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D. Jean Lodge · Mahajabeen Padamsee · P. Brandon Matheny · M. Catherine Aime · Sharon A. Cantrell · David Boertmann · Alexander Kovalenko · Alfredo Vizzini · Bryn T. M. Dentinger · Paul M. Kirk · A. Martyn Ainsworth · Jean-Marc Moncalvo · Rytas Vilgalys · Ellen Larsson · Robert Lücking · Gareth W. Griffith · Matthew E. Smith · Lorelei L. Norvell · Dennis E. Desjardin · Scott A. Redhead · Clark L. Ovrebo · Edgar B. Lickey · Enrico Ercole · Karen W. Hughes · Régis Courtecuisse · Anthony Young · Manfred Binder · Andrew M. Minnis · Daniel L. Lindner · Beatriz Ortiz-Santana · John Haight · Thomas Læssøe · Timothy J. Baroni · József Geml · Tsutomu Hattori

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Abstract Molecular phylogenies using 1–4 gene regions and information on ecology, morphology and pigment chemistry were used in a partial revision of the agaric family Hygrophoraceae. The phylogenetically supported genera we recognize here in the Hygrophoraceae based on these and previous analyses are: *Acantholichen*, *Ampulloclitocybe*, *Arrhenia*, *Cantharellula, Cantharocybe, Chromosera*, *Chrysomphalina, Cora*, *Corella*, *Cuphophyllus, Cyphellostereum*, *Dictyonema,*

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D. J. Lodge (✉)
Center for Forest Mycology Research, Northern Research Station, USDA-Forest Service, Luquillo, PR 00773-1377, USA
e-mail: djlodge@caribe.net

D. J. Lodge
e-mail: dlodge@fs.fed.us

M. Padamsee
Systematics Team, Landcare Research, 231 Morrin Road, Auckland 1072, New Zealand
e-mail: PadamseeM@landcareresearch.co.nz

P. B. Matheny · K. W. Hughes
Ecology & Evolutionary Biology, University of Tennessee, Knoxville, TN 37996-1610, USA

M. C. Aime
Department of Botany & Plant Pathology, Purdue University, West Lafayette, IN 47907, USA

S. A. Cantrell
Science and Technology, Universidad del Turabo, Gurabo, PR 00778-3030, USA

D. Boertmann
Department of Bioscience, Aarhus University, Frederiksborgvej 399, DK-4000 Roskilde, Denmark

A. Kovalenko
Komarov Botanical Institute of the Russian Academy of Sciences, 2 Prof. Popov Str., St. Petersburg 197376, Russia

A. Vizzini · E. Ercole
Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Viale P.A. Mattioli 25, 10125 Torino, Italy

B. T. M. Dentinger · P. M. Kirk · A. M. Ainsworth
Mycology, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3DS, UK

J.-M. Moncalvo
Royal Ontario Museum, 100 Queen's Park, Toronto, ON, Canada

R. Vilgalys
Biology Department, Duke University, Durham, NC 27708-0338, USA

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Eonema, *Gliophorus, Haasiella*, *Humidicutis, Hygroaster, Hygrocybe*, *Hygrophorus*, *Lichenomphalia, Neohygrocybe, Porpolomopsis* and *Pseudoarmillariella*. A new genus that is sister to *Chromosera* is described as *Gloioxanthomyces*. Revisions were made at the ranks of subfamily, tribe, genus, subgenus, section and subsection. We present three new subfamilies, eight tribes (five new), eight subgenera (one new, one new combination and one stat. nov.), 26 sections (five new and three new combinations and two stat. nov.) and 14 subsections (two new, two stat. nov.). Species of *Chromosera*, *Gliophorus, Humidicutis,* and *Neohygrocybe* are often treated within the genus *Hygrocybe;* we therefore provide valid names in both classification systems. We used a minimalist approach in transferring genera and creating new names and combinations. Consequently, we retain in the Hygrophoraceae the basal cuphophylloid grade comprising the genera *Cuphophyllus, Ampulloclitocybe* and *Cantharocybe,* despite weak phylogenetic support. We include *Aeruginospora* and *Semiomphalina* in Hygrophoraceae based on morphology though molecular data are lacking. The lower hygrophoroid clade is basal to Hygrophoraceae s.s., comprising the genera *Aphroditeola, Macrotyphula, Phyllotopsis, Pleurocybella, Sarcomyxa, Tricholomopsis* and *Typhula*.

Keywords Hygrophoraceae · Fungi · Revisionary systematics · Nomenclatural revision · Phylogenetics · Pigment chemistry · Lamellar trama construction · Hymenial morphology · Ecology

Introduction

This paper is a contribution towards revision of the agaric family Hygrophoraceae Lotsy that integrates new molecular phylogenetic and morphological analyses with old and current data on phylogeny, morphology, pigment chemistry and ecology. The primary aim is to provide a coherent, integrated, higher-level structure for this diverse family at the ranks of subfamily, tribe, genus, subgenus, section and subsection. Recent publications on ecology, chemotaxonomy and molecular phylogenies together with our own analyses of morphology and new molecular data and phylogenies have made this revision possible.

The Hygrophoraceae has a complex history. The family may be based on Roze (1876), but his name, Hygrophorées, had a French rather than a Latin ending and was therefore invalid according to Art. 18.4 of the International Code of

E. Larsson
Biological & Environmental Sciences, University of Gothenburg, Göteborg, Sweden

R. Lücking
Science & Eduaction, Integrative Research & Collections (Botany), The Field Museum of Natural History, 1400 Lake Shore Dr., Chicago, IL 60605-2496, USA

G. W. Griffith
University of Wales, Aberystwyth, Ceredigion SY23 3DD, UK

M. E. Smith
Department of Plant Pathology, University of Florida, Gainesville, FL 32611-0680, USA

L. L. Norvell
Pacific Northwest Mycology Service, 6720 NW Skyline Bvd, Portland, OR 97229-1309, USA

D. E. Desjardin
Department of Biology, San Francisco State University, 1600 Holloway Ave., San Francisco, CA 94132, USA

S. A. Redhead
National Mycological Herbarium (DAOM), Science and Technology Branch, Agriculture & Agri-Foods, Canada, 960 Carling Avenue, Ottawa, Ontario, Canada ONT K1A 0C6

C. L. Ovrebo
Department of Biology, University of Central Oklahoma, Edmond, OK 73034, USA

E. B. Lickey
Department of Biology, Bridgewater College, 402 E. College St., Bridgewater, VA 22812, USA

R. Courtecuisse
Department of Botany, Faculty of Pharmaceutical & Biological Sciences, Lille, France

A. Young
100 Langton Road, Blackbutt, Qld 4306, Australia

M. Binder
CBS Fungal Biodiversity Centre, Evolutionary Phytopathology, Inst. of the Royal Netherlands Academy of Arts & Sciences (KNAW), Uppsalalaan 8, 3584 CT Utrecht, The Netherlands

A. M. Minnis · D. L. Lindner · B. Ortiz-Santana · J. Haight
Center for Forest Mycology Research, USDA Forest Service, Northern Research Station, One Gifford Pinchot Dr., Madison, WI 53726-2398, USA

T. Læssøe
Ecology and Evolution, Department of Biology, University of Copenhagen, Universitetsparken 15, 2100 København Ø, Denmark

T. J. Baroni
Department of Biological Sciences, SUNY – College at Cortland, Cortland, NY 13054, USA

J. Geml
Naturalis Biodiversity Center, Section National Herbarium of the Netherlands, PO Box 9514, 2300 RA Leiden, The Netherlands

T. Hattori
Forestry & Forest Products Research Inst., Kansai Research Center, Tsukuba, Japan

Nomenclature for algae, fungi, and plants (Melbourne Code) (ICN 2012, http://www.iapt-taxon.org/nomen/main.php). Lotsy (1907) validly published Hygrophoraceae with supporting details in German, which was permissible under the ICBN rules at that time (Young 2003). The generic type for the family, the genus *Hygrophorus*, was published by Fries in 1836. Fries (1838) subsequently organized the species of *Hygrophorus* Fr. into three 'tribes' (a nomenclaturally unrecognized, infrageneric rank, not the currently recognized infra-familial rank of tribe): *Limacium, Camarophyllus,* and *Hygrocybe*. Kummer (1871) raised the Friesian tribes to genus rank as *Limacium* (Fr.) P. Kumm., *Camarophyllus* (Fr.) P. Kumm. and *Hygrocybe* (Fr.) P. Kumm. As noted by Young (2005), Kummer did not retain the genus name, *Hygrophorus*, but instead used *Limacium* for most of the ectomycorrhizal species with divergent lamellar trama that we now refer to as *Hygrophorus* s.s. Karsten (1876) recognized the genera *Hygrophorus* Fr. (rather than *Limacium* sensu Kummer), *Camarophyllus* and *Hygrocybe* (misspelled as '*Hydrocybe*'). That led to confusion with *Hydrocybe* Fr. – a segregate of *Cortinarius*. Karsten corrected his misspelling of *Hydrocybe* to '*Hygrocybe*' in later publications, but Murrill (1911–1942) perpetuated Karsten's spelling error. Murrill's *Hydrocybe* is regarded as an orthographic variant of *Hygrocybe* so his names are otherwise valid, legitimate, and corrected to *Hygrocybe* names and combinations.

The Hygrophoraceae was originally characterized by basidiomes with thick, distant, waxy lamellae, spores that were mostly smooth, hyaline and inamyloid, and basidia five or more times the length of their spores (Singer 1986). We now recognize these characters are not as reliable as they once seemed (Lawrey et al. 2009; Lodge et al. 2006; Matheny et al. 2006; Young 1997), leading Bas (1988) to transfer genera from the Hygrophoraceae to the Tricholomataceae. Subsequent phylogenetic analyses (i.e., Binder et al. 2010; Lawrey et al. 2009; Matheny et al. 2006; Moncalvo et al. 2002) placed most of the genera traditionally treated in Hygrophoraceae apart from the Tricholomataceae. Matheny et al. (2006) were first to show strong support for a monophyletic Hygrophoraceae. The Hygrophoraceae appears to be mostly biotrophic based on stable carbon and nitrogen isotope signatures, though only the type genus, *Hygrophorus,* forms ectomycorrhizal associations with tree roots (Seitzman et al. 2011; Tedersoo et al. 2010). *Acantholichen, Cora, Corella, Cyphellostereum, Dictyonema, Lichenomphalia* and *Semiomphalina* species form lichens with green algae or cyanobacteria (Lawrey et al. 2009; Matheny et al. 2006; Redhead et al. 2002), *Eonema* is associated with live ferns and grasses (Lawrey et al. 2009), and *Arrhenia* and *Cantharellula* are generally associated with bryophytes (Lawrey et al. 2009). Biotic relationships for the remaining genera of Hygrophoraceae are enigmatic (Seitzman et al. 2011). Currently, Hygrophoraceae comprises over 600 species (not all described) in 25 named genera and one new genus (Tables 1 and 2), and is thus one of the larger families in the Agaricales. Moncalvo et al. (2002) identified many phylogenetic clades that were later supported as belonging to the Hygrophoraceae by Lodge et al. (2006), Matheny et al. (2006), Lawrey et al. (2009) and Binder et al. (2010). Neither Binder et al. (2010) nor Seitzman et al. (2011) found support for a monophyletic family, but Matheny et al. (2006) found Bayesian support for a monophyletic Hygrophoraceae s.l. if *Camarophyllopsis* and *Neohygrophorus* were excluded.

