibid., on resin of *Picea* sp., *R. Thaxter*, *Reliquiae Farlowianae 669* (FH 00995493); ibid., *R. Thaxter 5573* (FH 00995499). *Massachusetts*: Bristol County, New Bedford, on pine [*Pinus* sp.] gum, 1865, *H. Willey* (FH 00965345); ibid., on white pine [*Pinus strobus*], 1882, *H. Willey 950* (FH 00965344); Essex County, Groveland, on *P*[*inus*] *rigida*, Aug. 1890, *W.G. Farlow* (FH 00979163); Middlesex County, Concord, Estabrook Woods, 42°28'59.96" N 71°21'24.97" W, on *Pinus strobus* resin, 19 September 2017, *J.K. Mitchell JM0015* (FH); Norfolk County, Blue Hills Reservation, on resin on bark, 18 Apr. 1993, *D.H. Pfister* (FH 00965333); Suffolk County, Boston, Arnold Arboretum, 42°17'55.53" N 71°07'31.63" W, on *Pinus strobus* 'Contorta' resin, 13 May 2017, *J.K. Mitchell JM0001* (FH); ibid., 42°17'55.34" N 71°07'33.38" W, on *Pinus tabuliformis* 16576N resin, 27 Jul. 2017, *J.K. Mitchell JM0011* (FH); Worcester County, Petersham, Harvard Forest, 42°32'15.03" N 72°10'58.94" W, on *Picea mariana* resin, 13 May 2018, *J.K. Mitchell & L. Quijada JM0082* (FH). *Minnesota*: Isanti County, Cedar Creek Ecosystem Science Reserve, 45°25'15.39" N 93°11'48.88" W, 292 m a.s.l., on *Pinus strobus* resin, 11 Aug. 2019, *J.K. Mitchell JM0108* (FH

00965393). *New Hampshire*: Carroll County, Intervale, *R. Thaxter* (FH 00979159); ibid., Tamworth, Chocorua, Sep. 1907, *W.G. Farlow* (FH 00995494); ibid., on *P*[*inus*] *strobus*, Aug. 1910, *W.G. Farlow* (FH 00979161); Coos County, Randolph, on fir [*Abies* sp.] gum, 1885, *H. Willey 1015* (FH 00979157); ibid., *H. Willey 1015* (FH 00965342); ibid., Shelburne, Sep. 1891, *W.G. Farlow* (FH 00995490); ibid., White Mountains National Forest, Tuckerman Ravine Trail, 44°15'41.45" N 71°16'02.38" W, 882 m a.s.l., on *Abies balsamea* resin, 16 Jun. 2018, *J.K. Mitchell JM0091* (FH 00965398); ibid., 44°15'49.75" N 71°16'40.29" W, 1049 m a.s.l., on *Picea rubens* resin, 16 Jun. 2018, *J.K. Mitchell JM0092* (FH 00965399). *North Carolina*: Swain County, Great Smoky Mountains National Park, 35°32'25-33'17" N 83°29'36"-44" W, 1768-1859 m a.s.l., 10 Oct. 2011, *E.A. Tripp & J.C. Lendemer 2261* (NY 01685454). *Tennessee*: Sevier County, Great Smoky Mountains National Park, Boulevard Trail, 35°38'03" N 83°24'50" W, 1814 m a.s.l., 7 Aug. 2012, *E.A. Tripp & J.C. Lendemer 3446* (NY 01685081); ibid., Bullhead Trail, 35°39'36"-40'32" N 83°27'02"-29'08" W, on *Picea* sap, 9 Oct. 2011, *J.C. Lendemer, E.A. Tripp & E. Darling 30379* (NY 01237252); ibid., Sugarland Mountain Trail, resinicolous on *Picea*, 26 Oct. 2017, *R.T. McMullin 19017* (NY 03303142). *Vermont*: Washington County, Calais, Chickering Bog Natural Area, 44°19'26.30" N 72°28'39.20" W, on *Picea* sp. resin, 21 Oct. 2017, *J.K. Mitchell & L. Quijada JM0031* (FH); ibid., 44°19'31.30" N 72°28'48.30" W, on *Larix laricina* resin, 21 Oct. 2017, *J.K. Mitchell & L. Quijada JM0032* (FH).

Zythia resinae: **Cape Verde**: *Santiago*: São Miguel, Serra Malagueta, 15°10'46.99" N 23°40'21.11" W, 1029 m a.s.l., on *Pinus canariensis* resin, 29 Jul. 2017, *I. Garrido-Benavent IGB456* (VAL). – **China**: *Heilongjiang*: Jixi, Hulin, Dōngfāng hóng, on *Pinus koraiensis* resin, 4 Sep. 1986, *T. Kobayashi & J.-Z. Zhao FPH-6930* (TFM); Mudanjiang, Ning'an, Dōngjīng zhèn,

on *Pinus koraiensis* resin, 11 Sep. 1986, *T. Kobayashi & J.-Z. Zhao FPH-6932* (TFM); ibid., Jiangshanjiao Experimental Forest Farm, on *Pinus koraiensis* resin, 9 Sep. 1986, *T. Kobayashi FPH-6926* (TFM); Qitaihe, Boli, on *Pinus koraiensis* resin, 15 Sep. 1986, *T. Kobayashi & J.-Z. Zhao FPH-6931* (TFM). *Yunnan*: Lijiang County, Lijiang, Elephant Mountain, 26°53'18" N 100°14'12" E, 2400 m a.s.l., on resinous trunk of *Pinus* sp., 20 Oct. 2002, *H. Sipman 49954* (B 600202098); ibid., 26°53'13" N 100°14'05" E, 2550 m a.s.l., on *Pinus* sp. resin, 20 Oct. 2002, *A. Aptroot 56089* (DUKE 0133124). – **Czechia**: *Central Bohemia*: Brdy Hills, 49°44'52" N 13°56'44" E, 650 m a.s.l., on resin of *Larix decidua*, 30 Aug. 2018, *J. Malíček & J. Vondrák 12020* (hb. Malíček); ibid., Jince, 49°45'44" N 13°56'21" E, 580 m a.s.l., on resin of *Larix decidua*, 27 Aug. 2018, *J. Malíček & J. Vondrák 12018* (hb. Malíček); ibid., Nepomuk, 49°40'06" N 13°49'34" E, 730 m a.s.l., on resin of *Picea abies*, 15 Aug. 2018, *J. Malíček & J. Vondrák 12005* (hb. Malíček); ibid., Strasice, 49°43'34" N 13°47'56" E, 610 m a.s.l., on resin of *Larix decidua*, 20 Aug. 2018, *J. Malíček & J. Vondrák 11998* (hb. Malíček). *Plzen*: Srby, 49°31'21" N 13°34'25" E, 550 m a.s.l., on resin of *Larix decidua*, 25 Oct. 2018, *J. Malíček & J. Vondrák 12159* (hb. Malíček). – **Dominican Republic**: *La Vega Province*: Parque Nacional Juan B. Perez, on resin of *Pinus occidentalis*, 7 Jan. 2002, *S. Cantrell, T. Iturriaga, J. Lodge, D.H. Pfister & M. de la Cruz DR-56* (FH 00965385). – **Japan**: *Ibaraki Prefecture*: Naka-gun, Hitachiota-shi, Mchiya, on *Pinus* bark and resin, 9 Nov. 2002, *T. Hosoya THX-134* (TNS-F-41522). – **Norway**: *Hedmark*: Furuberget Quarry, 60°49'01.11" N 11°02'23.53" E, on resin of fallen *Pinus sylvestris* attacked by *Cronartium flaccidum* or *Peridermium pini*, 14 Sep. 2017, *P. Vetlesen PV-D836-B* (FH 00965387). – **Spain**: *Santa Cruz de Tenerife*: Tenerife, Los Revolcaderos, on *Pinus radiata* resin, 16 Dec. 2017, *R.N. Piñero 17121601* (VAL); ibid., 11 Apr. 2018, *R.N. Piñero 18041101* (VAL). *Soria*: Abejar, Playa Pita, 41°50'16.42" N 2°46'43.85"

W, 1090 m a.s.l., on *Pinus sylvestris* resin, 16 Mar. 2014, *I. Garrido-Benavent IGB316* (VAL). *Valencia*: Barx, Pla de la Nevereta, 38°59'52.43" N 0°18'15.35" W, 677 m a.s.l., on *Pinus halapensis* resin, 4 Jan. 2018, *I. Garrido-Benavent IGB453* (VAL); Quatretonda, 38°57'46.35" N 0°22'31.18" W, 367 m a.s.l., on *Cupressus arizonica* resin, 20 Aug. 2013, *I. Garrido-Benavent IGB317* (VAL); ibid., Pla de Mora, 38°59'58.67" N 0°22'34.71" W, 223 m a.s.l., on *Pinus halapensis* resin, 27 Dec. 2017, *I. Garrido-Benavent IGB449* (VAL); ibid., on *Cupressus sempervirens* resin, 27 Dec. 2017, *I. Garrido-Benavent IGB450* (VAL). – **USA**: *Arizona*: Coconino County, San Francisco Peaks, 35°21' N 111°41' W, 3450 m a.s.l., on *Pinus aristata* resinous bark, 12 Jun. 1998, *M. Westberg 851* (LD 1356193). *California*: Del Norte County, Redwoods National Park, 41°32'05.6" N 124°04'16.0" W, 10 m a.s.l., on *Picea sitchensis* resin, 14 Dec. 2017, *J.K. Mitchell JM0074.2* (FH); Plumas County, Plumas National Forest, 39°42'26.7" N 121°11'39.8" W, 1060 m a.s.l., on *Pseudotsuga menziesii* resin, 8 Dec. 2017, *J.K. Mitchell JM0064.1* (FH); ibid., 39°42'31.9" N 121°11'40.3" W, 1056 m a.s.l., on *Pinus lambertiana* resin, 8 Dec. 2017, *J.K. Mitchell JM0065.1* (FH); San Diego County, Cleveland National Forest, 32°51'13.1" N 116°34'40.5" W, 1170 m a.s.l., on *Cupressus forbesii* bark and resin, 27 Dec. 2017, *J.K. Mitchell & M.D. Mitchell JM0077* (FH); Siskiyou County, Klamath National Forest, 41°50'03.6" N 123°25'42.1" W, 566 m a.s.l., on *Chamaecyparis lawsoniana* resin, 12 Dec. 2017, *J.K. Mitchell JM0068* (FH 00965406). *Georgia*: Douglas County, Sweetwater Creek State Park, 33°45'12.86" N 84°37'44.54" W, on *Pinus* cf. *taeda* resin, 21 Jul. 2017, *J.K. Mitchell & M. Barrios JM0010.2* (FH 00965391); White County, Unicoi State Park, 34°42'43.00" N 83°43'49.60" W, on *Pinus* sp. resin, 16 Jul. 2017, *J.K. Mitchell JM0009.1* (FH 00965388). *Idaho*: Clearwater County, 2 km NE of Southwick, 46°37'20.42" N 116°27'05.98" W, 785 m a.s.l., on resin on bark of bole of *Pseudotsuga menziesii*, 26 Aug. 2017, *M. Haldeman*

2514 (hb. Haldeman). *Maine*: Lincoln County, Southport, Pratts Island, on resin of *Picea*, 19 Feb. 1989, *D.H. Pfister* (FH 00965332); Washington County, Eagle Hill Institute, 44°27'36.00" N 67°55'49.40" W, on *Picea* cf. *glauca* resin, 3 Jul. 2017, *J.K. Mitchell JM0006* (FH); ibid., Milbridge, 44°32'24.10" N 67°52'52.60" W, on *Picea glauca* resin, 6 Jul. 2017, *J.K. Mitchell JM0008* (FH). *Massachusetts*: Barnstable County, Cape Cod National Seashore, Marconi Beach, 41°54'41.37" N 69°58'49.03" W, 9 m a.s.l., on resin of *Chamaecyparis thyoides*, 18 Oct. 2019, *J.K. Mitchell & D.E.W. Adamec JM0120* (FH); ibid., on *Chamaecyparis thyoides* canker, 15 Oct. 2011, *J.M. Karakehian 11101502* (FH); Essex County, Appleton Farms Grass Rides, 42°38'30.10" N 70°51'49.30" W, on *Pinus* sp. resin, 21 May 2017, *E. Kneiper & J.K. Mitchell JM0004* (FH); Middlesex County, Concord, Estabrook Woods, 42°29'00.15" N 71°21'23.47" W, 67 m a.s.l., on resin of *Pinus strobus*, 25 Jan. 2020, *J.K. Mitchell & D.E.W. Adamec JM0131* (FH); Norfolk County, Blue Hills Reservation, on resin on bark, 18 Apr. 1993, *D.H. Pfister* (FH 00965333); ibid., Webb Memorial State Park, 42°15'29.58" N 70°55'22.62" W, 1 m a.s.l., on resin of live *Pinus nigra* tree, 29 Mar. 2017, *A.C. Dirks & J.K. Mitchell BHI-F779* (FH); Plymouth County, Grape Island, 42°16'15.67" N 70°55'07.43" W, on resin flow of *Pinus strobus* tree, 3 May 2017, *L.A. Kappler & J.K. Mitchell BHI-F871* (FH); Suffolk County, Arnold Arboretum, 42°17'55.49" N 71°07'33.83" W, on *Pinus sylvestris* 438-57-B resin, 27 Jul. 2017, *J.K. Mitchell JM0012* (FH); ibid., 42°17'54.93" N 71°07'29.95" W, on *Chamaecyparis obtusa* resin, 30 Oct. 2017, *J.K. Mitchell & L. Quijada JM0036* (FH); Worcester County, Devens Reserve Forces Training Area, 42°28'22.60" N 71°39'11.34" W, 87 m a.s.l., on hardened trunk resin of *Pinus rigida*, 10 Sep. 1998, *E. Kneiper K987694* (FH 00405294); ibid., Petersham, Harvard Forest, 42°32'09.37" N 72°11'16.15" W, on resin of a live *Pinus strobus* tree, 18 Aug. 2017, *J.K. Mitchell JM0014* (FH); ibid., Princeton, Mass Audubon's Wachusett Meadow