In this paper, we attempt to establish correct, legitimate, validly published names that correspond to phylogenetic clades in Hygrophoraceae. In some cases, we note a lack of correspondence between clades and previously established classifications. We used a conservative approach, and changed the status of names or made new combinations for names used previously in other genera or at unassigned ranks, created new names for clades or changed the placement of named taxa only when the phylogenetic evidence was strong, compelling, and consistent with morphology.

This is the culmination of a large international collaborative effort spanning 20 years and reflects both the consensus as well as the differing opinions of the many coauthors. Our efforts began in 1988–1990 with two separate collaborations formed by the Vilgalys – Moncalvo lab, one with Lodge and Cantrell, and the other with Kovalenko. The collaboration expanded greatly in 2002 with a Hygrophoraceae Systematics, Ecology and Conservation workshop at the International Mycological Congress in Oslo, Norway that was co-organized by Lodge, Cantrell, Boertmann, Courtecuisse and Kovalenko. The preliminary molecular phylogenies by Moncalvo that were presented in 2002 served as the basis for seeking specific additional sequences and for further phylogenetic analyses by Matheny. The complete data set analysis was presented at the Mycological Society of America meeting in Quebec, Canada (Lodge et al. 2006, web link), while a smaller, mostly independent data set was used in the Matheny et al.'s (2006) Assembling the Fungal Tree of Life (AFTOL) paper on Agaricales published in Mycologia. Padamsee and Aime were recruited for final analyses. Our four-gene region backbone analysis builds upon all of these previous iterations plus recent papers by Lawrey et al. (2009), Ovrebo et al. (2011) and the six-gene analysis by Binder et al. (2010). Our aim was to use two representatives per clade in the backbone analysis so as to reduce long-branch attractions while minimizing loss of bootstrap support with increasing taxa. We attempted to include a basal and a terminal representative from each clade to determine if the morphological characters used to distinguish taxonomic groups were synapomorphic. We also use independent four-gene analyses of *Hygrophorus* s.s. presented by Larsson (2010, and unpublished data).

In this paper, we used four gene regions: nuclear ribosomal ITS (ITS 1–2 and 5.8S), LSU (25S), and SSU (18S), and added the nuclear rpb2 6F to 7.1R region to as many of the

Table 1 Alternative classifications for Hygrophoraceae, subfamily *Hygrocyboideae* using the segregate genera accepted in this paper versus the aggregate genus, *Hygrocybe* s.l. The order in this table is by branching order in the 4-gene backbone and Supermatrix analyses (Figs. 1 and 2)

Segregate genera accepted here	Aggregate genus *Hygrocybe* s.l.
Subfamily *Hygrocyboideae* Padamsee & Lodge, subf. nov., type genus: *Hygrocybe* (Fr.) P. Kumm. Führ. Pilzk. (Zerbst): 111 (1871). *Hygrocybe* (Fr.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871) [≡ *Hygrophorus* subg. *Hygrocybe* Fr., Summa veg. Scand., Section Post. (Stockholm): 308 (1849)].	
Tribe *Hygrocybeae* Kühner, Bull. Soc. Linn. Lyon 48: 621 (1979), emended here by Lodge. Type genus: *Hygrocybe* (Fr.) P. Kumm., Führ. Pilzk. (Zwickau): 26 (1871)	
Genus *Hygrocybe* (Fr.) P. Kumm., Führ. Pilzk. (Zwickau): 26 (1871) [≡ *Hygrophorus* subg. *Hygrocybe* Fr. (1849)], type species: *Hygrocybe conica* (Schaeff.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871) [≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838)]	**Genus *Hygrocybe*** (Fr.) P. Kumm., Führ. Pilzk. (Zwickau): 26 (1871) [≡ *Hygrophorus* subg. *Hygrocybe* Fr. (1849)], type species: *Hygrocybe conica* (Schaeff.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871) [≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838)]
Subgenus *Hygrocybe*, [autonym] (1976), type species *Hygrocybe conica* (Schaeff.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871) [≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838) [1836–1838]]	**Subgenus *Hygrocybe***, [autonym] (1976), type species *Hygrocybe conica* (Schaeff.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871) [≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838) [1836–1838]]
Section *Hygrocybe* [autonym] (1889), type species *Hygrocybe conica* (Schaeff.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871) [≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838) [1836–1838]]	**Section *Hygrocybe*** [autonym] (1889), type species *Hygrocybe conica* (Schaeff.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871) [≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838) [1836–1838]]
Subsection *Hygrocybe* [autonym] (1951), type species *Hygrocybe conica* (Schaeff.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871) [≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838) [1836–1838]]	**Subsection *Hygrocybe***, [autonym] (1951), type species *Hygrocybe conica* (Schaeff.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871) [≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838) [1836–1838]]
Subsection *Macrosporae* R. Haller Aar. ex Bon, Doc. Mycol. 24(6): 42 (1976), type species *Hygrocybe acutoconica* (Clem.) Singer (1951) (as *Hygrocybe acuticonica* Clem.) [= *Hygrocybe persistens* (Britzelm.) Singer (1940)]	**Subsection *Macrosporae*** R. Haller Aar. ex Bon, Doc. Mycol. 24(6): 42 (1976), type species *Hygrocybe acutoconica* (Clem.) Singer (1951) (as *Hygrocybe acuticonica* Clem.) [= *Hygrocybe persistens* (Britzelm.) Singer (1940)]
Section *Velosae* Lodge, Ovrebo & Padamsee, sect. nov., type species *Hygrophorus hypohaemactus* Corner, Trans. Br. Mycol. Soc. 20(2): 180, Figs. 5, 6, 8a (1936) [≡ *Hygrocybe hypohaemacta* (Corner) Pegler & Fiard, Kew Bull. 32(2): 299 (1978)]	**Section *Velosae*** Lodge, Ovrebo & Padamsee
Section *Pseudofirmae* Lodge & Padamsee, sect. nov., type species *Hygrophorus appalachianensis* Hesl. & A.H. Sm., North American Species of *Hygrophorus*: 147 (1963) [≡ *Hygrocybe appalachianensis* (Hesl. & A.H. Sm.) Kronaw. (as '*appalachiensis*'), in Kronawitter & Bresinsky, Regensb. Mykol. Schr. 8: 58 (1998)]	**Section *Pseudofirmae*** Lodge & Padamsee
Section *Microsporae* Boertm., The genus *Hygrocybe*. Fungi of Northern Europe (Greve) 1: 16 (1995), type species *Hygrocybe citrinovirens* (J.E. Lange) Jul. Schäff., Ber. bayer.bot. Ges. 27: 222 (1947)	**Section *Microsporae*** Boertm., The genus *Hygrocybe*. Fungi of Northern Europe (Greve) 1: 16 (1995), type species *Hygrocybe citrinovirens* (J.E. Lange) Jul. Schäff., Ber. bayer.bot. Ges. 27: 222 (1947)
Section *Chlorophanae* (Herink) Arnolds ex Candusso, *Hygrophorus*. Fungi europ. (Alassio 6: 464 (1997), type species *Hygrocybe chlorophana* (Fr.) Wünsche, Die Pilze: 112 (1877) [≡ *Agaricus chlorophanus* Fr. : Fr., Syst. mycol. (Lundae) 1: 103 (1821)]	**Section *Chlorophanae*** (Herink) Arnolds ex Candusso, *Hygrophorus*. Fungi europ. (Alassio) 6: 464 (1997), type species *Hygrocybe chlorophana* (Fr.) Wünsche, Die Pilze: 112 (1877) [≡ *Agaricus chlorophanus* Fr. : Fr., Syst. mycol. (Lundae) 1: 103 (1821)]
Subgenus *Pseudohygrocybe* Bon, Doc. Mycol. 6 (24): 42 (1976), type species *Hygrocybe coccinea* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 330 (1838) [1836–1838]] ≡ *Agaricus coccineus* Schaeff. Fung. Bavar. Palat. 4: 70 (1774), ([NOT *Agaricus coccineus* Scop., Fl. carniol., (Wein) Edn. 2: 436 (1772), an earlier homonym of a sanctiond name]	**Subgenus *Pseudohygrocybe*** Bon, Doc. Mycol. 6 (24): 42 (1976), type species *Hygrocybe coccinea* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 330 (1838) [1836–1838]] ≡ *Agaricus coccineus* Schaeff. Fung. Bavar. Palat. 4: 70 (1774), ([NOT *Agaricus coccineus* Scop., Fl. carniol., (Wein) Edn. 2: 436 (1772), an earlier homonym of a sanctiond name]
Section *Coccineae* Fayod, Proc. Hist. Nat. Agar. Ann. Scient. Nat. 7(9): 309 (1889), type species *Hygrocybe coccinea* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 330 (1838) [1836–1838], ≡ *Agaricus coccineus* Schaeff. Fung. Bavar. Palat. 4: 70 (1774) [= *Hygrocybe* sect. *Puniceae* Fayod (1889), illeg., = *H.* sect. '*Inopodes*" Singer (1943), nom. invalid]	**Section *Coccineae*** Fayod, Proc. Hist. Nat. Agar. Ann. Scient. Nat. 7(9): 309 (1889), type species *Hygrocybe coccinea* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 330 (1838) [1836–1838], ≡ *Agaricus coccineus* Schaeff. Fung. Bavar. Palat. 4: 70 (1774) [= *Hygrocybe* sect. *Puniceae* Fayod (1889), illeg., = *H.* sect. "*Inopodes*" Singer (1943), nom. invalid]
Subsection *Coccineae* (Bataille) Singer, Lilloa 22: 152 (1951) [1949], type species: *Hygrocybe coccinea* (Schaeff.) Fr., Epicr. syst. mycol.	**Subsection *Coccineae*** (Bataille) Singer, Lilloa 22: 152 (1951) [1949], type species: *Hygrocybe coccinea* (Schaeff.) Fr., Epicr. syst. mycol.

Table 1 (continued)

Segregate genera accepted here	Aggregate genus *Hygrocybe* s.l.
(Upsaliae): 330 (1838) [1836–1838] ≡ *Agaricus coccineus* Schaeff. Fung. Bavar. Palat. 4: 70 (1774) [= *Hygrocybe* subsect. *Puniceae* (Fayod) Arnolds ex Candusso (1997), superfluous, nom. illeg., = *Hygrocybe* subsect. "*Inopodes*" Singer (1952), nom. invalid]	(Upsaliae): 330 (1838) [1836–1838] ≡ *Agaricus coccineus* Schaeff. Fung. Bavar. Palat. 4: 70 (1774) [= *Hygrocybe* subsect. *Puniceae* (Fayod) Arnolds ex Candusso (1997), superfluous, nom. illeg., = *Hygrocybe* subsect. "*Inopodes*" Singer (1952), nom. invalid]
Subsection *Siccae* Boertm., The genus *Hygrocybe*. Fungi of Northern Europe - Vol. 1: 15 (1995), type species *Hygrocybe reidii* Kühner, Bull. trimest. Soc. mycol. Fr. 92: 463 (1976)	**Subsection *Siccae*** Boertm., The genus *Hygrocybe*. Fungi of Northern Europe - Vol. 1: 15 (1995), type species *Hygrocybe reidii* Kühner, Bull. trimest. Soc. mycol. Fr. 92: 463 (1976)
Subsection *Squamulosae* (Bataille) Singer, Lilloa 22: 152 (1951)[1949], type species *Hygrocybe turunda* (Fr.) P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 235 (1879), ≡ *Hygrophorus turundus* (Fr.: Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 330 (1838), ≡ *Agaricus turundus* Fr., Observationes mycologicae 2: 199 (1818), [≡ *Hygrocybe* subsect. *Turundae* (Herink) Bon, Doc. Mycol. 19(75): 56 (1989), superfluous, nom. illeg.]	**Subsection *Squamulosae*** (Bataille) Singer, Lilloa 22: 152 (1951)[1949], type species *Hygrocybe turunda* (Fr.) P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 235 (1879), ≡ *Hygrophorus turundus* (Fr.: Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 330 (1838), ≡ *Agaricus turundus* Fr., Observationes mycologicae 2: 199 (1818), [≡ *Hygrocybe* subsect. *Turundae* (Herink) Bon, Doc. Mycol. 19(75): 56 (1989), superfluous, nom. illeg.]
Section *Firmae* Heinem., Bull. Jard. bot. État Brux. 33 (4): 441 (1963), emend. here by Lodge, type species *Hygrocybe firma* (Berk. & Broome) Singer, Sydowia 11: 355 (1958), ≡ *Hygrophorus firmus* Berk. & Broome, J. Linn. Soc., Bot. 11(56): 563 (1871)	**Section *Firmae*** Heinem., Bull. Jard. bot. État Brux. 33 (4): 441 (1963), type species *Hygrocybe firma* (Berk. & Broome) Singer, Sydowia 11: 355 (1958), ≡ *Hygrophorus firmus* Berk. & Broome, J. Linn. Soc., Bot. 11(56): 563 (1871)
Genus *Hygroaster* Singer 1955, *Sydowia* 9(1–6): 370, type species *Hygroaster nodulisporus* (Dennis) Singer, Sydowia 9(1–6: 370 (1955), ≡ *Hygrophorus nodulisporus* Dennis Kew Bull. 8(2): 259 (1953)	Subgenus or sect. *Hygroaster*, ined. This change would need to be made to prevent *Hygrocybe* s.l. from being rendered polyphyletic if the aggregate genus *Hygrocybe* is used.
***Tribe* Humidicuteae** Padamsee & Lodge, tribe nov., type genus *Humidicutis* (Singer) Singer, Sydowia 12(1–6): 225 (1959) [1958]	
***Genus* Neohygrocybe** Herink Sb., Severocesk. Mus., Prír. Vedy 1: 71 (1959), emend. here by Lodge, type species *Neohygrocbye ovina* (Bull. : Fr.) Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 72 (1959), ≡ *Hygrophorus ovinus* (Bull. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 328 (1838) [1836–1838], ≡ Agaricus ovinus Bull., Herbier de la France 13: t. 580 (1793) : Fr.	**Subgenus *Neohygrocybe*** (Herink) Bon, Doc. Mycol. 19 (75): 56 (1989), type species *Hygrocybe ovina* (Bull.) Kühner, *Botaniste* 17: 43 (1926), ≡ *Hygrophorus ovinus* (Bull. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 328 (1838) [1836–1838], ≡ *Agaricus ovinus* Bull., Herbier de la France 13: t. 580 (1793) : Fr.
Section *Neohygrocybe* [autonym] type species *Neohygrocybe ovina* (Bull. ex Fr.) Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 72 (1959), ≡ *Hygrocybe ovina* (Bull.) Kühner, Botaniste 17: 43 (1926), ≡ *Hygrophorus ovinus* (Bull. : Fr.) Fr., Anteckn. Sver. Ätl. Svamp.: 45, 47 (1836), ≡ *Agaricus ovinus* Bull., Herbier de la France 13: t. 580 (1793)] [≡ *Neohygrocybe* sect. "*Ovinae*" Herink (1959), nom. invalid],	**Section *Neohygrocybe*** (Herink) Bon, 1989, Doc. Mycol. 19 (75): 56 (1989), type species *Hygrocybe ovina* (Bull.) Kühner, *Botaniste* 17: 43 (1926), ≡ *Hygrophorus ovinus* (Bull. : Fr.) Fr., Anteckn. Sver. Ätl. Svamp.: 45, 47 (1836), ≡ *Agaricus ovinus* Bull., Herbier de la France 13: t. 580 (1793), [≡ *Hygrocybe* sect. *Neohygrocybe* (Herink) Candusso 1997, superfluous, nom. illeg.],
Section *Tristes* (Bataille) Lodge & Padamsee, comb. nov., emended here by Lodge to include only the type species. Lectoype designated by Singer, Lilloa 22: 151 (1951): *Hygrocybe nitrata* (Pers.) Wünsche, Die Pilze: 112 (1877), ≡ *Agaricus nitratus* Pers., Syn. meth. fung. (Göttingen) 2: 356 (1801), ≡ *Neohygrocybe nitrata* (Pers.) Kovalenko, Opredelitel' Gribov SSSR (Leningrad): 40 (1989), [≡ "*Neohygrocybe nitrata*" (Pers.) Herink (1959), nom. invalid., Art. 33.2]. Basionym: *Hygrocybe* section *Tristes* (Bataille) Singer, Lilloa 22: 151 (1951) [1949] [≡ *Hygrophorus* Fr. subgen. *Hygrocybe* Fr. [unranked] *Tristes* Bataille, Mém. Soc. émul. Doubs, sér. 8 4:183 (1910), [≡ *Neohygrocybe* sect. "*Nitratae*" Herink, superfluous, nom. illeg., Art. 52.1]	**Section *Tristes*** (Bataille) Singer, Lilloa 22: 151(1951) [1949]. Lectotype designated by Singer, Lilloa 22: 151 (1951) [1949]: *Hygrocybe nitrata* (Pers.) Wünsche, [≡ *Agaricus nitratus* Pers. (1801), ≡ *Neohygrocybe nitrata* (Pers.) Kovalenko (1989), [≡ *"Neohygrocybe nitrata"* (Pers.) Herink (1959), nom. invalid. Art. 33.2]
	Subgenus *Humidicutis* (Singer) Boertm., Fungi of Europe, 2nd ed., Vol. 1: 17 (2010), type species *Hygrocybe marginata* (Peck) Murrill [as '*Hydrocybe*'], N. Amer. Fl. (New York) 9(6): 378 (1916), ≡ *Hygrophorus marginatus* Peck, Ann. Rpt. N.Y. State Mus. Nat. Hist. 28: 50 (1876)
Genus *Porpolomopsis* Bresinsky, Regensb. Mykol. Schr. 15: 145 (2008), type species *Porpolomopsis calyptriformis* (Berk.) Bresinsky Regensb. Mykol. Schr. 15: 145, (2008), ≡ *Hygrocybe calyptriformis* (Berk.) Fayod, Annls. Sci. Nat. Bot., sér. 7 9: 309 (1889), ≡ *Agaricus calyptriformis* Berk., Ann. Mag. Nat. Hist., Ser. 1 1: 198 (1838)	
Genus *Humidicutis* (Singer) Singer, Sydowia 12(1–6): 225 (1959) [1958], emended here by Lodge, type species *Humidicutis marginata* (Peck) Singer (1959), ≡ *Hygrophorus marginatus* Peck, Ann. Rpt. N.Y. State Mus. Nat. Hist. 28: 50 (1876)	

Table 1 (continued)