Wildlife Sanctuary, 42°27'20.1" N 71°54'18.7" W, 312 m a.s.l., on resin of planted *Juniperus virginiana*, 28 Dec. 2019, *J.K. Mitchell JM0125* (FH). *Michigan*: Washtenaw County, Ann Arbor, University of Michigan North Campus, 42°17'43.8" N 83°43'29.9" W, 289 m a.s.l., on resin of *Pinus sylvestris*, 9 Nov. 2019, *A.C. Dirks ACD0229* (MICH 139997). *Minnesota*: Isanti County, Cedar Creek Ecosystem Science Reserve, 45°25'15.39" N 93°11'48.88" W, 292 m a.s.l., on resin of *Pinus strobus*, 11 Aug. 2019, *J.K. Mitchell JM0107* (FH 00965392). *North Carolina*: Camden County, North River Game Land, 36°21'24" N 76°13'06" W, 0 m a.s.l., on *Taxodium* exudate, 12 Apr. 2012, *B. P. Hodkinson, J. Allen, R. C. Harris & J. C. Lendemer 18239* (NY 01886893); Onslow County, Jacksonville, on *Juniperus scopulorum* 'SkyRocket' resinous wound, 7 Apr. 2006, *J. Morton* (NCSLG 17391). *Oregon*: Lane County, Eugene, Hendricks Park, on *Pseudotsuga* resin, 5 Aug. 1978, *M.A. Sherwood* (FH 00965334). *Rhode Island*: Washington County, Ell Pond Preserve, 41°30'22.00" N 71°46'46.66" W, on *Chamaecyparis thyoides* resin, 26 Nov. 2017, *J.K. Mitchell & L. Quijada JM0044* (FH). *Washington*: Whatcom County, Baker Lake, 48°42'53" N 121°41'40" W, 287 m a.s.l., on resin on bole of 71 cm diameter *Pseudotsuga menziesii*, 12 Mar. 2018, *M. Haldeman 2747* (hb. Haldeman). *Wisconsin*: Dane County, Mazomanie Bottoms State Natural Area, 43°13'34.7" N 89°48'14.0" W, 225 m a.s.l., on resin of *Pinus* sp., 4 May 2019, *A.C. Dirks ACD0083* (MICH 139995); Door County, Whitefish Dunes State Park, 44°55'22.8" N 87°11'39.8" W, 190 m a.s.l., on resin of *Thuja occidentalis*, 10 May 2019, *A.C. Dirks ACD0147* (MICH 139996).

Appendix C

Chapter 5 PCR Protocols Used

PCR recipes (including specific components) and cycling parameters used for amplification of sequences used in this study. Protocols are listed under the primer pair they apply to.

ITS1F-LR3:

PCR Solution

Component	Concentration	Volume (µL)
EconoTaq	5 U/µL	0.125
dNTPs	10 mM each	0.5
BSA	1% in H_2O	1
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	10×	2.5
DNA Template	.01-1×	5
ddH_2O	—	13.375
Total	—	25

PCR Program:

8. 95°C, 5 minutes
9. 95°C, 1 minute
10. 53°C, 30 seconds
11. 72°C, 2 minutes
12. Go to 2, repeat 2-4, 35 times
13. 72°C, 10 minutes
14. 4°C, ∞

LR0R-LR5:

PCR Solution

Component	Concentration	Volume (µL)
EconoTaq	5 U/µL	0.125
dNTPs	10 mM each	0.5
BSA	1% in H_2O	1
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	10×	2.5
DNA Template	.01-1×	5

ddH_2O	—	13.375
Total	—	25

PCR Program:

8. 95°C, 4 minutes
9. 95°C, 1 minute
10. 53°C, 1 minute
11. 72°C, 1 minute 30 seconds
12. Go to 2, repeat 2-4, 40 times
13. 72°C, 7 minutes
14. 4°C, ∞

Mcm7-709for-Mcm7-1348rev or Mcm7-CalicF-Mcm7-CalicR:

PCR Solution

Component	Concentration	Volume (µL)
EconoTaq	5 U/µL	0.2
dNTPs	10 mM each	0.5
BSA	1% in H_2O	1
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	10×	2.5
DNA Template	.01-1×	5
ddH_2O	—	13.3
Total	—	25

PCR Program:

1. 94°C, 5 minutes
2. 94°C, 45 seconds
3. 55°C, 50 seconds
4. 72°C, 1 minute
5. Go to 2, repeat 2-4, 40 times
6. 72°C, 5 minutes
7. 4°C, ∞

EF1-983F-EF1-2218R:

PCR Solution

Component	Concentration	Volume (µL)
DMSO	—	0.25
ddH_2O	—	0.45
BSA	1% in H_2O	1
Forward Primer	10 µM	2.5
Reverse Primer	10 µM	2.5
DNA Template	.01-1×	5

REDExtract-N-Amp PCR ReadyMix	1×	13.3
Total	—	25

PCR Program:

12. 94°C, 10 minutes
13. 94°C, 2 minutes
14. 69°C, 1 minute, -1°C/cycle
15. 72°C, 3 minutes
16. Go to 2, repeat 2-4, 10 times
17. 94°C, 30 seconds
18. 59°C, 30 seconds
19. 72°C, 2 minutes
20. Go to 2, repeat 6-8, 37 times
21. 72°C, 10 minutes
22. 4°C, ∞

RPB2:

PCR Solution

Component	Concentration	Volume (µL)
Q5	2 U/µL	0.25
dNTPs	10 mM each	0.5
BSA	1% in H_2O	1
Forward Primer	10 µM	1.25
Reverse Primer	10 µM	1.25
PCR Buffer	5×	5
DNA Template	.01-1×	5
ddH_2O	—	10.75
Total	—	25

fRPB2-5F-fRPB2-7cR:

PCR Program:

1. 98°C, 30 seconds
2. 98°C, 10 seconds
3. 67.5°C, 30 seconds, -1°C/cycle
4. 72°C, 40 seconds
5. Go to 2, repeat 2-4, 10 times
6. 98°C, 10 seconds
7. 63°C, 30 seconds
8. 72°C, 40 seconds
9. Go to 2, repeat 6-8, 35 times
10. 72°C, 2 minutes
11. 4°C, ∞

RPB2-5FCal-RPB2-7RCal:

PCR Program:

1. 98°C, 30 seconds
2. 98°C, 10 seconds
3. 64°C, 30 seconds
4. 72°C, 30 seconds
5. Go to 2, repeat 2-4, 35 times
6. 72°C, 2 minutes
7. 4°C, ∞

RPB2-5FEus-RPB2-7REus:

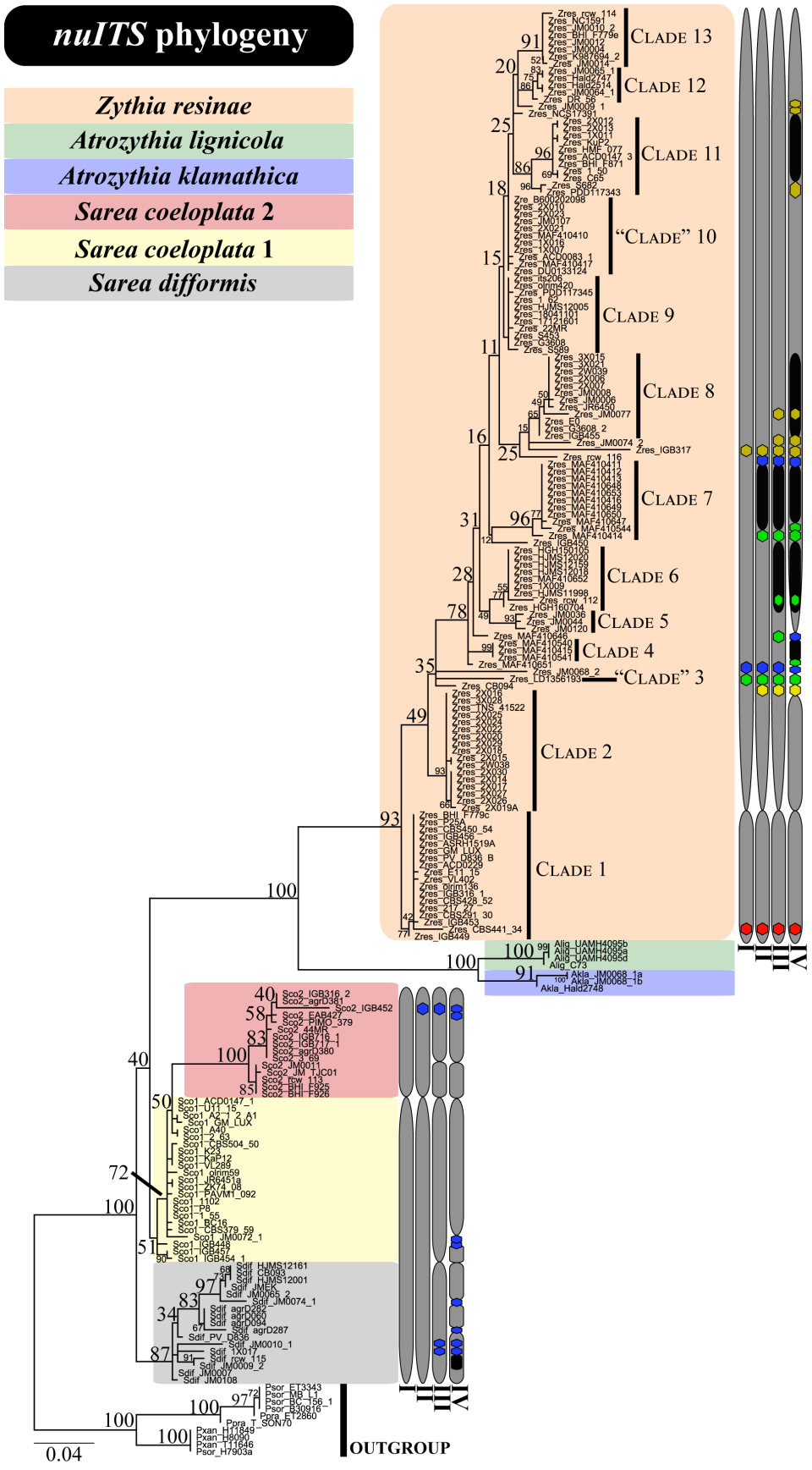
PCR Program:

1. 98°C, 30 seconds
2. 98°C, 10 seconds
3. 65.5°C, 30 seconds
4. 72°C, 30 seconds
5. Go to 2, repeat 2-4, 35 times
6. 72°C, 2 minutes
7. 4°C, ∞