Segregate genera accepted here	Aggregate genus *Hygrocybe* s.l.
Genus *Gliophorus* Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 80 (1959), type species *Gliophorus psittacinus* (Schaeff. : Fr.) Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 72 (1959), ≡ *Hygrocybe psittacina* (Schaeff. : Fr.) P. Kumm., Führ. Pilzk. (Zwickau): 112 (1871), ≡ *Hygrophorus psittacinus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 332 (1838), ≡ *Agaricus psittacinus* Schaeff. : Fr., Fung. Bavar. Palat. 4: 70, t. 301 (1774)	**Subgenus *Gliophorus*** (Herink) Heinem., Bull. Jardin bot. État. Brux.33: 452 (1963), type species *Hygrocybe psittacina* (Schaeff. : Fr.) P. Kumm., Führ. Pilzk. (Zwickau): 112 (1871), ≡ *Hygrophorus psittacinus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 332 (1838), ≡ *Agaricus psittacinus* Schaeff. : Fr., Fung. Bavar. Palat. 4: 70, t. 301 (1774)
Section *Gliophorus*, [autonym] (1958), type species: *Gliophorus psittacinus* (Schaeff.) Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 82 (1959), ≡ *Hygrocybe psittacina* (Schaeff.) P. Kumm. (1871), ≡ *Hygrophorus psittacinus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 332 (1838), ≡ *Agaricus psittacinus* Schaeff., Fung. Bavar. Palat. 4: 301 (1774)]. [= *Gliophorus* sect. '*Psittacinae*"(Bataille) Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 81 (1959), nom. invalid, Art. 22.2].	Section *Gliophorus*, pro parte, combination in *Hygrocybe* not yet made, [≡ *Hygrocybe* sect. *Psittacinae* (Bataille) Arnolds ex Candusso 1997, illeg., Art. 52.1]
Section *Glutinosae* (Kühner) Lodge & Padamsee, comb. nov., emend. here to exclude *G. unguinosus* (Fr. : Fr.) Kovalenko, Lectotype: *Gliophorus laetus* (Pers. : Fr.) Herink (1958) [1959], Sb. Severocesk. Mus., Prír. Vedy 1: 84, [≡ *Hygrocybe laeta* (Pers. : Fr.) P. Kumm. (1871), ≡ *Hygrophorus laetus* (Pers.) Fr., Epicr. syst. mycol. (Upsaliae): 328 (1838) [1836–1838], ≡ *Agaricus laetus* Pers., Observ. Mycol. (Lipsiae) 2: 48 (1800) [1779] : Fr.]. Lectotype [*H. laeta* (Pers.) P. Kumm.] was inadvertently selected by Candusso, *Hygrophorus*. Fungi europ. (Alassio) 6: 591 (1997). Basionym: *Hygrocybe* sect. *Glutinosae* Kühner, *Botaniste* 17: 53 (1926). [≡ *Gliophorus* sect. *Laetae* (Bataille) Kovalenko 1989, based on *Hygrocybe* sect. *Laetae* (Bataille) Singer (1949) 1951, is superfluous, nom. illeg.].	**Section *Glutinosae*** Kühner, Botaniste 17: 53 (1926), Lectotype species inadvertently selected by Candusso 1997: *Hygrocybe laeta* (Pers.) P. Kumm. (1871), ≡ *Agaricus laetus* Pers. (1800) [1779], [≡ *Hygrocybe* sect. *Laetae* (Battaille) Singer 1951, superfluous, nom. illeg.].
Section *Unguinosae* Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 81 (1959), type species *Agaricus unguinosus* Fr. : Fr., Syst. mycol. (Lundae) 1: 101 (1821), ≡ *Gliophorus unguinosus* (Fr.) Kovalenko, Mikol. Fitopatol. 22(3): 209 (1988), [≡ "*Gliophorus unguinosus*" Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 81 (1959), nom. invalid, Art. 41.5], ≡ *Hygrocybe unguinosa* (Fr.: Fr.) P. Karst Bidr. Känn. Finl. Nat. Folk 32: 237 (1879), = *Hygrocybe irrigata* (Pers.: Fr.) Bon, Docums Mycol. 6(no. 24): 4 (1976)	Section *Gliophorus,* ined, pro parte, combination in *Hygrocybe* not yet made
Tribe *Chromosereae* Vizzini, Lodge Norvell & Redhead, tribe nov., type genus *Chromosera* Redhead, Ammirati & Norvell, Beih. Sydowia 10: 161 (1995), emend. Vizzini & Ercole, Micol. Veget. Medit. 26(2): 97 (2012) [2011]	
Genus *Chromosera* Redhead, Ammirati & Norvell, Beih. Sydowia 10: 161 (1995), emend. Vizzini & Ercole, Micol. Veget. Medit. 26(2): 97 (2012) [2011], type species *Agaricus cyanophyllus* Fr. Öfvers. Kongl. Svensk Vet.-Akad. Förh. 18(1): 23 (1861), ≡ *Chromosera cyanophylla* (Fr.) Redhead, Ammirati & Norvell, Mycotaxon 118: 456 (2012) [2011].	**Subgenus *Oreocybe*** (Boertm.) Beis. Regensburger Mykologische Schriften 10: 11 (2002), type species *Hygrocybe citrinopallida* (A.H. Sm. & Hesler) Kobayasi, Bull. natn. Sci. Mus., Tokyo 14(1): 62 (1971), ≡ *Hygrophorus citrinopallidus* A.H. Sm. & Hesler (1954)
Subgenus *Chromosera*, [autonym], type species *Agaricus cyanophyllus* Fr. Öfvers. K. Svensk. Vetensk.-Akad. Förhandl. 18(1): 23 (1861), ≡ *Chromosera cyanophylla* Redhead, Ammirati & Norvell (2012) [2011] in Redhead, Ammirati, Norvell, Vizzini & Contu, Mycotaxon 118: 456	*Omphalina cyanophylla* (Fr.) Quél. ≡ *Chromosera cyanophylla* (not yet combined in *Hygrocybe*)
Subgenus *Oreocybe* (Boertm.) Vizzini, Lodge & Padamsee, comb. nov., type species: *Chromosera citrinopallida* (A.H. Sm. & Hesler) Vizzini & Ercole, Micol. Veget. Medit. 26(2): 97 (2012) [2011], ≡ *Gliophorus citrinopallidus* (A.H. Sm. & Hesler) Kovalenko (1999), ≡ *Hygrocybe citrinopallida* (A.H. Sm. & Hesler) Kobayasi, Bull. natn. Sci. Mus., Tokyo 14(1): 62 (1971), ≡ *Cuphophyllus citrinopallidus* (A.H. Sm. & Hesler) Bon, Docums. Mycol. 21(no. 81): 56 (1991), ≡ *Hygrophorus citrinopallidus* A.H. Sm. & Hesler, Sydowia (1–6): 327 (1954)]. Basionym: *Hygrocybe sect. Oreocybe* Boertm., Nordic Jl. Bot. 10(3): 315 (1990), [≡ *Hygrocybe* subg. *Oreocybe* (Boertm.) Beis., Regensburger Mykologische Schriften 10: 11 (2002)]	**Section *Oreocybe*** Boertm., pro parte, Nordic J. Botany 10(3): 315 (1990), type species *Hygrocybe citrinopallida* (A.H. Sm. & Hesler) Kobayasi, Bull. natn. Sci. Mus., Tokyo 14(1): 62 (1971), ≡ *Hygrophorus citrinopallidus* A.H. Sm. & Hesler, Sydowia (1–6): 327 (1954)
Subgenus *Subomphalia* Vizzini, Lodge & Padamsee, subg. nov., type species: *Chromosera viola* (J. Geesink & Bas) Vizzini & Ercole, Micol. Veget. Medit. 26(2): 97 (2012) [2011], ≡ *Hygrocybe viola* J. Geesink & Bas, in Arnolds, Persoonia 12(4): 478 (1985a), ≡ *Cuphophyllus viola* (J. Geesink & Bas) Bon, Doc. Mycol. 19(76): 73 (1989)	**Section *Oreocybe*** Boertm., 1990, pro parte, Nordic Jl. Bot. 10(3): 315, type species *Agaricus cyanophyllus* Fr. (1861), ≡ *Chromosera cyanophylla* Redhead, Ammirati & Norvell (2012) [2011] in Redhead, Ammirati, Norvell, Vizzini and Contu, Mycotaxon 118: 456

Table 1 (continued)

Segregate genera accepted here	Aggregate genus *Hygrocybe* s.l.
***Genus* Gloioxanthomyces** Lodge, Vizzini, Ercole & Boertm., gen. nov., type species *Hygrophorus vitellinus* Fr., Monogr. Hymenomyc. Suec. (Upsaliae) 2(2): 312 (1863), ≡ *Gloioxanthomyces vitellinus* (Fr.) Lodge, Vizzini, Ercole & Boertm. Lectotype designated here is an illustration cited in Fries, Monogr. Hymenomyc. Suec. (Upsaliae) 2(2): 312 (1863): Icon. t. 167, f. 3. Epitype selected by Lodge, Vizzini, Ercole & Boertmann: Sweden, coll. K. Bergelin, 8 Oct. 2011, LD 1617064	**Genus *Gloioxanthomyces*** Lodge, Vizzini, Ercole & Boertm., [or a new subgenus or section for *Hygrocybe nitida* and *H. vitellina*]

backbone representatives as possible. We augmented the dataset used for the backbone with additional species and specimens that had at least an LSU sequence and performed a supermatrix analysis. In addition, we present paired ITS-LSU phylogenies that have greater species representation for four overlapping segments of the Hygrophoraceae. We have included more species and genera than previous analyses, though not all of the species or collections that we sequenced are presented. Our initial analyses revealed many cases where the same name has been applied to multiple, molecularly distinguishable species. We therefore sought collections from the same region as the type location to serve as reference taxa. We have retained some unknown taxa with misapplied names, however, to show the depth of the taxonomic problems that exist. We have resolved some previously known issues, while others have been raised or are in need of further work. The ITS analyses in Dentinger et al. (unpublished data) has been especially helpful in resolving species complexes and misapplied names in *Hygrocybe* s.l. We use this paper to establish a higher-level taxonomic framework for the Hygrophoraceae and to show where the remaining issues lie.

Methods

Species selection Lodge and Cantrell targeted several species per clade using previous unpublished preliminary analyses by Moncalvo, Vilgalys, Hughes and Matheny together with published molecular phylogenies by Moncalvo et al. (2000, 2002), Matheny et al. (2006), Lawrey et al. (2009) and Binder et al. (2010). Preference was for one basal and one distal taxon per clade and for types of genera and sections. In clades comprising difficult species complexes, we selected at least one named species known from a restricted geographic range (e.g., *Hygrocybe graminicolor, Humidicutis lewellianae*). The sequences that were generated in this study together with those from GenBank and UNITE are given in Online Resource 1. We generated 306 sequences for this work: 90 ITS, 109 LSU, 65 SSU and 42 RPB2. The rpb2 sequences we analyzed contain indels that caused reading frame shifts so they are not accessible in GenBank using the BLASTx protocol. The taxa for the backbone analysis were winnowed to two (rarely three) per clade based on whether all or most of the four gene regions could be sequenced, preferably from the same collection. When it was necessary to use multiple collections to obtain all the sequences, these were matched by the ITS region (> 97 % similar), except for some of Kovalenko's Russian collections that were matched by LSU sequences (> 99.5 % similar in the LROR to LR7 section). Most of the names for *Hygrocybe* s.l. used in North America are those of species originally described from Europe/UK/Scandinavia. Many of the sequences in our initial iterations were from North American collections, but we found that they often did not match ITS sequences of European/Scandinavian/UK collections by us, and later, published ITS sequences by Brock et al. (2009) from UK collections deposited at Kew, and Babos et al. (2011) from Hungarian collections. We therefore replaced many of our original sequences of American collections with sequences of correctly named collections from Europe/UK/Scandinavia.