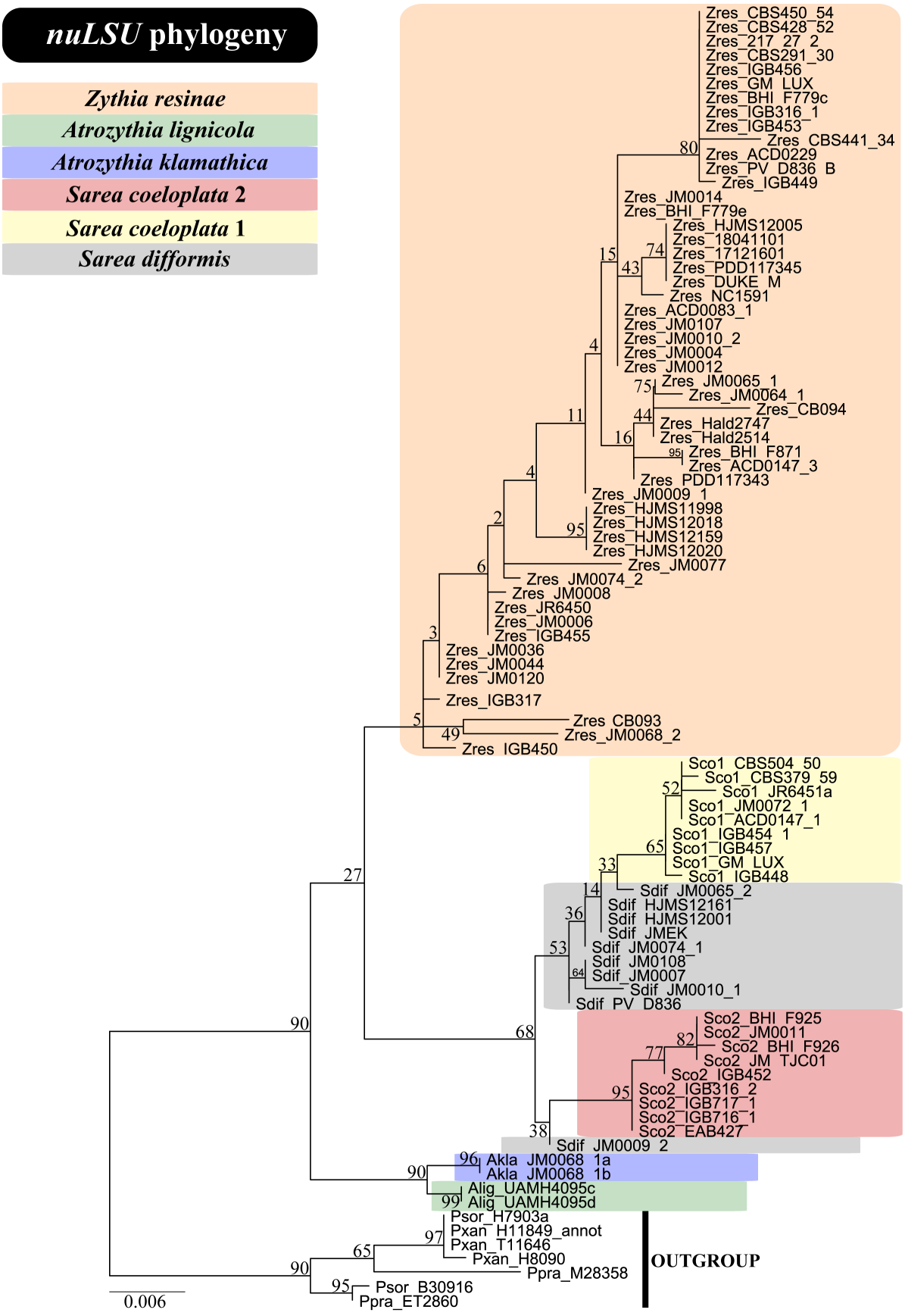
Appendix D

Supplementary Figures

Supplementary Figure 4.S1. *Sareomycetes* nuITS phylogram and species delimitation scenarios based on ABGD. Maximum likelihood tree reconstruction obtained with RAxML based on nuITS data that depicts phylogenetic relationships among the studied *Sareomycetes* specimens. The voucher code of each sample is provided. Coloured boxes delineate the different taxa (genus, species) considered in the present study; full Latin names are available in the legend on the upper-left corner. Bootstrap support values are shown for each node. On the right margin of *Zythia*, species delimitation schemes are based on ABGD 6 (column I), 10 (II), 15 (III), and 24 (IV) putative species solutions. On the right margin of *Sarea*, the schemes are based on ABGD 2 (column I), 3 (II), 7 (III), and 16 (IV) putative species solutions.


nuITS phylogeny
Zythia resinae
Atrozythia lignicola
Atrozythia klamathica
Sarea coeloplata 2
Sarea coeloplata 1
Sarea difformis
Clade 13
Clade 12
Clade 11
"Clade" 10
Clade 9
Clade 8
Clade 7
Clade 6
Clade 5
Clade 4
"Clade" 3
Clade 2
Clade 1
OUTGROUP
0.04
I
II
III
IV
V

Supplementary Figure 4.S2. *Sareomycetes* nuLSU phylogram. Maximum likelihood tree reconstruction obtained with RAxML based on nuLSU data that depicts phylogenetic relationships among the studied *Sareomycetes* specimens. The voucher code of each sample is provided. Coloured boxes delineate the different taxa (genus, species) considered in the present study; full Latin names are available in the legend on the upper-left corner. Bootstrap support values are shown for each node.


nuLSU phylogeny
Zythia resinae
Atrozythia lignicola
Atrozythia klamathica
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Sarea coeloplata 1
Sarea difformis
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Zres_CBS428_52
Zres_217_27_2
Zres_CBS291_30
Zres_IGB456
Zres_GM_LUX
Zres_BHI_F779c
Zres_IGB316_1
Zres_IGB453
Zres_CBS441_34
Zres_ACD0229
Zres_PV_D836_B
Zres_IGB449
Zres_JM0014
Zres_BHI_F779e
Zres_HJMS12005
Zres_18041101
Zres_17121601
Zres_PDD117345
Zres_DUKE_M
Zres_NC1591
Zres_ACD0083_1
Zres_JM0107
Zres_JM0010_2
Zres_JM0004
Zres_JM0012
Zres_JM0065_1
Zres_JM0064_1
Zres_CB094
Zres_Hald2747
Zres_Hald2514
Zres_BHI_F871
Zres_ACD0147_3
Zres_PDD117343
Zres_JM0009_1
Zres_HJMS11998
Zres_HJMS12018
Zres_HJMS12159
Zres_HJMS12020
Zres_JM0077
Zres_JM0074_2
Zres_JM0008
Zres_JR6450
Zres_JM0006
Zres_IGB455
Zres_JM0036
Zres_JM0044
Zres_JM0120
Zres_IGB317
Zres_CB093
Zres_JM0068_2
Zres_IGB450
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Sco1_CBS379_59
Sco1_JR6451a
Sco1_JM0072_1
Sco1_ACD0147_1
Sco1_IGB454_1
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Sco1_GM_LUX
Sco1_IGB448
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Sdif_HJMS12001
Sdif_JMEK
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Sdif_JM0108
Sdif_JM0007
Sdif_JM0010_1
Sdif_PV_D836
Sco2_BHI_F925
Sco2_JM0011
Sco2_BHI_F926
Sco2_JM_TJC01
Sco2_IGB452
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Sco2_IGB717_1
Sco2_IGB716_1
Sco2_EAB427
Sdif_JM0009_2
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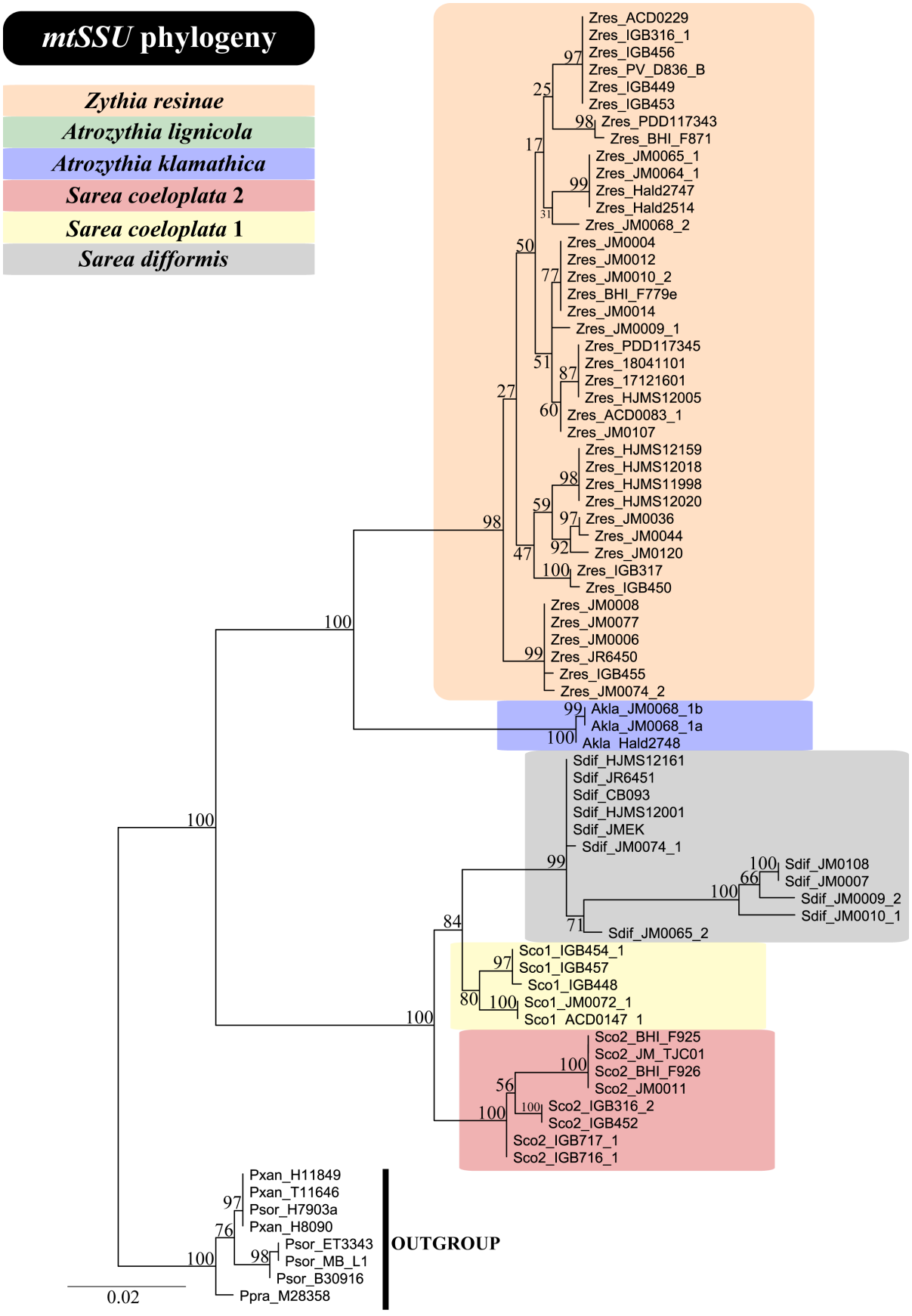
Akla_JM0068_1b
Alig_UAMH4095c
Alig_UAMH4095d
Psor_H7903a
Pxan_H11849_annot
Pxan_T11646
Pxan_H8090
Ppra_M28358
Psor_B30916
Ppra_ET2860
OUTGROUP
0.006

Supplementary Figure 4.S3. *Sareomycetes* mtSSU phylogram. Maximum likelihood tree reconstruction obtained with RAxML based on mtSSU data that depicts phylogenetic relationships among the studied *Sareomycetes* specimens. The voucher code of each sample is provided. Coloured boxes delineate the different taxa (genus, species) considered in the present study; full Latin names are available in the legend on the upper-left corner. Bootstrap support values are shown for each node.