DNA extraction and amplification Molecular methods generally followed either Mata et al. (2007) or Lindner and Banik (2009) with the following modifications for DNA isolation, PCR, cloning and sequencing. Small fragments of fruiting bodies, typically stipe apex or hymenial tissue, were placed in 1.5 mL microcentrifuge tubes with approximately 500 μL filter-sterilized cell lysis solution (CLS) containing 1.4 M NaCl, 0.1 M Tris–HCl, 20 mM EDTA, and 2 % hexadecyltrimethylammonium bromide (CTAB) and homogenized with plastic or glass pestles. Ground samples at the Center for Forest Mycology Research (CFMR) were stored at –20 C overnight. Tubes were then incubated at 65 C for 1 or 2 h. Following incubation the tubes were centrifuged at 16 110 rcf for 5 min and the supernatants transferred to clean 1.5 mL microcentrifuge tubes. Five-hundred μL of −20 C 2-propanol (isopropanol) was added to each supernatant, tubes were inverted, incubated at −80 C for 15 min (or at 0 C overnight by JEH at CFMR) and then centrifuged at 10 621 rcf for 20 min at 0 C (or 15 000 rcf for 30 min at 0C by JEH at CFMR). Supernatants were discarded, 500 μL of 75 %

Table 2 Taxonomy of Hygrophoraceae, subfamilies *Hygrophoroideae* and *Lichenomphalioideae* and the cuphophylloid grade. Taxa are organized in this table hierarchically and by the branching order in the 4-gene backbone and Supermatix analyses (Figs. 1 and 2) and the *Hygrophorus* ITS analysis (Online Resource 9)

Subfamily *Hygrophoroideae* E. Larss., Lodge, Vizzini, Norvell & Redhead, subf. nov., type genus *Hygrophorus* Fr., Fl. Scan.: 339 (1836) [1835]

Tribe *Chrysomphalineae* Romagn., Bull. Soc., Mycol. Fr. 112(2): 135 (1996), emend. Lodge, Padamsee, Norvell, Vizzini & Redhead, Transferred from Cantharellaceae tribe *Chrysomphalineae* Romagn., Doc. Mycol. 25(98–100): 135 (1996), type genus *Chyrsomphalina* Clémençon, Z. Mykol. 48(2): 202 (1982) [≡ Cantharellaceae tribe "*Paracantharelleae*" Romagn., Doc. Mycol. Fr. 25(98–100): 418 (1995) nom. invalid, Art. 18.1]

Genus *Chrysomphalina* Clémençon, Z. Mykol. 48(2): 202 (1982), type species *Chrysomphalina chrysophylla* (Fr. : Fr.) Clémençon, Z. Mykol. 48(2): 203 (1982), ≡ *Agaricus chrysophyllus* Fr. : Fr., Syst. mycol. (Lundae) 1: 167 (1821)

Genus *Haasiella* Kotl. & Pouzar, Ceská Mykol. 20(3): 135 (1966), type species *Haasiella venustissima* (Fr.) Kotl. & Pouzar ex Chiaffi & Surault (1996), ≡ *Agaricus venustissimus* Fr., Öfvers Kongl. Svensk Vet.-Akad, Förh. 18: 21 (1861)

Genus *Aeruginospora* Höhn. Sber. Akad. Wiss. Wein, Math.-naturw. Kla., Abt. 1 117: 1012 (1908), type species *Aeruginospora singularis* Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 117: 1012 (1908)

Tribe *Hygrophoreae* P. Henn., in A. Engler & E.A. Prantl, Nat. Pflanzenfam. 1: 209 (1898), emend. Kühner, Bull. mens. Soc. linn. Lyon 48: 617 (1979), type genus *Hygrophorus* Fr., Fl. Scan.: 339 (1836) [1835]

Genus *Hygrophorus* Fr., Fl. Scan.: 339. (1836) [1835], type species *Hygrophorus eburneus* (Bull. : Fr.) Fr., *Epicr. syst. mycol.* (Upsaliae): 321 (1836) [1836–1838], ≡ *Agaricus eburneus* Bull., Herb. Fr. 3: tab. 118, tab. 551, fig. 2 (1783)

Subgenus *Hygrophorus* [autonym] (1849), Emended here by E. Larss., type species *Hygrophorus eburneus* (Bull.) Fr., Epicr. syst. mycol. (Upsaliae): 321 (1836) [1836–1838], ≡ *Agaricus eburneus* Bull., Herb. Fr. 3: tab. 118, tab. 551, fig. 2 (1783)

Section *Hygrophorus* [autonym] type species *Hygrophorus eburneus* (Bull.) Fr., Epicr. syst. mycol. (Upsaliae): 321 (1836) [1836–1838], ≡ *Agaricus eburneus* Bull., Herb. Fr. 3: tab. 118, tab. 551, fig. 2 (1783)

Subsection *Hygrophorus* [autonym] type species *Hygrophorus eburneus* (Bull.) Fr., Epicr. syst. mycol. (Upsaliae): 321 (1836) [1836–1838], ≡ *Agaricus eburneus* Bull., Herb. Fr. 3: tab. 118, tab. 551, fig. 2 (1783)

Subsection *Fulventes* (Fr.) E. Larss., sect. nov., type species *Hygrophorus arbustivus* (Fr.) Fr., Anteckn. Sver. Ätl. Svamp.: 46 (1836) [= *Hygrophorus*, 'Tribus' *Limacium* [unranked] Fulventes l. flavi. Fries 1874, Hymen. Eur.: 408]

Section *Discoidei* (Bataille) Konrad & Maubl., Icon. Sel. Fung. 6: 428 (1937), type species *Hygrophorus discoideus* (Pers. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 323 (1838) [1836–1838],≡ *Agaricus discoideus* (Pers. : Fr.) : Fr., Syn. meth. fung. (Göttingen) 2: 365 (1801). Basionym: *Hygrophorus* [unranked] *Discoidei* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 162 (1910)

Section *Picearum* E. Larss., sect. nov., type species *Hygrophorus piceae* Kühner, Bull. mens. Soc. linn. Lyon 18: 179 (1949)

Subgenus *Colorati* (Bataille) E. Larss., stat. nov., type section *Olivaceoumbrini* (Bataille) Konrad & Maubl., Icon. Sel. Fung. 6: 137 (1937). Type species *Hygrophorus olivaceoalbus* (Fr. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 324 (1838) [1836–1838], ≡ *Agaricus olivaceoalbus* Fr., Observ. Mycol. (Havniae) 1: 5 (1815)], designated by Singer, Lilloa 22: 148 (1951) [1949]. Basionym *Hygrophorus* subg. *Limacium* [unranked] *Colorati* Bataille, Mém. Soc. Émul. Doubs, sér. 8 4: 158 (1910) [1909],

Section *Olivaceoumbrini* (Bataille) Konrad & Maubl., Icon. Sel. Fung. 6: 137 (1937), type species *Hygrophorus olivaceoalbus (*Fr. :Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 324 (1838), ≡ *Agaricus olivaceoalbus* Fr., Observ. Mycol. (Havniae) 1: 5 (1815). Basionym: *Hygrophorus* [unranked] *Olivaceo-umbrini* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 163 (1910) [≡ sect. *Olivaceo-umbrini* (Bataille) Bon 1990, superfluous, nom. illeg. ≡ sect. *Colorati* (Bataille) Singer (1951)[1949], superfluous, nom. illeg., Art. 52.1]

Subsection *Olivaceoumbrini* (Bataille) Singer, Lilloa 22: 146 (1951) [1949], type species *Hygrophorus olivaceoalbus* (Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 324 (1838), ≡*Agaricus olivaceoalbus* Fr. (1815) : Fr., Observ. Mycol. (Havniae) 1: 5 (1815). Basionym: *Hygrophorus* [unranked] *Olivaceo-umbrini* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 163 (1910)

Subsection *Tephroleuci* (Bataille) Singer, Lilloa 22: 146 (1951) [1949], type species *Hygrophorus tephroleucus* (Pers.) Fr., Epicr. syst. mycol. (Upsaliae): 325 (1838), ≡ *Agaricus tephroleucus* Pers. (1801) : Fr. = *Hygrophorus pustulatus* (Pers.) Fr. (1838), = *Agaricus pustulatus* Pers. (1801) : Fr., [Bataille's name is automatically typified by the type species epithet upon which the taxon name was based, thus type NOT *Hygrophorus agathosmus* (Fr. : Fr.) Fr., as in Singer (1951, 1986) and Candusso (1997), Art. 22.6]. Basionym: *Hygrophorus* [unranked] *Tephroleuci* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 164 (1910)

Section *Pudorini* (Bataille) Konrad & Maubl., Sel. Fung. 6: 427 (1937), type species *Hygrophorus pudorinus* (Fr.) Fr. Anteckn. Sver. Ätl. Svamp.: 46 (1836), ≡ *Agaricus pudorinus* Fr., *Syst. mycol.* (Lundae) 1: 33 (1821), = *Hygrophorus persicolor* Ricek, Z. Pilzk. 40(1–2): 6 (1974). Basionym: *Hygrophorus* [unranked] *Pudorini* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 158 (1910)

Subsection *Clitocyboides* (Hesler & A.H. Sm.) E. Larss., stat. nov., type species: *Hygrophorus sordidus* Peck, Torrey Bot. Club Bull. 25: 321 (1898). Basionym: *Hygrophorus* [section *Hygrophorus* subsection *Hygrophorus*] series *Clitocyboides* Hesler & A.H. Sm., North American Species of *Hygrophorus*: 309 (1963) [= subsect. "*Pallidi*" A.H. Sm. & Hesler, Llyodia 2:32 (1939) invalid, Art. 36.1]

Subsection *Pudorini* (Bataille) Candusso, *Hygrophorus*. Fungi europ. (Alassio) 6: 72 (1997), type species *Hygrophorus pudorinus* (Fr.) Fr., Anteckn. Sver. Ätl. Svamp.: 46 (1836), ≡ *Agaricus pudorinus* Fr., *Syst. mycol.* (Lundae) 1: 33 (1821), = *Hygrophorus persicolor* Ricek, Z. Pilzk. 40(1–2): 6 (1974). Basionym: *Hygrophorus* [unranked] *Pudorini* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 158 (1910) [= Hygrophorus subsect. "*Erubescentes*" A.H. Sm. & Hesler, Llyodia 2: 4 (1939), invalid, Art. 36.1]

Subection *Salmonicolores* E. Larss., subsect. nov., type species *Hygrophorus abieticola* Krieglsteiner ex Gröger et Bresinsky, Krieglsteiner ex Gröger et Bresinsky, Regensb. Mykol. Schr.: 15: 211 (2008)