mtSSU phylogeny
Zythia resinae
Atrozythia lignicola
Atrozythia klamathica
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Sarea coeloplata 1
Sarea difformis
Zres_ACD0229
Zres_IGB316_1
Zres_IGB456
Zres_PV_D836_B
Zres_IGB449
Zres_IGB453
Zres_PDD117343
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Zres_JM0065_1
Zres_JM0064_1
Zres_Hald2747
Zres_Hald2514
Zres_JM0068_2
Zres_JM0004
Zres_JM0012
Zres_JM0010_2
Zres_BHI_F779e
Zres_JM0014
Zres_JM0009_1
Zres_PDD117345
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Zres_HJMS12005
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Zres_JM0107
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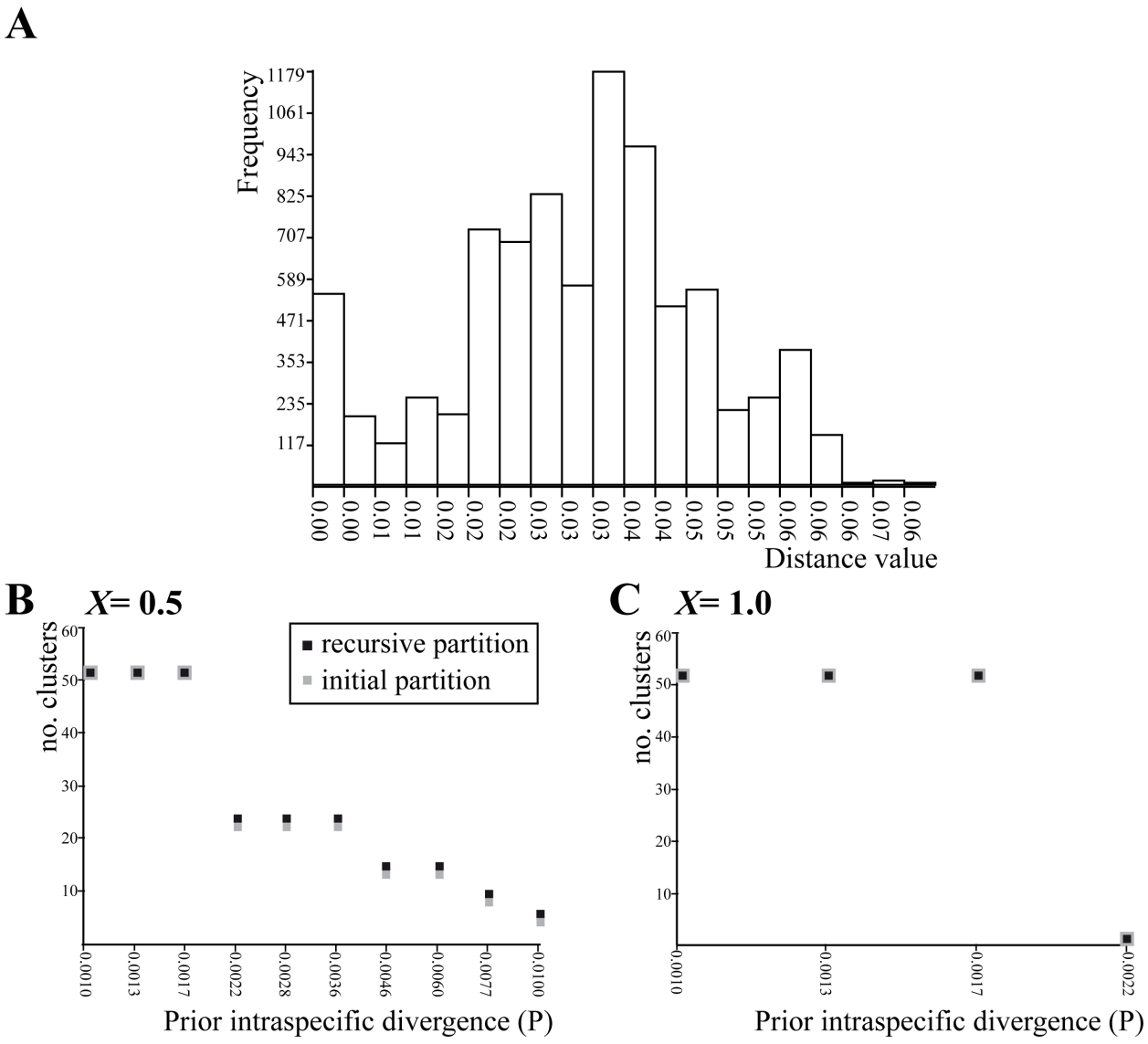
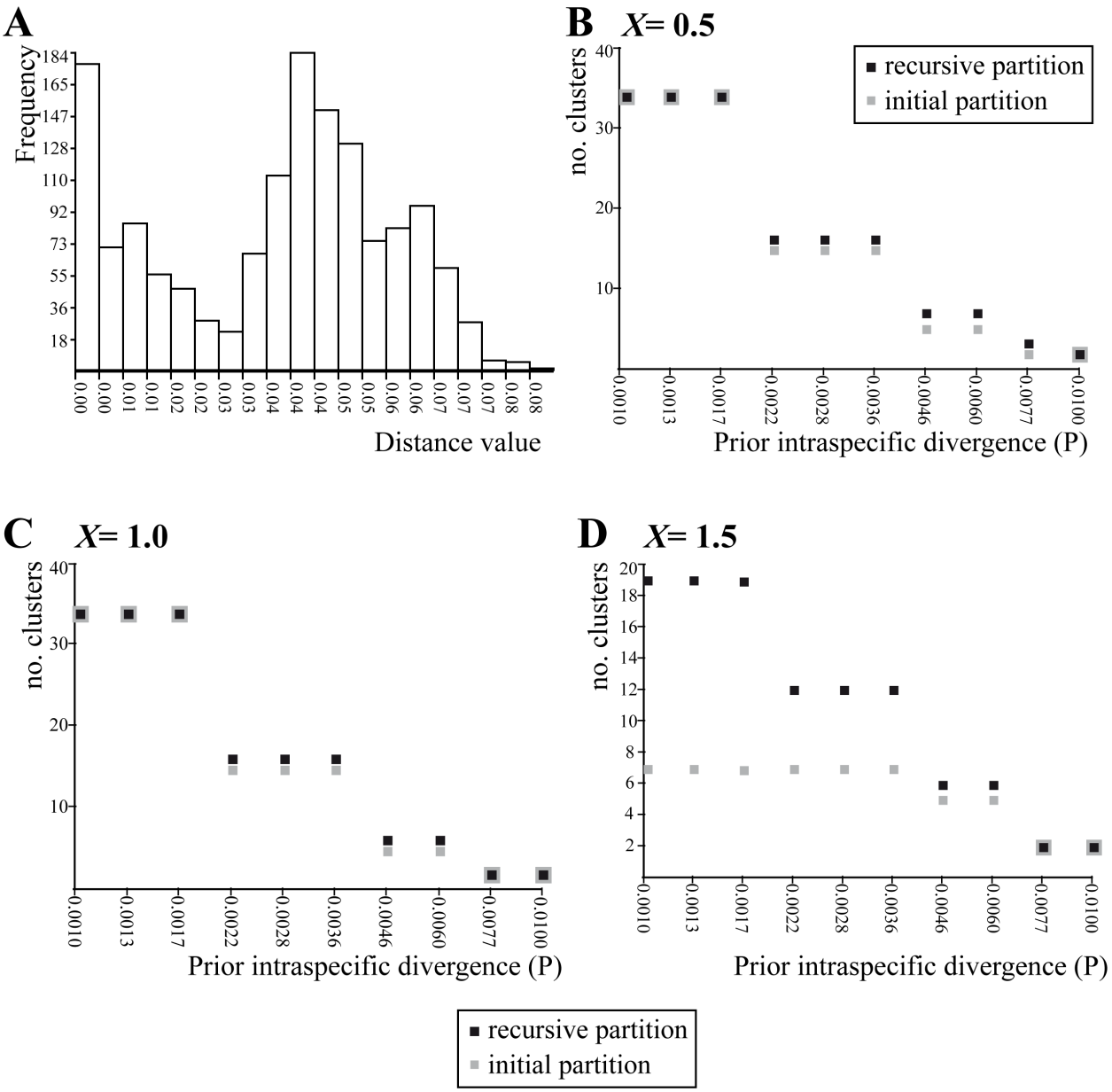
Zres_JM0036
Zres_JM0044
Zres_JM0120
Zres_IGB317
Zres_IGB450
Zres_JM0008
Zres_JM0077
Zres_JM0006
Zres_JR6450
Zres_IGB455
Zres_JM0074_2
Akla_JM0068_1b
Akla_JM0068_1a
Akla_Hald2748
Sdif_HJMS12161
Sdif_JR6451
Sdif_CB093
Sdif_HJMS12001
Sdif_JMEK
Sdif_JM0074_1
Sdif_JM0108
Sdif_JM0007
Sdif_JM0009_2
Sdif_JM0010_1
Sdif_JM0065_2
Sco1_IGB454_1
Sco1_IGB457
Sco1_IGB448
Sco1_JM0072_1
Sco1_ACD0147_1
Sco2_BHI_F925
Sco2_JM_TJC01
Sco2_BHI_F926
Sco2_JM0011
Sco2_IGB316_2
Sco2_IGB452
Sco2_IGB717_1
Sco2_IGB716_1
Pxan_H11849
Pxan_T11646
Psor_H7903a
Pxan_H8090
Psor_ET3343
Psor_MB_L1
Psor_B30916
Ppra_M28358
OUTGROUP
0.02

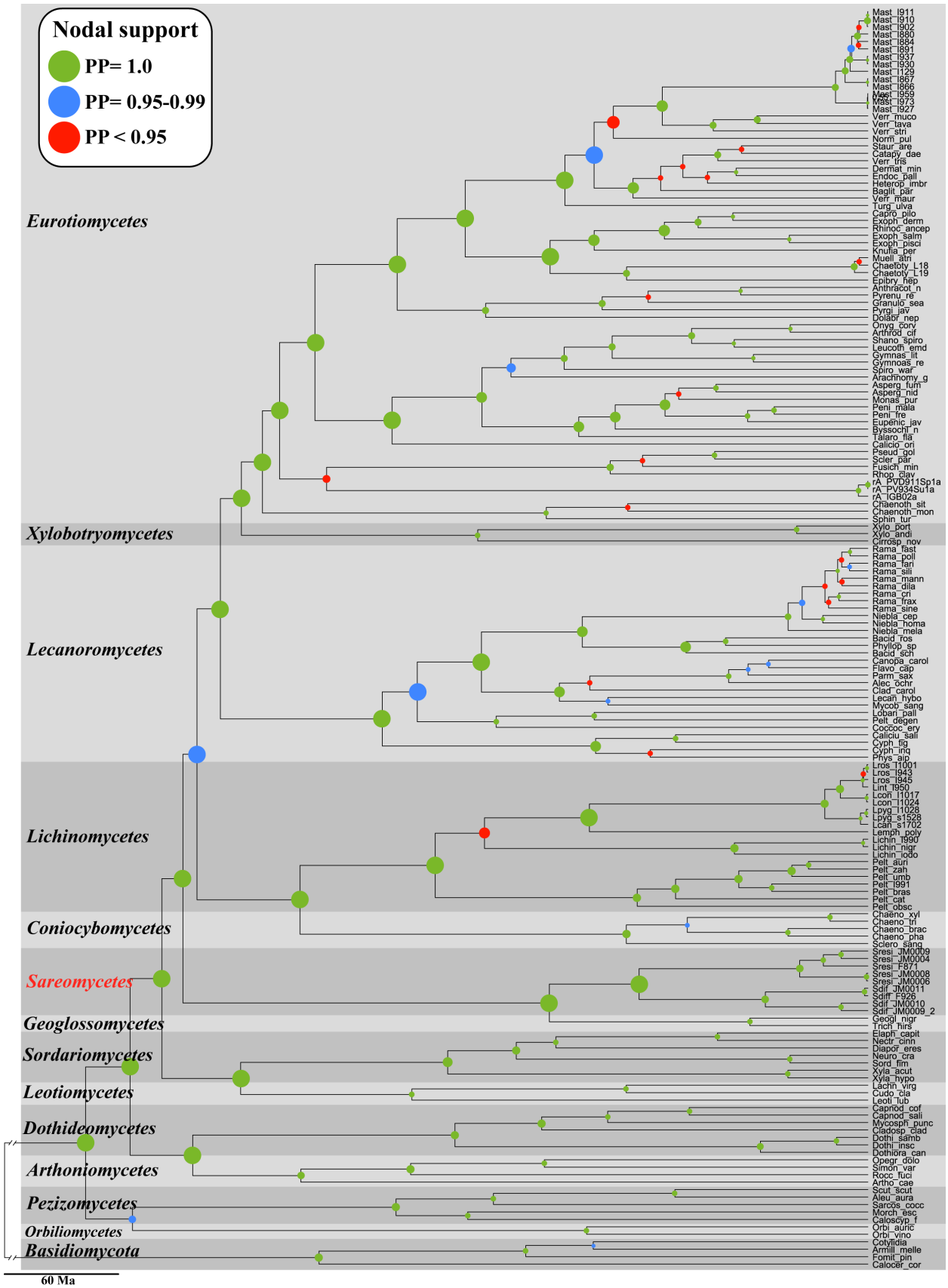
Supplementary Figure 4.S4. ABGD results for species delimitation in *Zythia*. A Histogram showing the distribution of pairwise genetic distances (K2P) among sequences (specimens). B–C Graphs showing the inferred number of clusters (*i.e.*, ABGD partitions or putative species) with different Prior intraspecific divergence (P) values. Analyses in B and C used a value for the relative gap width (*X*) of 0.5 and 1.0, respectively.



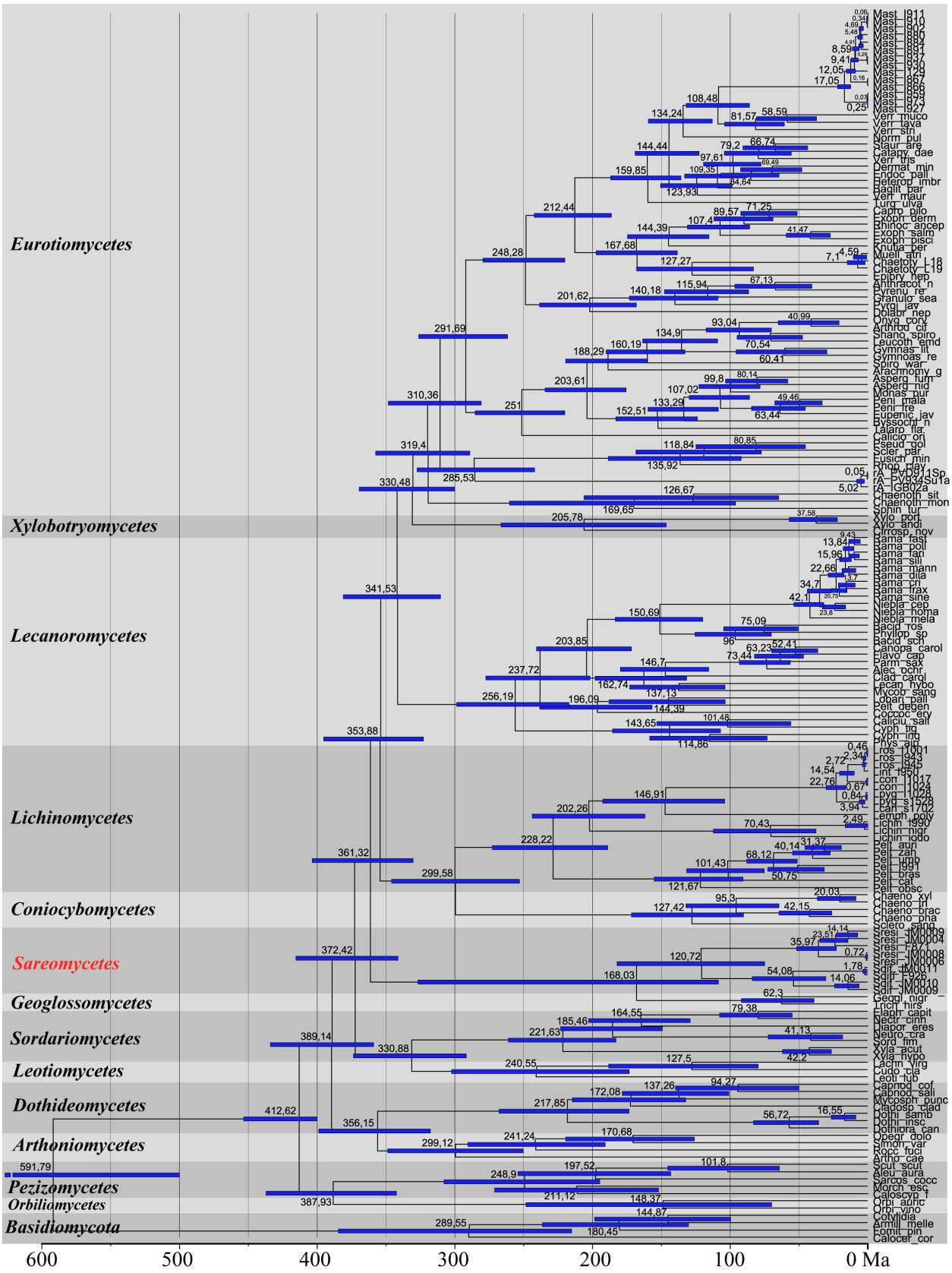
Supplementary Figure 4.S5. ABGD results for species delimitation in *Sarea*. A Histogram showing the distribution of pairwise genetic distances (K2P) among sequences (specimens). B–D Graphs showing the inferred number of clusters (*i.e.*, ABGD partitions or putative species) with different Prior intraspecific divergence (P) values. Different values for the relative gap width (*X*) were used: 0.5 (B), 1.0, and 1.5 (C).



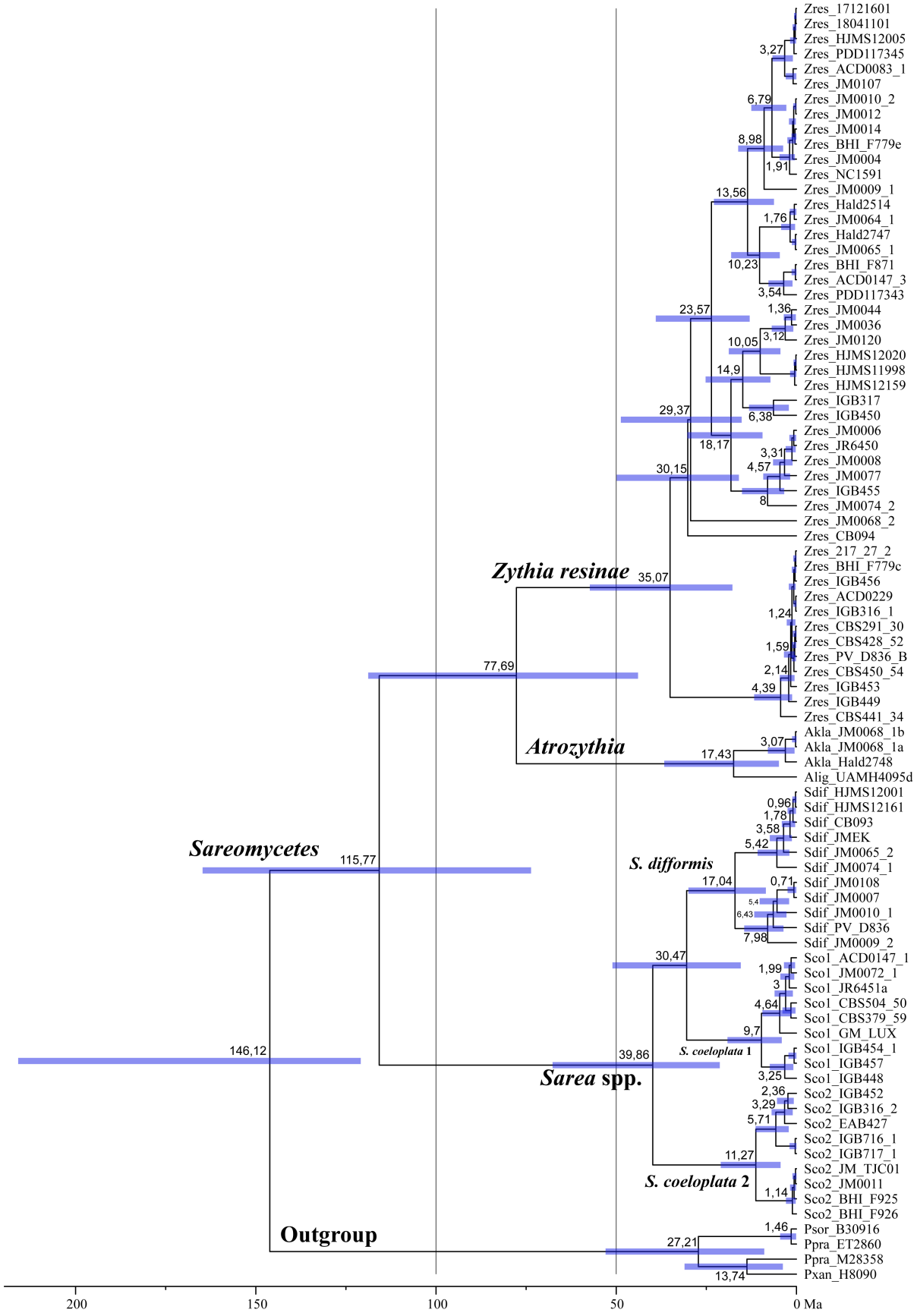
Supplementary Figure 4.S6. Six-locus phylogram for *Ascomycota* with nodal support. Nodal support calculated for the time-calibrated MCC tree constructed in BEAST using a six-locus dataset and 169 fungal taxa, including representatives of the main *Ascomycota* lineages and *Basidiomycota* (outgroup). The colour of circles indicates the strength of nodal support (see legend on the upper-left corner); the size of each circle was deliberately chosen to fit the size of the node, and therefore has no associated information. The class *Sareomycetes*, which represents the focal group of the present study, is highlighted in red. Accession numbers for each marker and considered species are available in Table 4.S3. Ma: million years ago.


Nodal support
PP= 1.0
PP= 0.95-0.99
PP < 0.95
Eurotiomycetes
Xylobotryomycetes
Lecanoromycetes
Lichinomycetes
Coniocybomycetes
Sareomycetes
Geoglossomycetes
Sordariomycetes
Leotiomycetes
Dothideomycetes
Arthoniomycetes
Pezizomycetes
Orbiliomycetes
Basidiomycota
60 Ma

Supplementary Figure 4.S7. Six-locus phylogram for *Ascomycota* with 95% HPD intervals. Nodal 95% Highest Posterior Density (HPD) intervals estimated for divergence ages in the time-calibrated MCC tree constructed in BEAST using a six-locus dataset and 169 fungal taxa, including representatives of the main *Ascomycota* lineages and *Basidiomycota* (outgroup). The class *Sareomycetes*, which represents the focal group of the present study, is highlighted in red. Accession numbers for each marker and considered species are available in Table 4.S3. Ma: million years ago.


Eurotiomycetes
Xylobotryomycetes
Lecanoromycetes
Lichinomycetes
Coniocybomycetes
Sareomycetes
Geoglossomycetes
Sordariomycetes
Leotiomycetes
Dothideomycetes
Arthoniomycetes
Pezizomycetes
Orbiliomycetes
Basidiomycota
600
500
400
300
200
100
0 Ma

Supplementary Figure 4.S8. Three-locus MCC tree calibrated using a date inferred from the six-locus analysis.Time-calibrated MCC tree estimated from a concatenated dataset of ribosomal (nuITS and nuLSU) and mitochondrial (mtSSU) markers from specimens belonging into class *Sareomycetes* using BEAST. The tree was calibrated imposing a time estimate of 120.88 Ma (181.35–75.76 Ma, 95 % HPD) on the crown node of *Sareomycetes* based on results of our six-locus dating analysis. Nodal blue bars show the 95% HPD intervals for the estimated divergence ages. The voucher code of each sample is provided. Ma: million years ago.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Zres_18041101
Zres_HJMS12005
Zres_PDD117345
Zres_ACD0083_1
Zres_JM0107
Zres_JM0010_2
Zres_JM0012
Zres_JM0014
Zres_BHI_F779e
Zres_JM0004
Zres_NC1591
Zres_JM0009_1
Zres_Hald2514
Zres_JM0064_1
Zres_Hald2747
Zres_JM0065_1
Zres_BHI_F871
Zres_ACD0147_3
Zres_PDD117343
Zres_JM0044
Zres_JM0036
Zres_JM0120
Zres_HJMS12020
Zres_HJMS11998
Zres_HJMS12159
Zres_IGB317
Zres_IGB450
Zres_JM0006
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Zres_JM0008
Zres_JM0077
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Zres_JM0074_2
Zres_JM0068_2
Zres_CB094
Zres_217_27_2
Zres_BHI_F779c
Zres_IGB456
Zres_ACD0229
Zres_IGB316_1
Zres_CBS291_30
Zres_CBS428_52
Zres_PV_D836_B
Zres_CBS450_54
Zres_IGB453
Zres_IGB449
Zres_CBS441_34
Akla_JM0068_1b
Akla_JM0068_1a
Akla_Hald2748
Alig_UAMH4095d
Sdif_HJMS12001
Sdif_HJMS12161
Sdif_CB093
Sdif_JMEK
Sdif_JM0065_2
Sdif_JM0074_1
Sdif_JM0108
Sdif_JM0007
Sdif_JM0010_1
Sdif_PV_D836
Sdif_JM0009_2
Sco1_ACD0147_1
Sco1_JM0072_1
Sco1_JR6451a
Sco1_CBS504_50
Sco1_CBS379_59
Sco1_GM_LUX
Sco1_IGB454_1
Sco1_IGB457
Sco1_IGB448
Sco2_IGB452
Sco2_IGB316_2
Sco2_EAB427
Sco2_IGB716_1
Sco2_IGB717_1
Sco2_JM_TJC01
Sco2_JM0011
Sco2_BHI_F925
Sco2_BHI_F926
Psor_B30916
Ppra_ET2860
Ppra_M28358
Pxan_H8090
3,27
6,79
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13,56
1,76
10,23
3,54
23,57
1,36
3,12
10,05
14,9
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18,17
3,31
4,57
30,15
8
35,07
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1,59
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17,04
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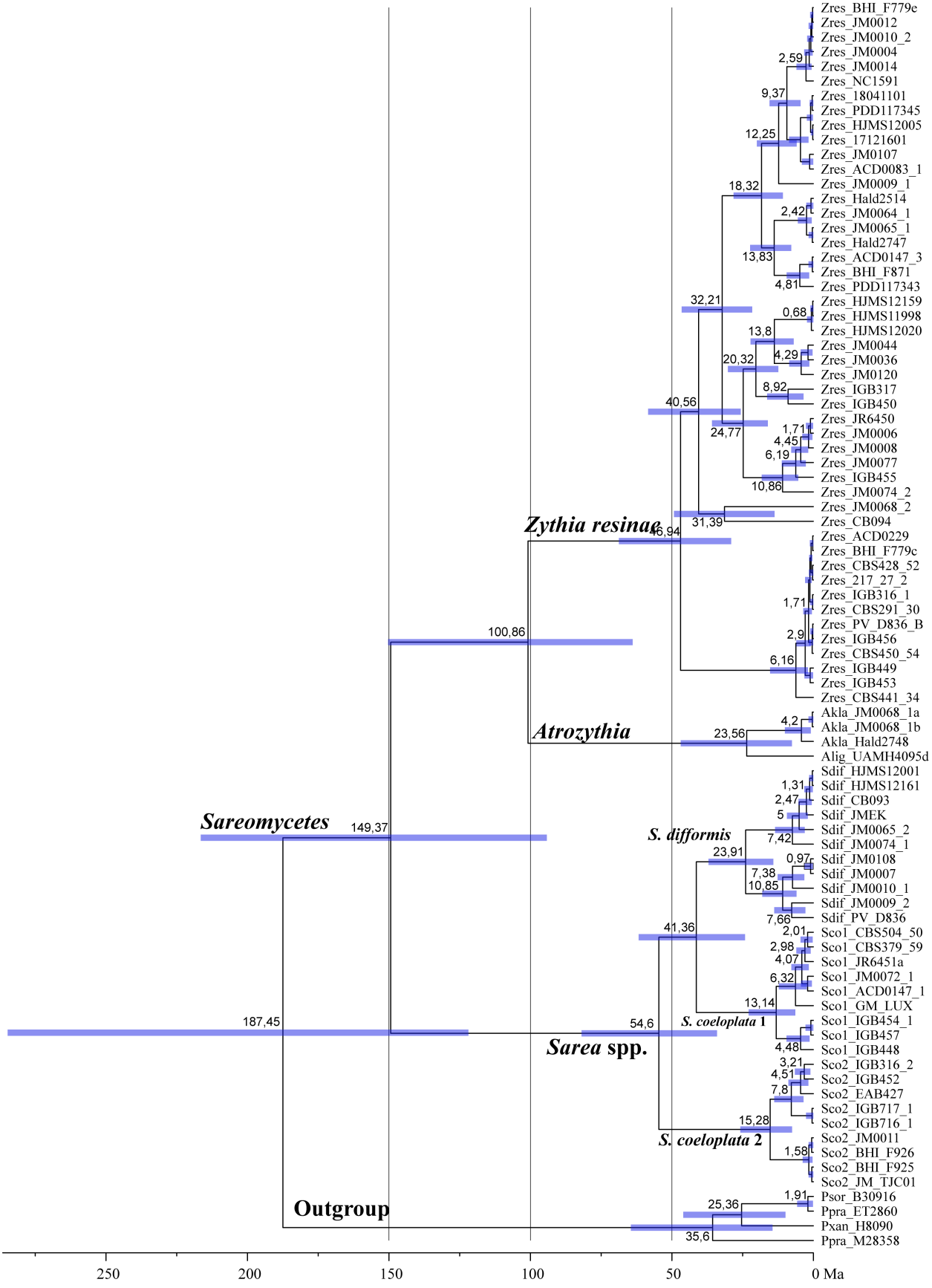
1,99
3
4,64
9,7
146,12
39,86
3,25
2,36
3,29
5,71
11,27
1,14
1,46
27,21
13,74
Zythia resinae
Atrozythia
Sareomycetes
S. difformis
S. coeloplata 1
Sarea spp.
S. coeloplata 2
Outgroup
200
150
100
50
0 Ma