Table 2 (continued)

Section *Aurei* (Bataille) E. Larss., stat. nov., type species *Hygrophorus aureus* (Arrh.) Fr., Monogr. Hymenomyc. Suec. (Upsaliae) 2: 127 (1863), ≡ *Hygrophorus hypothejus* (Fr. : Fr.) Fr., var. *aureus* (Arrh.) Imler, Bull. trimest. Soc. mycol. Fr. 50: 304 (1935) [1934]. Basionym *Hygrophorus* [unranked] *Aurei,* Bataille, Mém. Soc. ému. Doubs sér 8 4: 161 (1910) [1909]

Subsection *Aurei* (Bataille) Candusso (1997), *Hygrophorus*. Fungi Europaei 6: 222, type species *Hygrophorus aureus* Arrh. in Fr., Monogr. Hymenomyc. Suec. (Upsaliae) 2: 127 (1863), ≡ *Hygrophorus hypothejus* (Fr. : Fr.) Fr., var. *aureus* (Arrh.) Imler, Bull. trimest. Soc. mycol. Fr. 50: 304 (1935) [1934], = *Hygrophorus hypothejus* (Fr. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 324 (1838), ≡ *Agaricus hypothejus* Fr., Observ. Mycol. (Havniae) 2: 10 (1818)]. Basionym *Hygrophorus* [unranked] *Aurei,* Bataille, Mém. Soc. ému. Doubs sér 8 4: 161 (1910) [1909]

Subsection *Discolores* E. Larss., subsect. nov., type species *Hygrophorus karstenii* Sacc. & Cub., Syll. fung. (Abellini) 5: 401 (1887)

Subgenus *Camarophylli* (as *Camarophyllus*) Fr., Summa veg. Scand., Section Post. (Stockholm): 307 (1849), Emended here by E. Larss. to exclude *A. pratensis* and related species now place in *Cuphophyllus*, type species *Agaricus camarophyllus* Alb. & Schwein.: Fr., Consp. Fung. Lusat.: 177 (1805), [Art. 22.6], ≡ *Hygrophorus camarophyllus* (Alb. & Schwein. : Fr.) Dumée, Grandjean & L. Maire, Bull. Soc. mycol. Fr. 28: 292 (1912), [= *Hygrophorus caprinus* (Scop.) Fr. (1838), illeg., superfluous to a sanctioned name]

Section *Camarophylli* (as *Camarophyllus*) (Fr.) E. Larss., stat. nov., type species *Hygrophorus camarophyllus* (Alb. & Schwein.) Dumée, Grandjean & L. Maire. Basionym: *Hygrophorus* subg. *Camarophylli* (as *Camarophyllus*) Fr., Summa veg. Scand., Section Post. (Stockholm): 307 (1849)

Section *Chrysodontes* (Singer) E. Larss., stat. nov., type species *Hygrophorus chrysodon* (Batsch : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 320 (1838) [1836–1838], ≡ *Agaricus chrysodon* Batsch, Elench. Fung., cont. sec. (Halle): 79 (1789) : Fr.. Basionym *Hygrophorus* sect. *Hygrophorus* subsect. *Chrysodontes* Singer (as *Chrysodontini*), Ann. Mycol. 3: 41 (1943)

Section *Rimosi* E. Larss., sect. nov., type species *Hygrophorus inocybiformis* A.H. Sm., Mycologia 36: 246 (1944)

Subfamily *Lichenomphalioideae* Lücking & Redhead subf. nov., type genus *Lichenomphalia* Redhead, Lutzoni, Moncalvo & Vilgalys Mycotaxon 83: 36 (2002)

Tribe *Arrhenieae* Lücking, tribe nov., type genus *Arrhenia* Fr., Summa. veg. Scand., Section Post. (Stockholm): 312 (1849)

Genus *Acantholichen* P.M. Jørg., Bryologist 101: 444 (1998), type species *Acantholichen pannarioides* P.M. Jørg., Bryologist 101: 444 (1998)

Genus *Cora* Fr., Syst. orb. veg. (Lundae) 1: 300 (1825), type species *Cora pavonia* (Sw.) Fr. Syst. orb. veg. (Lundae) 1: 300 (1825), ≡ *Thelephora pavonia* Sw., Fl. Ind. Occid. 3: 1930 (1806)

Genus *Dictyonema* C. Agardh ex Kunth, Syn. pl. (Paris) 1: 1 (1822), type species *Dictyonema excentricum* C. Agardh in Kunth, Syn. pl. (Paris) 1: 1 (1822), = *Dictyonema thelephora* (Spreng.) Zahlbr., Cat. Lich. Univers. 7: 748 (1931) [current name], = *D. sericeum* (Sw.) Berk., London J. Bot. 2: 639 (1843), ≡ *Dictyonema sericeum* f. *thelephora* (Spreng.) Parmasto, Nova Hedwigia 29: 111 (1978) [1977]

Genus *Cyphellostereum* D.A. Reid, Nova Hedwigia, Beih. 18: 336 (1965), type species *Cyphellostereum pusiolum* (Berk. & M.A. Curtis) D.A. Reid, Beih. Nova Hedwigia 18: 342 (1965) ≡ *Stereum pusiolum* Berk. & M.A. Curtis, J. Linn. Soc., Bot. 10 (no. 46): 330 (1869) [1868]

Genus *Arrhenia* Fr., Summa veg. Scand., Section Post. (Stockholm): 312 (1849), type species *Arrhenia auriscalpium* (Fr.) Fr., Summa Veg. Scand., Section Post. (Stockholm): 312 (1849), ≡ *Cantharellus auriscalpium* Fr., Elench. Fung. (Greifswald) 1: 54 (1829), ≡ *Cantharellus auriscalpium* Fr., Elench. fung. (Greifswald) 1: 54 (1828)]

Genus *Corella* Vain., Acta Soc. Fauna Flora fenn. 7(2): 243 (1890), type species *Corella brasiliensis* Vain., Acta Soc. Fauna Flora fenn. 7(2): 243 (1890), ≡ *Dictyonema pavonium* f. *brasiliense* (Vain.) Parmasto, Nova Hedwigia 29 (1–2): 106 (1978)

Genus *Eonema* Redhead, Lücking & Lawrey, Mycol. Res. 113(10): 1169 (2009), type species *Eonema pyriforme* (M.P. Christ.) Redhead, Lücking & Lawrey, ≡ *Athelia pyriformis* (M.P. Christ.) Jülich, Willdenowia, Beih. 7: 110 (1972), ≡ *Xenasma pyrifome* M.P. Christ., Dansk bot. Ark. 19(2): 108 (1960)

Tribe *Lichenomphalieae* Lücking & Redhead, tribe. nov., type genus *Lichenomphalia* Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 36 (2002)

Genus *Lichenomphalia* Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 36 (2002), type species *Lichenomphalia hudsoniana* (H.S. Jenn) Redhead et al., Mycotaxon 83: 38 (2002), ≡ *Hygrophorus hudsonianus* H.S. Jenn, Mem. Carn. Mus., III 12: 2 (1936)

Subgenus *Lichenomphalia* [autonym], type species *Lichenomphalia hudsoniana* (H.S. Jenn) Redhead et al., Mycotaxon 83: 38 (2002), ≡ *Hygrophorus hudsonianus* H.S. Jenn, Mem. Carn. Mus., III 12: 2 (1936)

Subgenus *Protolichenomphalia* Lücking, Redhead & Norvell, subg. nov., type species *Lichenomphalia umbellifera* (L.) Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 38 (2002), ≡ *Agaricus umbelliferus* L., Sp. pl. 2: 1175 (1753), sanctioned by Fr., Elench. fung. 1: 22 (1828)

Genus *Semiomphalina* Redhead, Can. J. Bot. 62 (5): 886 (1984), type species *Semiomphalina leptoglossoides* (Corner) Redhead, ≡ *Pseudocraterellus leptoglossoides* Corner, Monogr. Cantharelloid Fungi: 161 (1966)

Tribe *Cantharelluleae* Lodge, Redhead & Desjardin, tribe. nov., type genus *Cantharellula* Singer, Revue Mycol., Paris 1: 281 (1936)

Genus *Cantharellula* Singer, Revue Mycol., Paris 1: 281 (1936), type species *Cantharellula umbonata* (J.F. Gmel.) Singer, Revue Mycol., Paris 1: 281 (1936), ≡ *Merulius umbonatus* J.F. Gmel., Systema Naturae, Edn. 13, 2: 1430 (1792). Basionym: *Cantharellula* subg. *Pseudoarmillariella* Singer, Mycologia 48(5): 725 (1956)

Genus *Pseudoarmillariella* Singer, Mycologia 48: 725 (1956), type species *Pseudoarmillariella ectypoides* (Peck) Singer [as *P* '*ectyloides*'], Mycologia 48(5): 725 (1956), ≡ *Agaricus ectypoides* Peck, Ann. Rep. N.Y. St. Mus. 24: 61 (1872) [1871]

Cuphophylloid grade

Genus *Cuphophyllus* (Donk) Bon, Doc. Mycol. 14(56): 10 (1985) [1984], type species: *Cuphophyllus pratensis* (Fr.) Bon Doc. Mycol. 14(56): 10 (1985)[1984], ≡ *Hygrocybe pratensis* (Fr.) Murrill, Mycologia 6(1): 2 (1914), ≡ *Agaricus pratensis* Fr., Observ. Mycol. (Havniae) 2: 116 (1818),

Table 2 (continued)

sanctioned by Fr., Syst. mycol. 1: 99 (1821). Basionym: *Hygrocybe* subg. *Cuphophyllus* Donk (1962), Beih. Nova Nedwigia 5: 45 (1962) [*Camarophyllus* P. Kumm., (1871) is an incorrect name for this group]

Section *Fornicati* (Bataille) Vizzini & Lodge, comb. nov., type species: *Hygrophorus fornicatus* Fr., Epicr. syst. mycol. (Upsaliae): 327 (1838), ≡ *Cuphophyllus fornicatus* (Fr.) Lodge, Padamsee & Vizzini, comb. nov. Basionym: *Hygrophorus* Fr. [subg. *Camarophyllus* Fr.] [unranked] *Fornicati* Bataille, Mém. Soc. émul. Doubs. ser. 8 4: 170 (1909) [1910], ≡ *Hygrocybe* [subg. *Neohygrocybe* (Herink) Bon (1989)] sect. *Fornicatae* (Bataille) Bon, Doc. Mycol 14 (75): 56 (1989), ≡ *Dermolomopsis* Vizzini, Micol. Veget. Medit. 26(2): 100 (2012) [2011]