Supplementary Figure 4.S9. Three-locus MCC tree calibrated using a mtSSU rate inferred from the six-locus analysis. Time-calibrated MCC tree estimated from a concatenated dataset of ribosomal (nuITS and nuLSU) and mitochondrial (mtSSU) markers from specimens belonging into class *Sareomycetes* using BEAST. The tree was calibrated imposing a mtSSU rate of 3.28×10^{-10} s/s/y inferred for the *Sareomycetes* clade in the six-locus dating approach. Nodal blue bars show the 95% HPD intervals for the estimated divergence ages. The voucher code of each sample is provided. Ma: million years ago.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Zres_HJMS12005
Zres_17121601
Zres_JM0107
Zres_ACD0083_1
Zres_JM0009_1
Zres_Hald2514
Zres_JM0064_1
Zres_JM0065_1
Zres_Hald2747
Zres_ACD0147_3
Zres_BHI_F871
Zres_PDD117343
Zres_HJMS12159
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Zres_ACD0229
Zres_BHI_F779c
Zres_CBS428_52
Zres_217_27_2
Zres_IGB316_1
Zres_CBS291_30
Zres_PV_D836_B
Zres_IGB456
Zres_CBS450_54
Zres_IGB449
Zres_IGB453
Zres_CBS441_34
Akla_JM0068_1a
Akla_JM0068_1b
Akla_Hald2748
Alig_UAMH4095d
Sdif_HJMS12001
Sdif_HJMS12161
Sdif_CB093
Sdif_JMEK
Sdif_JM0065_2
Sdif_JM0074_1
Sdif_JM0108
Sdif_JM0007
Sdif_JM0010_1
Sdif_JM0009_2
Sdif_PV_D836
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Sco1_CBS379_59
Sco1_JR6451a
Sco1_JM0072_1
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Sco1_IGB448
Sco2_IGB316_2
Sco2_IGB452
Sco2_EAB427
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Sco2_IGB716_1
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Sco2_BHI_F925
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Pxan_H8090
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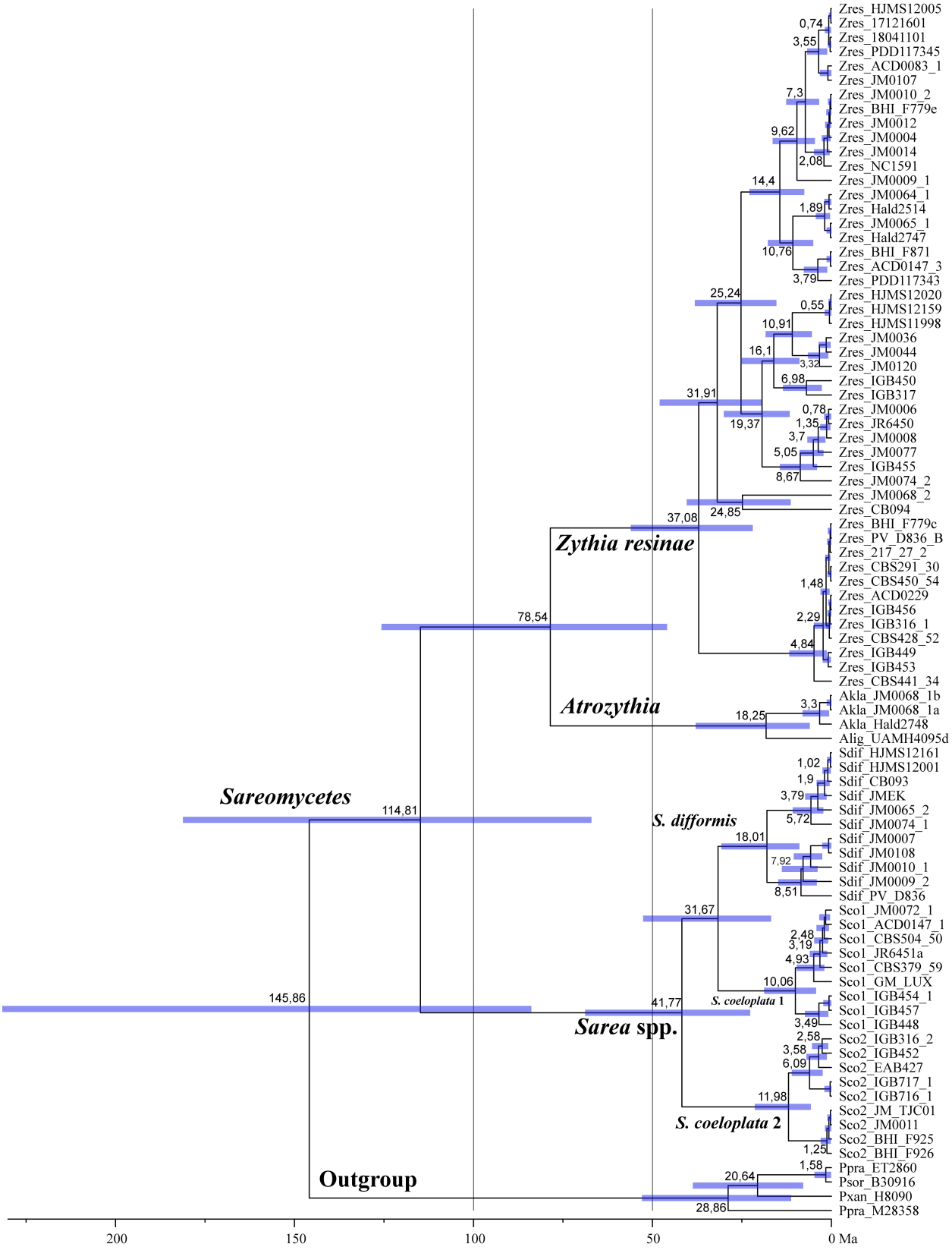
187,45
149,37
Zythia resinae
Atrozythia
Sareomycetes
S. difformis
S. coeloplata 1
Sarea spp.
S. coeloplata 2
Outgroup
250
200
150
100
50
0 Ma

Supplementary Figure 4.S10. Three-locus MCC tree calibrated using a nuLSU rate inferred from the six-locus analysis. Time-calibrated MCC tree estimated from a concatenated dataset of ribosomal (nuITS and nuLSU) and mitochondrial (mtSSU) markers from specimens belonging into class *Sareomycetes* using BEAST. The tree was calibrated imposing a nuLSU rate of 2.68×10^{-10} s/s/y inferred for the *Sareomycetes* clade in the six-locus dating approach. Nodal blue bars show the 95% HPD intervals for the estimated divergence ages. The voucher code of each sample is provided. Ma: million years ago.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Zres_IGB455
Zres_JM0074_2
Zres_JM0068_2
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Zres_BHI_F779c
Zres_PV_D836_B
Zres_217_27_2
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Zres_ACD0229
Zres_IGB456
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Zres_CBS428_52
Zres_IGB449
Zres_IGB453
Zres_CBS441_34
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Akla_JM0068_1a
Akla_Hald2748
Alig_UAMH4095d
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Sdif_HJMS12001
Sdif_CB093
Sdif_JMEK
Sdif_JM0065_2
Sdif_JM0074_1
Sdif_JM0007
Sdif_JM0108
Sdif_JM0010_1
Sdif_JM0009_2
Sdif_PV_D836
Sco1_JM0072_1
Sco1_ACD0147_1
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Sco1_IGB457
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Sco2_IGB452
Sco2_EAB427
Sco2_IGB717_1
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Sco2_JM_TJC01
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Psor_B30916
Pxan_H8090
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Zythia resinae
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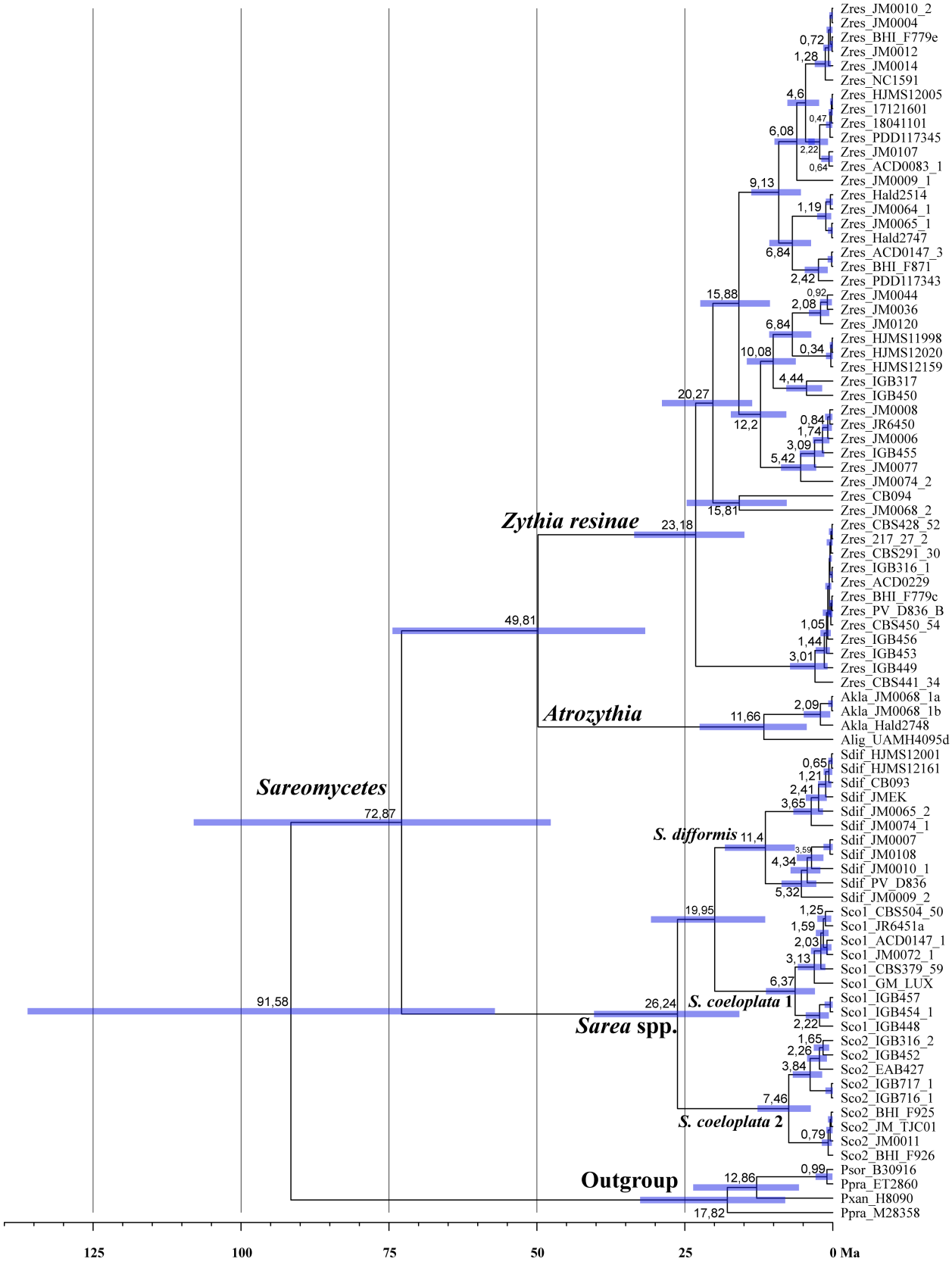
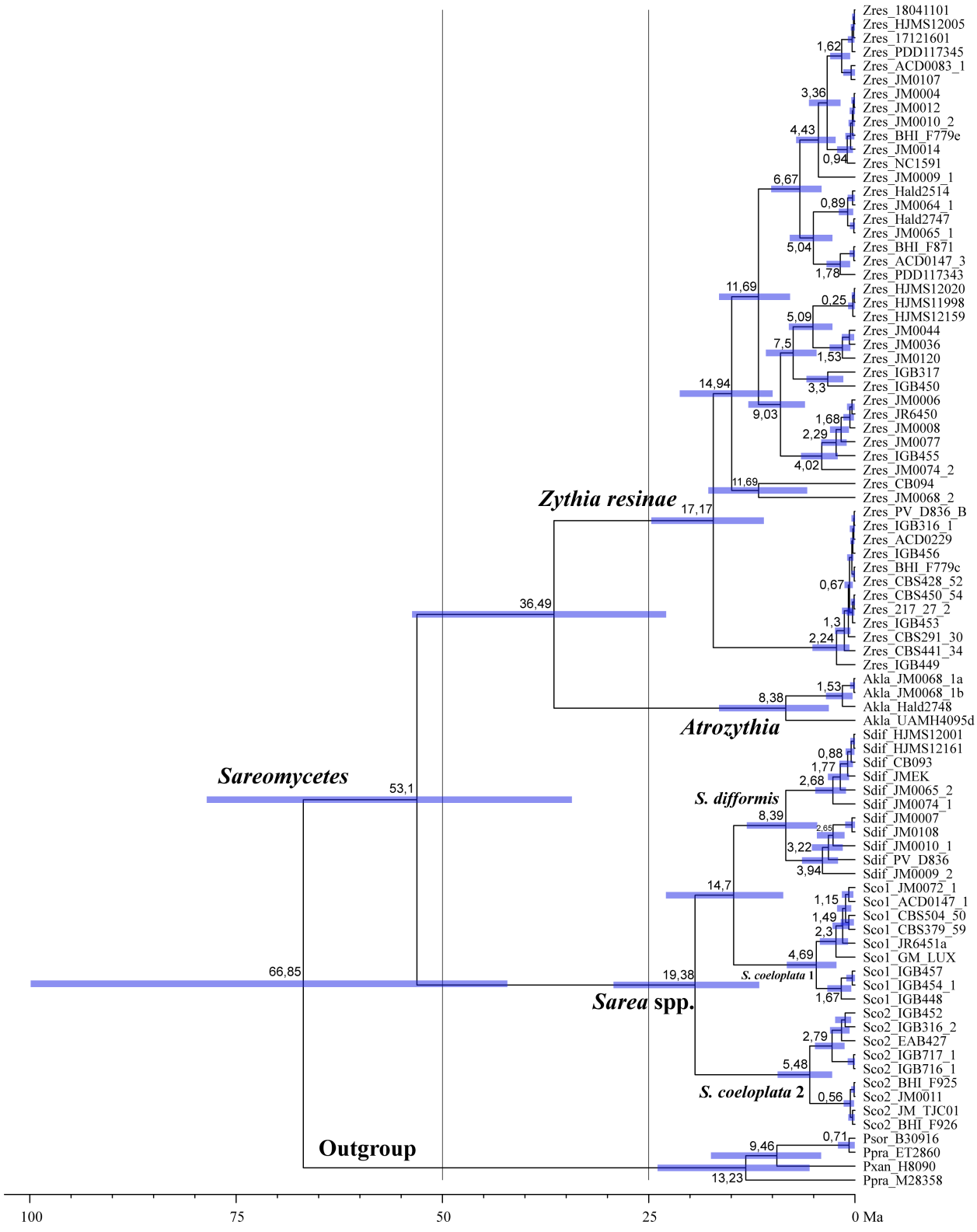
2,29
4,84
Atrozythia
3,3
18,25
Sareomycetes
114,81
S. difformis
1,02
1,9
3,79
5,72
18,01
7,92
8,51
31,67
2,48
3,19
4,93
10,06
145,86
41,77
S. coeloplata 1
Sarea spp.
3,49
2,58
3,58
6,09
11,98
S. coeloplata 2
1,25
1,58
20,64
28,86
Outgroup
200
150
100
50
0 Ma

Supplementary Figure 4.S11. Three-locus MCC tree calibrated using a nuITS rate estimated for *Erysiphales*. Time-calibrated MCC tree estimated from a concatenated dataset of ribosomal (nuITS and nuLSU) and mitochondrial (mtSSU) markers from specimens belonging into class *Sareomycetes* using BEAST. The tree was calibrated imposing a nuITS rate of 2.52×10^{-9} s/s/y calculated for the fungal order *Erysiphales* by Takamatsu and Matsuda (2004). Nodal blue bars show the 95% HPD intervals for the estimated divergence ages. The voucher code of each sample is provided. Ma: million years ago.


Zres_JM0010_2
Zres_JM0004
Zres_BHI_F779e
Zres_JM0012
Zres_JM0014
Zres_NC1591
Zres_HJMS12005
Zres_17121601
Zres_18041101
Zres_PDD117345
Zres_JM0107
Zres_ACD0083_1
Zres_JM0009_1
Zres_Hald2514
Zres_JM0064_1
Zres_JM0065_1
Zres_Hald2747
Zres_ACD0147_3
Zres_BHI_F871
Zres_PDD117343
Zres_JM0044
Zres_JM0036
Zres_JM0120
Zres_HJMS11998
Zres_HJMS12020
Zres_HJMS12159
Zres_IGB317
Zres_IGB450
Zres_JM0008
Zres_JR6450
Zres_JM0006
Zres_IGB455
Zres_JM0077
Zres_JM0074_2
Zres_CB094
Zres_JM0068_2
Zres_CBS428_52
Zres_217_27_2
Zres_CBS291_30
Zres_IGB316_1
Zres_ACD0229
Zres_BHI_F779c
Zres_PV_D836_B
Zres_CBS450_54
Zres_IGB456
Zres_IGB453
Zres_IGB449
Zres_CBS441_34
Akla_JM0068_1a
Akla_JM0068_1b
Akla_Hald2748
Alig_UAMH4095d
Sdif_HJMS12001
Sdif_HJMS12161
Sdif_CB093
Sdif_JMEK
Sdif_JM0065_2
Sdif_JM0074_1
Sdif_JM0007
Sdif_JM0108
Sdif_JM0010_1
Sdif_PV_D836
Sdif_JM0009_2
Sco1_CBS504_50
Sco1_JR6451a
Sco1_ACD0147_1
Sco1_JM0072_1
Sco1_CBS379_59
Sco1_GM_LUX
Sco1_IGB457
Sco1_IGB454_1
Sco1_IGB448
Sco2_IGB316_2
Sco2_IGB452
Sco2_EAB427
Sco2_IGB717_1
Sco2_IGB716_1
Sco2_BHI_F925
Sco2_JM_TJC01
Sco2_JM0011
Sco2_BHI_F926
Psor_B30916
Ppra_ET2860
Pxan_H8090
Ppra_M28358
Zythia resinae
Atrozythia
Sareomycetes
S. diffformis
S. coeloplata 1
Sarea spp.
S. coeloplata 2
Outgroup
125
100
75
50
25
0 Ma

Supplementary Figure 4.S12. Three-locus MCC tree calibrated using a nuITS rate estimated for *Melanohalea*. Time-calibrated MCC tree estimated from a concatenated dataset of ribosomal (nuITS and nuLSU) and mitochondrial (mtSSU) markers from specimens belonging into class *Sareomycetes* using BEAST. The tree was calibrated imposing a nuITS rate of 3.41×10^{-9} s/s/y calculated for the lichenised fungal genus *Melanohalea* by Leavitt et al. (2012). Nodal blue bars show the 95% HPD intervals for the estimated divergence ages. The voucher code of each sample is provided. Ma: million years ago.


Zres_18041101
Zres_HJMS12005
Zres_17121601
Zres_PDD117345
Zres_ACD0083_1
Zres_JM0107
Zres_JM0004
Zres_JM0012
Zres_JM0010_2
Zres_BHI_F779e
Zres_JM0014
Zres_NC1591
Zres_JM0009_1
Zres_Hald2514
Zres_JM0064_1
Zres_Hald2747
Zres_JM0065_1
Zres_BHI_F871
Zres_ACD0147_3
Zres_PDD117343
Zres_HJMS12020
Zres_HJMS11998
Zres_HJMS12159
Zres_JM0044
Zres_JM0036
Zres_JM0120
Zres_IGB317
Zres_IGB450
Zres_JM0006
Zres_JR6450
Zres_JM0008
Zres_JM0077
Zres_IGB455
Zres_JM0074_2
Zres_CB094
Zres_JM0068_2
Zres_PV_D836_B
Zres_IGB316_1
Zres_ACD0229
Zres_IGB456
Zres_BHI_F779c
Zres_CBS428_52
Zres_CBS450_54
Zres_217_27_2
Zres_IGB453
Zres_CBS291_30
Zres_CBS441_34
Zres_IGB449
Akla_JM0068_1a
Akla_JM0068_1b
Akla_Hald2748
Akla_UAMH4095d
Sdif_HJMS12001
Sdif_HJMS12161
Sdif_CB093
Sdif_JMEK
Sdif_JM0065_2
Sdif_JM0074_1
Sdif_JM0007
Sdif_JM0108
Sdif_JM0010_1
Sdif_PV_D836
Sdif_JM0009_2
Sco1_JM0072_1
Sco1_ACD0147_1
Sco1_CBS504_50
Sco1_CBS379_59
Sco1_JR6451a
Sco1_GM_LUX
Sco1_IGB457
Sco1_IGB454_1
Sco1_IGB448
Sco2_IGB452
Sco2_IGB316_2
Sco2_EAB427
Sco2_IGB717_1
Sco2_IGB716_1
Sco2_BHI_F925
Sco2_JM0011
Sco2_JM_TJC01
Sco2_BHI_F926
Psor_B30916
Ppra_ET2860
Pxan_H8090
Ppra_M28358
Zythia resinae
Atrozythia
Sareomycetes
S. difformis
S. coeloplata 1
Sarea spp.
S. coeloplata 2
Outgroup
1,62
3,36
4,43
0,94
6,67
0,89
5,04
1,78
11,69
0,25
5,09
7,5
1,53
3,3
14,94
9,03
1,68
2,29
4,02
11,69
17,17
0,67
36,49
1,3
2,24
1,53
8,38
0,88
1,77
2,68
53,1
8,39
2,65
3,22
3,94
14,7
1,15
1,49
2,3
4,69
66,85
19,38
1,67
2,79
5,48
0,56
0,71
9,46
13,23
100
75
50
25
0 Ma

Appendix E

Supplementary Tables

Supplementary Table 2.S1. List of taxa used in this study with GenBank accession numbers and voucher information.

Available at:

https://www.ingentaconnect.com/content/wfbi/fuse/2020/00000006/00000001/art00003/supp-data/content-f2_fuse_vol6_art2-supp#

Supplementary Table 2.S2. PCR primers and PCR conditions used in this study.

Primer name/Publication	Primer sequence	PCR conditions
ITS1F/Gardes and Bruns 1993	5'-CTT GGT CAT TTA GAG GAA GTA A-3'	(1) 95 °C for 2 min (2) 35 cycles of 45s at 95°C, 45s at 52°C and 45s at 72°C (3) 72°C for 10 min
ITS4/White et al. 1990	5'-TCC TCC GCT TAT TGA TAT GC-3'	
LR0R/Rehner and Samuels 1994	5'-ACCCGCTGAACTTAAGC-3'	(1) 95 °C for 2 min (2) 35 cycles of 45s at 95°C, 45s at 52°C and 45s at 72°C (3) 72°C for 10 min
LR5/Vilgalys and Hester 1990	5'-TCCTGAGGGAAACTTCG-3'	
LR7/Vilgalys and Hester 1990	5'-TACTACCACCAAGAT CT-3'	(1) 95 °C for 2 min (2) 35 cycles of 45s at 95°C, 50s at 52°C and 60s at 72°C (3) 72°C for 10 min
LR3R/Moncalvo et al. 2000	5'-GTCTTGAAACACGGA CC-3'	
Mcm7-709/Schmitt et al. 2009	5'-ACI MGI GTI TCV GAY GTH AAR CC-3'	(1) 95 °C for 2 min (2) 35 cycles of 45s at 95°C, 50s–60s at 50°C–52°C and 60s at 72°C (3) 72°C for 10 min
Mcm7-1348/Schmitt et al. 2009	5'-GAY TTD GCI ACI CCI GGR TCW CCC AT-3'	
NS1/White et al. 1990	5'- GTA GTC ATA TGC TTG TCT C-3'	(1) 95 °C for 2 min (2) 35 cycles of 45s at 95°C, 50s–60s at 50°C–52°C and 60s at 72°C (3) 72°C for 10 min
NS4/White et al. 1990	5'-CTTCCGTCAATTCCTTTAAG-3'	
RPB1-AFasc/Hofstetter et al. 2007	5'-ADTGYCCYGGYCATTTYGGT-3'	(1) 95 °C for 2 min (2) 40 cycles of 50s at 95°C, 60s at 52°C–55°C and 60 s at 72°C (3) 10 min at 72°C.
RPB1-6R2asc/Hofstetter et al. 2007	5'-ATGACCCATCATRGAYTCCT-3'	
RPB1-DF2asc/Hofstetter et al. 2007	5'-CAYAAGGARTCYATGATGG-3'	
RPB1G1R/Hofstetter et al. 2007	5'-ACNCCNACCATYTCNCCNGG-3'	
fRPB2-5F/Liu et al. 1999	5'-GAYGAYMGWGATCAYTTYGG-3'	(1) 95 °C for 2 min (2) 40 cycles of 50s at 95°C, 60s at 50°C–55°C and 60 s at 72°C (3) 10 min at 72°C.
fRPB2-7cR/Liu et al. 1999	5'-CCCATRGCTTGYTTRCCCAT-3'	
TSR1453/Schmitt et al. 2009	5'-GAR TTC CCI GAY GAR ATY GAR CT-3'	(1) 95 °C for 2 min (2) 35–40 cycles of 45s at 95°C, 50s at 52°C and 60s at 72°C (3) 10 at 72°C.
TSR2308/Schmitt et al. 2009	5'-CTT RAA RTA ICC RTG IGT ICC-3'	