Section *Adonidum* (Singer) Lodge & M.E. Sm., comb. nov., type species *Camarophyllus adonis* Singer, Sydowia 6(1–4): 172 (1952), ≡ *Cuphophyllus adonis* (Singer) Lodge & M.E. Sm., comb. nov. Basionym *Camarophyllus* sect. *Adonidum* (as *Adonidi*) Singer, Sydowia Beih. 7: 2 (1973)

Section *Cuphophyllus* [autonym], type species *Cuphophyllus pratensis* (Fr.) Bon, Doc. Mycol. 14(56): 10 (1985)[1984], ≡ *Hygrocybe pratensis* (Fr.) Murrill, Mycologia 6(1): 2 (1914), ≡ *Agaricus pratensis* Fr., Observ. mycol. (Havniae) 2: 116 (1818), sanctioned by Fr., Syst. mycol. 1: 99 (1821)

Section *Virginei* (Bataille) Kovalenko, in Nezdoiminogo, Opredelitel Gribov SSSR (Leningrad): 37 (1989), type species *Cuphophyllus virgineus* (Wulfen : Fr.) Kovalenko (1989), ≡ *Hygrocybe virginea* P.D. Orton & Watling, Notes R. bot. Gdn Edinb. 29(1): 132 (1969), ≡ *Agaricus virgineus* Wulfen, in Jacquin, Miscell. austriac. 2: 104 (1781), sanctioned by Fr., Syst. mycol. 1: 100 (1821)

Genus *Ampulloclitocybe* Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 36 (2002), type species *Ampulloclitocybe clavipes* (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 36 (2002), ≡ *Clitocybe clavipes* (Pers.) P. Kumm., *Führ. Pilzk.* (Zwickau): 124 (1871), ≡ *Agaricus clavipes* Pers., *Syn. meth. fung.* (Göttingen) 2: 353 (1801), [≡ *Clavicybe clavipes* (Pers.) Harmaja, *Karstenia* 42(2): 42 (2002), nom. illeg., Art. 52.1]

Genus *Cantharocybe* H.E. Bigelow & A.H. Sm., Mycologia 65(2): 486 (1973), emend. Ovrebo, Lodge & Aime, Mycologia 103(5): 1103 (2011), type species *Cantharocybe gruberi* (A.H. Sm.) H.E. Bigelow, Mycologia 65: 486 (1973), ≡ *Clitocybe gruberi* A.H. Sm., Mycologia 36(3): 245 (1944)

ethanol (v/v) was added and tubes were centrifuged at 16 110 rcf for 5 min at room temperature. Supernatants were removed, pellets air dried at room temperature for 10 min and pellets resuspended in 50 μL sterile water.

DNA in aqueous solution was then cleaned at CFMR using GeneClean III kits (Qbiogene) following the manufacturer's protocol with the following modifications. Fifty μL of aqueous DNA solution was combined with 150 μL of NaI solution and 5 μL of glassmilk provided with kit. Tubes were agitated followed by centrifugation at 16 110 rcf for 8 s. The supernatant was discarded and the pellet washed three times using 1 mL of New Wash solution provided with the kit. After removal of New Wash, pellets were air-dried for 15 min and template DNA eluted in 50 μL of water. DNA was extracted at the University of Tennessee in Knoxville (UTK) using the chloroform method as described in Mata et al. (2007), so further cleaning was not needed.

PCR amplification of the ribosomal ITS1-5.8S-ITS2 region was carried out with primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990). PCR of the ribosomal large subunit 3′ end was carried out with primers LR7 (Moncalvo et al. 2000) and LROR or rarely LR3R (CFMR) or ITS3 (UTK & CFMR) (White et al. 1990). Amplification of the nuclear ribosomal small subunit (SSU) at CFMR was carried out using primer sets NS1 and NS2, NS3 and NS4, NS5 and NS8 or ITS2. Primers used for PCR of the most variable region of the nuclear ribosomal rpb2 gene between domains 6 and 7 were rpb2-b6F and rpb2-b7.1R (Matheny 2005). PCR was performed using 1×Green GoTaq reaction buffer or GoTaq DNA polymerase (Promega, Madison, Wisconsin) and 0.025 units of GoTaq DNA polymerase were added per μL of reaction volume. Each primer had a final concentration of 0.2 μM and each dNTP (Promega, Madison, Wisconsin) had a final concentration of 200 μM. Template DNA was typically diluted 1:50 in the final reaction volume. Thermocycler conditions for ITS and LSU primers were as follows: initial denaturing at 94 C for 3 min; 30 cycles of denaturing at 94 C for 1 min, annealing at 53 or 50 C for 40 s, and extension at 72 C for 1.5 min; and a final extension step of 72 C for 10 min. For SSU, annealing was changed to 53 C for 2 min with a 2 min extension time. Samples with poor amplification were rerun using a touchdown program with annealing temperatures ranging from 63 C down to 45 C. Thermocycler conditions for RPB2 primers followed the less stringent, stepped protocol of Matheny (2005).

Following amplification 3 μL of product was run on a 1.5 % or 1.8 % agarose gel stained with ethidium bromide to verify the presence of amplification products. In preparation for sequencing, amplification products were treated with Exonuclease I (EXO) and Shrimp Alkaline Phosphatase (SAP) (USB Corporation, Cleveland, Ohio) as follows: for 15 μL PCR reactions, a solution containing 3.12 μL water, 0.80 μL SAP and 0.08 μL EXO was added to each reaction; the reactions with EXO/SAP were heated to 37 C for 15 min and then heated to 80 C for 20 min.; after cooling, 35 μL of water was added to each reaction.

Sequencing reactions were performed following the BigDye terminator protocol (ABI Prism) with the following sequencing primers: ITS1F, ITS2, ITS3, ITS4, and ITS5 (White et al. 1990; ITS primers); LR5, LR3R, and LROR (Moncalvo et al. 2000; LSU primers); the same NS primer sets that were used for PCR of the SSU (SSU primers); rpb2-b6F and rpb2-b7.1R, rpb2 primers. Sequencing products were cleaned using CleanSeq (Agencourt) magnetic beads following the manufacturer's protocol. Sequencing products were analyzed at the University of Wisconsin Biotech Center and final sequences were aligned using Sequencher 4.2 (GeneCodes Corporation).

Cloning Cloning of ITS PCR products at CFMR and UTK was accomplished using pGEM-T Vector System II kits and JM109 competent cells from Promega (Madison, Wisconsin) following manufacturer's instructions when direct sequencing did not resolve a sequence. To amplify cloned regions from bacterial colonies at CFMR, a PCR reaction was prepared as previously described with the exception that template DNA was added by placing a small amount of a transformed bacterial colony into the reaction using a sterile 200 μL pipette tip. To amplify cloned regions at UTK, the bacterial colony was transferred to water, boiled, followed by PCR; PCR was repeated on dilutions of boiled DNA if no product was obtained. Thermocycler conditions were as follows: initial denaturing at 94 C for 10 min; 30 cycles of denaturing at 94 C for 40 s, annealing at 53 C for 40 s, and extension at 72 C for 90 s; and a final extension step of 72 C for 10 min. Following PCR the reactions were checked for product, treated with EXO/SAP and sequenced as previously described. Five clones per collection were sequenced.

Consensus sequences Consensus sequences were produced using multiple sequences in Sequencher 4.8. Self-chimeric LSU sequences (containing out-of-sequence partial forward and back reads) were used to correct bp in the full sequences by segmenting them at splices and aligning them to reference sequences together with full sequences.

Phylogenetic analyses Three sets of alignments were constructed from the resulting sequences. The first set consisted of the nuclear ribosomal large subunit (LSU, 25S, D1, D2 and D3), and PhyML analysis rooted with *Typhula phacorrhiza*. The second set comprised four partially overlapping data sets from the Hygrophoraceae constructed from the nuclear ribosomal internal transcribed spacer (ITS) region (ITS 1–2 and 5.8S) together with the LSU and an outgroup based on phylogenies in Binder et al. (2010), Matheny et al. (2006) and the LSU analysis above; each data set was aligned separately to minimize loss of data from the ITS, and ML analysis was used. Outgroups were *Hygroaster albellus* for Group 1 (*Hygrocybe* s.s.); *Hygrophorus eburneus* for Group 2 (*Neohygrocybe, Porpolomopsis, Gliophorus, Gloioxanthomyces, Haasiella, Humidicutis, Chromosera* and *Chrysomphalina*); *Neohygrocybe ingrata* for Group 3 (*Hygrophorus* ss, *Neohygrocybe, Chromosera, Chrysomphalina, Arrhenia, Dictyonema, Lichenomphalia* and *Pseudoarmillariella*); *Macrotyphula fistulosa* for Group 4 (*Ampullocliticybe, Cantharocybe* and *Cuphophyllus*). Sequences were initially aligned using the default settings in MAFFT version 6 (Katoh and Toh 2008) and then manually aligned using SeAl version 2.0a11 (Rambaut 2002). Ambiguously aligned positions and sequence ends were pruned from the datasets before running maximum likelihood (ML) analyses in GARLI v0.951 (Zwickl 2006) using a general time reversible model of nucleotide substitution with a gamma distributed rate heterogeneity and a proportion of invariant sites (GTR+G γ+I). ML searches were repeated three times for each dataset. GARLI was used to generate 100 ML nonparametric bootstrap replicates (MLBP) with the generation threshold halved to 5,000 as suggested by the program; the replicates were used to calculate a majority rule consensus tree in PAUP* 4.0b10 (Swofford 2002) to assess clade support.