References:

Hofstetter V, Miadlikowska J, Kauff F, Lutzoni F (2007) Phylogenetic comparison of protein-coding versus ribosomal RNA-coding sequence data: a case study of the *Lecanoromycetes* (*Ascomycota*). Molecular Phylogenetics and Evolution 44(1):412–426. https://doi.org/10.1016/j.ympev.2006.10.016

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. Molecular Ecology 2(2):113–118. https://doi.org/10.1111/j.1365-294X.1993.tb00005.x

Liu YJ, Whelen S, Hall BD (1999) Phylogenetic relationships among ascomycetes: evidence from an RNA polymerse II subunit. Molecular Biology and Evolution 16(12):1799–1808. https://doi.org/10.1093/oxfordjournals.molbev.a026092

Moncalvo JM, Lutzoni FM, Rehner SA, Johnson J, Vilgalys R (2000) Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. Systematic Biology 49(2):278-305. https://doi.org/10.1093/sysbio/49.2.278

Rehner S, Samuels, GJ (1994) Taxonomy and phylogeny of *Gliocladium* analyzed from nuclear large subunits ribosomal DNA sequences. Mycological Research 98(6):625–634. https://doi.org/10.1016/S0953-7562(09)80409-7

Schmitt I, Crespo A, Divakar PK, et al (2009) New primers for promising single-copy genes in fungal phylogenetics and systematics. Persoonia 23(1):35–40. https://doi.org/10.3767/003158509X470602

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172(8):4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

White TJ, Bruns T, Lee S, Taylor J (1990) 38 - Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) PCR Protocols: A Guide to Methods and Applications. Academic Press, Inc., San Diego: 315–322

Supplementary Table 4.S1. Sequences used in three-locus analyses. Specimens and sequences used in phylogenetic analyses for Figs. 4.4, 4.5, 4.6B, 4.S1-4.S5, and 4.S8-4.S12, with updated identifications, identifiers, holding institutions, collecting localities, host data, and associated references. Unmarked sequences were downloaded from GenBank (https://www.ncbi.nlm.nih.gov/genbank/), * indicates a sequence from the UNITE database (https://unite.ut.ee/), and † indicates a sequence from the NARO Genebank (https://www.gene.affrc.go.jp/databases-micro_search_en.php).

Available at: https://static-content.springer.com/esm/art%3A10.1186%2Fs43008-021-00056-0/MediaObjects/43008_2021_56_MOESM3_ESM.xlsx

Supplementary Table 4.S2. Tests for strict molecular clock. Test for strict molecular clock for each locus conducted in MEGA 5 prior to perform the three-locus dating analyses (see section "Inferring a Time Frame for The Diversification of *Sareomycetes*" in Material and Methods). Tested under two different topologies (ML and Bayesian). *denotes rejection of the null hypothesis (*i.e.*, equal rates).

	ML estimate				MrBayes consensus			
nrITS K2+Γ+I	**ln*L***	**Param**	**(+Γ)**	**(+I)**	**ln*L***	**Param**	**(+Γ)**	**(+I)**
With Clock	-2936.883	86	0.755	0.60	-2907.169	86	0.564	0.37
Without Clock	-2799.163	168	0.75	0.52	-2685.295	168	0.66	0.44
P (Ho: = rates)		$1.15e^{-7}$*				$1.28e^{-27}$*		
nuLSU K2+Γ+I	**ln*L***	**Param**	**(+Γ)**	**(+I)**	**ln*L***	**Param**	**(+Γ)**	**(+I)**
With Clock	-2630.479	87	0.145	0.74	-2502.123	87	0.316	0.83
Without Clock	-2282.383	170	0.70	0.82	-2399.594	170	0.31	0.83
P (Ho: = rates)		$4.81e^{-66}$*				0.02*		
mtSSU HKY+Γ	**ln*L***	**Param**	**(+Γ)**		**ln*L***	**Param**	**(+Γ)**	
With Clock	-2469.963	71	0.219		-2441.517	71	0.180	
Without Clock	-2377.089	136	0.20		-2380.866	136	0.20	
P (Ho: = rates)		0.001*				0.695		

Supplementary Table 4.S3. Sequences used in six-locus analyses. GenBank sequences used for dating analyses in Figs. 4.6A, 4.S6, and 4.S7 arranged alphabetically by class.

Available at: https://static-content.springer.com/esm/art%3A10.1186%2Fs43008-021-00056-0/MediaObjects/43008_2021_56_MOESM5_ESM.xlsx

Supplementary Table 4.S4. Calibration fossils. List of the six fossil calibrations used to estimate the age of the crown node of *Sareomycetes* with BEAST based on a six-locus dataset with 169 different fungal taxa. (Ma: million years ago).

Calibration		Evidence	Age (Ma)	Geological Time	Prior distribution and settings	References
A	Crown of family *Parmeliaceae*	*Anzia electra* Rikkinen & Poinar is a lichenized fungus that was found in Baltic amber	55–35	Early Oligocene to Late Eocene	Exponential (mean= 45, offset= 40; initial: 43)	Rikkinen and Poinar 2002; Lücking and Nelsen 2018
B	*Cyphelium-Calicium* clade	*Calicium* sp. fossil			Exponential (mean= 40, offset= 35; initial: 37)	Rikkinen 2003; Pérez-Ortega et al. 2016
C	Crown of class *Coniocybomycetes*	*Chaenotheca* sp. fossil from Baltic amber			Exponential (mean= 98.9, offset= 35; initial: 70)	Rikkinen 2003; Pérez-Ortega et al. 2016
D	Crown of family *Aspergillaceae*	*Aspergillus collembolorum* Dörfelt & A.R. Schmidt was found overgrowing a springtail (suborder *Entomobryomorpha*) in Baltic amber			Exponential (mean= 40, offset= 35; initial: 37)	Dörfelt and Schmidt 2005; Lutzoni et al. 2018; Samarakoon et al. 2019
E	Common ancestor of *Capnodiales*	*Metacapnodium succinum* (Dörfelt, A.R. Schmidt & J. Wunderl.) Rikkinen, Dörfelt, A.R. Schmidt & J. Wunderl.	~100 (minimum age of 100 Mya for the crown age of *Capnodiales*)		truncated normal distribution mean = 100, standard deviation = 150, confidence interval = 400; truncated upper = infinit; lower: 100	Schmidt et al. 2014; Samarakoon et al. 2019
F	Crown of *Pezizomycotina*	*Paleopyrenomycites devonicus* fossil			Exponential (mean= 67.8, offset= 400; initial: 400)	Taylor et al. 2005; Prieto and Wedin 2013; Beimforde et al. 2014; Pérez-Ortega et al. 2016; Samarakoon et al. 2019

References:

Beimforde C, Feldberg K, Nylinder S, et al (2014) Estimating the Phanerozoic history of the *Ascomycota* lineages: combining fossil and molecular data. Molecular Phylogenetics and Evolution 78:386–398. https://doi.org/10.1016/j.ympev.2014.04.024

Dörfelt H, Schmidt AR (2005) A fossil *Aspergillus* from Baltic amber. Mycological Research 109(8):956–960. https://doi.org/10.1017/S0953756205003497

Lücking R, Nelsen MP (2018) Ediacarans, Protolichens, and Lichen-Derived *Penicillium*. In: Krings M, Harper CJ, Cuneo NR, Rothwell GW (eds) Transformative Paleobotany: Papers to Commemorate the Life and Legacy of Thomas N. Taylor. San Diego: Elsevier Science & Technology, pp 551–590

Lutzoni F, Nowak MD, Alfaro ME, et al (2018) Contemporaneous radiations of fungi and plants linked to symbiosis. Nature Communications 9:5451. https://doi.org/10.1038/s41467-018-07849-9

Pérez-Ortega S, Garrido-Benavent I, Grube M, et al (2016) Hidden diversity of marine borderline lichens and a new order of fungi: *Collemopsidiales* (*Dothideomyceta*). Fungal Diversity 80(1):285–300. https://doi.org/10.1007/s13225-016-0361-1

Prieto M, Wedin M (2013) Dating the diversification of the major lineages of *Ascomycota* (*Fungi*). PLoS ONE 8(6):e65576. https://doi.org/10.1371/journal.pone.0065576

Rikkinen J (2003) Calicioid lichens from European Tertiary amber. Mycologia 95(6):1032–1036. https://doi.org/10.1080/15572536.2004.11833019

Rikkinen J, Poinar GO (2002) Fossilised *Anzia* (*Lecanorales*, lichen-forming *Ascomycota*) from European Tertiary amber. Mycological Research 106(8):984–990. https://doi.org/10.1017/S0953756202005907

Samarakoon MC, Hyde KD, Hongsanan S, et al (2019) Divergence time calibrations for ancient lineages of *Ascomycota* classification based on a modern review of estimations. Fungal Diversity 96(1):285–346. https://doi.org/10.1007/s13225-019-00423-8

Schmidt AR, Beimforde C, Seyfullah LJ, et al (2014) Amber fossils of sooty moulds. Review of Palaeobotany and Palynology 200:53–64. https://doi.org/10.1016/j.revpalbo.2013.07.002

Taylor TN, Hass H, Kerp H, et al (2005) Perithecial ascomycetes from the 400 million year old Rhynie chert: an example of ancestral polymorphism. Mycologia 97(1):269–285. https://doi.org/10.1080/15572536.2006.11832862

Supplementary Table 4.S5. Divergence time estimates of lineages in *Sareomycetes*. Divergence time estimates (Ma) of *Sareomycetes* and the main lineages within obtained using five different secondary calibration approaches with BEAST. The median (in millions of years, Ma) and 95% HPD intervals (in brackets) are given for each divergence time estimate. For simplicity, the "Epochs" interval for each row is based on the five median estimates and it does not consider the corresponding 95% HPD intervals.

	Calibrated node with Age estimate	mtSSU subst. rate	nuLSU subst. rate	*Erysiphales* nuITS subst. rate	*Melanohalea* nuITS subst. rate	Epochs
Sareomycetes crown node	115.77 (164.75–73.62)	149.37 (216.5–94.19)	114.81 (181.16–67.04)	72.87 (107.99–47.87)	53.1 (78.55–34.31)	Upp. Jurassic–Eocene
Zythia crown node	35.07 (57.32–17.76)	46.94 (68.7–29.06)	37.08 (56.05–21.99)	23.18 (33.56–14.96)	17.17 (24.68–11.04)	Eocene–Miocene
Atrozythia crown node	17.43 (36.66–4.87)	23.56 (46.85–7.57)	18.25 (37.92–6.04)	11.66 (22.5–4.41)	8.38 (16.47–3.18)	Oligocene–Miocene
Sarea crown node	39.86 (67.66–21.28)	54.6 (81.94–34.04)	41.77 (68.81–22.7)	26.24 (40.35–15.78)	19.38 (29.25–11.6)	Eocene–Miocene
Zythia-Atrozythia split	77.69 (118.81–43.95)	100.86 (150.32–63.85)	78.54 (125.67–45.89)	49.81 (74.41–31.71)	36.49 (53.68–22.89)	Low. Cretaceous–Eocene
A. klamathica-A. lignicola split	17.43 (36.66–4.87)	23.56 (46.85–7.57)	18.25 (37.92–6.04)	11.66 (22.5–4.41)	8.38 (16.47–3.18)	Oligocene–Miocene
S. differmis crown	17.04 (29.97–8.49)	23.91 (37.03–14.16)	18.01 (30.74–8.95)	11.4 (18.23–6.42)	8.39 (13.11–4.58)	Oligocene–Miocene
S. coeloplata 1 crown	9.7 (19.12–4.09)	13.14 (22.88–6.37)	10.06 (18.77–4.3)	6.37 (11.29–3.02)	4.69 (8.25–2.25)	Miocene–Pliocene
S. coeloplata 2 crown	11.27 (20.99–4.4)	15.28 (25.81–7.52)	11.98 (21.41–5.73)	7.46 (12.72–3.73)	5.48 (9.38–2.77)	Miocene

Supplementary Table 4.S6. Prior host records for *Sarea* spp. and *Zythia resinae*. Some representative literature and specimen database host reports of species in *Zythia* and *Sarea* prior to this study. Host genera are arranged alphabetically by family, and *Cupressus* is given in both its broad sense (encompassing *Callitropsis*, *Cupressus s.str.*, *Hesperocyparis*, and *Xanthocyparis*) and its strict sense, differentiated from *Hesperocyparis*. * indicates a report which is ambiguous.

Available at: https://static-content.springer.com/esm/art%3A10.1186%2Fs43008-021-00056-0/MediaObjects/43008_2021_56_MOESM8_ESM.xlsx

Supplementary Table 4.S7. Taxonomic history of *Sareomycetes*. Historical taxonomic placements of genera accepted here in *Sareomycetes*, arranged chronologically with references.

Available at: https://static-content.springer.com/esm/art%3A10.1186%2Fs43008-021-00056-0/MediaObjects/43008_2021_56_MOESM9_ESM.xlsx