The third set, henceforth referred to as the 4-gene backbone analysis, consisted of four loci including the nuclear ribosomal gene regions (5.8S, 18S, and 25S) and the RNA polymerase II (rpb2) region between conserved domains 5 and 7. Positions deemed ambiguous in alignment were pruned from the nexus file before conversion to Phylip format using SeaView 4.2.4 (Gouy et al. 2010). Nexus and Phylip files of the four-gene region data set can be obtained from http://www.bio.utk.edu/matheny/Site/Alignments_%26_Data_Sets.html. In the final concatenated alignment, rRNA gene regions occupied positions 1–2854; the *rpb2* region comprised positions 2855–3995. The four-gene region data set was analyzed using maximum likelihood (ML) in RAxML 7.0.3 (Stamatakis 2006a) with rapid bootstrapping (Stamatakis et al. 2008) and by Bayesian inference using the parallel version of MrBayes 3.1.2 (Altekar et al. 2004; Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003) on the Newton cluster at the University of Tennessee. For both ML and Bayesian analyses, the rRNA gene regions were treated as a single partition following Aime et al. (2006; see Appendix I). First, second, and third codon partitions of *rpb2* were partitioned separately. Thus, four partitions were assigned and modeled separately. One thousand rapid bootstraps and a thorough ML search were conducted in RAxML using four distinct models/partitions with joint branch length optimization. All free model parameters were estimated by RAxML and incorporated a GAMMA+P-Invar model of rate heterogeneity, a GTR substitution rate matrix, and empirical base frequencies for the final ML search. Rapid bootstrapping was done using a GTRCAT model (Stamatakis 2006b). Bayesian inference was performed using a mixed models analysis run in parallel for up to 50 million generations. Four chains were run with trees sampled every 5,000 steps with the heating temperature set to 0.1. Convergence diagnostic features were used to guide burn-in choice. All analyses were rooted with *Plicaturopsis crispa* (Amylocorticiales; Binder et al. 2010).

The fourth data set used a Supermatrix with 1,000 bootstrap replicates (SMBS) to analyze a more comprehensive data set comprising multiple representatives of taxa from various geographic regions, and utilizing all the available ITS, LSU, SSU and RPB2 sequences except those with only ITS sequences. All sequences were from single collections. The four gene partitions used were: rRNA 1–3164, rpb2 1st

codon pos 3165–3915/3, rpb2 2nd codon pos 3166–3915/3, rpb2 3rd codon pos 3167–3915/3. In the rRNA partition, SSU comprised pos 1–1754, 5.8S 1755–1956, LSU 1957–3164. A GTRGAMMA model was assigned to each partition. This analysis was restricted to the hygrophoroid clade as delineated by the 4-gene ML analysis above. Trees were rooted with *Cantharocybe* based on the 4-gene backbone analysis above. The data set was divided into four parts and examined to ensure a minimum representation of each gene region in each part of the tree to prevent skewing: 59–95 % for ITS, 91–98 % for LSU, 32–83 % SSU, and 29–54 % RPB2 except for the *Hygrophorus-Chromosera* group with 15 % rpb2.

Specimens examined and drawings All of the cited types, specimens sequenced, and the specimens illustrated by drawings were examined by DJ Lodge with the exceptions noted below. *Aeruginospora singularis* had a type study by E Horak (FH). Types and collections of *Hygrophorus* spp. s.s. were examined by E Larsson, except A Kovalenko examined those from Russia and DJ Lodge examined those from Belize, the Dominican Republic and Japan. Types and collections sequenced in subf. *Lichenomphalioideae* were examined by R Lücking, SA Redhead and LL Norvell, except for *Lichenomphalia hudsoniana* and *L. umbellifera* which were collected and examined by J Geml, and *Cantharellula umbonata* and *C. humicola* which were examined by DE Desjardin and DJ Lodge. T Læssøe collected and examined *Chromosera* and *Haasiella* from Russia and Danish collections of *Chrysomphalina* and *Pseudoomphalina*. G Griffith examined collections from Wales. Collections at Kew were matched to reference ITS sequences, and M Ainsworth (B Dentinger et al., unpublished) re-determined them with microscopy. D Boertmann examined some collections from Hungary, but they are not deposited in recognized fungaria. Drawings of hand cut sections were made by DJ Lodge with the aid of an Olympus microscope and drawing tube.

Locations where collections that were sequenced are deposited are given in Online Resource 1. Collection numbers for drawings are given in the figure captions; these collections are deposited at CFMR, except for *Aeruginospora singularis* (BO); *Cantharellula umbonata* and *C. humicola* (SFSU); *Hygrocybe appalachianensis* (DMWV); *Humidicutis pura* (K); *Ampulloclitocybe clavipes*, *Cuphophyllus acutoides* var. *pallidus*, *C.* aff. *pratensis*, *Gloioxanthomyces vitellinus, Humidicutis auratocephalus* and *Pseudoarmillariella ectypoides* (TENN).

Results and discussion

Ecology The Hygrophoraceae is known to comprise genera with different nutritional strategies, including known biotrophic associations with ectomycorrhizal plants, algae, cyanobacteria and mosses (Lawrey et al. 2009; Seitzman et al. 2011; Tedersoo et al. 2010). The remaining genera in Hygrophoraceae were putatively regarded as saprotrophic, but recent data derived from stable isotope ratios are at variance with that assumption (Griffith et al. 2002; Griffith 2004; Seitzman et al. 2011). Knowledge about nutritional strategies is important for conservation of species of Hygrophoraceae, and many species are reported as threatened in Europe and Australia (Boertmann 2010; Gärdenfors 2010; Griffith 2004; Griffith et al. 2002, 2004; Kearney and Kearney 2000; Young 2005). Furthermore, nutritional strategies are moderately conserved within lineages in Hygrophoraceae (Seitzman et al. 2011), and are more likely to be adaptive than many morphological features used in agaric systematics. Ecology may therefore provide informative synapomorphic characters if new nutritional strategies were the foundation of adaptive radiations. Hence, we summarize results of studies on the ecology of genera in Hygrophoraceae below, with emphasis on nutritional strategies.

Hygrophorus s.s. represents an independent evolutionary acquisition of the ectomycorrhizal lifestyle in basidiomycete fungi (Tedersoo et al. 2010), though recent micromorphological evidence indicates the relationship in *H. olivaceoalbus* may be parasitic rather than mutualistic (Agerer 2012). Individual species of *Hygrophorus* s.s. are considered host specialists but this has only been definitively shown for a handful of species (Jacobsson and Larsson 2007; Larsson and Jacobsson 2004; Molina et al. 1992). Thus they represent an adaptive radiation within Hygrophoraceae. Species of *Hygrophorus* s.s. fruit primarily in undisturbed forest habitats dominated by ectomycorrhizal (ECM) plants (Visser 1995; Singer 1949). While the genus has long been considered symbiotic with roots (e.g. Frank 1888; Noack 1889), Kropp and Trappe (1982) provided definitive proof when they synthesized ECM of *Hygrophorus purpurascens* in pure culture with *Tsuga heterophylla*. More recently, molecular methods have confirmed the presence of *Hygrophorus* species on the roots of both angiosperms and gymnosperms from a variety of habitats in the Northern Hemisphere (see Online Resource 2). According to Hobbie and Agerer (2010), species of *Hygrophorus* s.s. form "contact", "short", or "medium-smooth" exploration-type ECM that are hydrophilic and lack rhizomorphs. The restricted soil volume exploited by *Hygrophorus* ectomycorrhizae may explain why some species are considered "nitrophilic" and respond positively to high nitrogen inputs (Lilleskov et al. 2001, 2002; Vineis et al. 2010) and why some respond negatively to liming (Kjøller and Clemmensen 2009; Pena et al. 2010). In addition to limitations of potential benefits to the host from *Hygrophorus* mycorrhizae due to limited soil exploration by the fungus, Agerer (2012) showed that the intracellular development of *H. olivaceoalbus* in *Picea* roots was characteristic

of a parasitic infection. Proliferation of *H. olivaceoalbus* in defensive tannin droplets within host cells was also consistent with the high activity of phenoloxidase (Agerer et al. 2000) and laccase (Agerer 2012) in that species. Further evidence for parasitic rather than mutualistic association comes from the low isotopic ∂^{15}N of *H. olivaceoalbus* basidiomes (−3.6—0.1 % in Taylor et al. 2003; 2.7±3.5 % in Trudell et al. 2004), which is generally below the range of ∂^{15}N found in typical ectomycorrhizal fungal basidiomes (3—18 % ∂^{15}N, Taylor et al. 2003; Trudell et al. 2004; Agerer et al. 2012; Seitzman et al. 2011). While such low ∂^{15}N signatures might indicate saprobic growth in litter low in ^{15}N (Hobbie et al. 1999; Zeller et al. 2007), Agerer (2012) argued that partial digestion of host-derived nitrogen during intracellular growth was a more likely source given the limited extraradical growth of *H. olivaceoalbus*.

Hygrophorus s.s. species are mostly restricted to the temperate regions of the world and the highest species diversity is in the Northern Hemisphere (Arora 1986; Tedersoo et al. 2010; Singer 1949). A few species of *Hygrophorus* s.s. are present in Australia and in the montane *Quercus* forests of Central America and Columbia (Halling and Mueller 2005; Young and Wood 1997), but they are largely absent from ECM forests in lowland tropical habitats. An exception is represented by an uncultured clone from *Pisonia grandis* (Nyctaginaceae) roots in the Seychelles (FN296256, Online Resources 2). That most species occur at high latitude or altitude is consistent with the habit of *Hygrophorus* s.s. to fruit preferentially during the coldest parts of the mushroom season (Cooke 1891). In Europe, *Hygrophorus* forms ectomycorrhiza with trees in the Fagaceae, Corylaceae, Betulaceae, Cistaceae, Tiliaceae and Pinaceae. Many species show strong host specificity and also associations with certain environmental conditions such as nutrient rich soil on calcareous ground (e.g. *H. chrysodon* and *H. poetarum*), nutrient poor *Pinus* forests (*H. calophyllus*) or *Picea* forest on calcareous ground (*H. discoideus*) (Larsson, unpublished data). Eighteen of the ca. 40 *Hygrophorus* species in the Nordic countries (Kovalenko 2012; Larsson et al. 2011) are rare and declining and are listed as threatened in the Red List of Swedish species (Gärdenfors 2010, www.artdata.slu.se/rodlista). The reason for this decline is unclear but may be caused by acidification or eutrophication of forest soils resulting from nitrogen inputs in air pollution.

Members of the genus *Hygrocybe* s.l. (*Hygrocybe, Neohygrocybe, Gliophorus, Porpolomopsis*) and *Cuphophyllus* fall into distinct clades but occur together and are therefore often treated as a group for conservation purposes (e.g., Boertmann 2010). The ecology of this group is enigmatic as they are generally found in contrasting habitats in Europe versus the Americas and elsewhere. In northern Europe, Greenland and Newfoundland, these species are associated with nutrient-poor grasslands where they are often the dominant macrofungal component (based on basidiocarp abundance), whereas in most other parts of the world the same or sister species are usually less abundant and found in forests from the tropics to the boreal zone. Additionally a few species are associated with tundra habitats or are found in bryophyte dominated bogs.

Historically, species in genera of the Hygrophoraceae that are not known to be ectomycorrhizal or moss or lichen symbionts s.l. have been considered as saprotrophs (Keizer 1993) based on the absence of consistent associations with known ectomycorrhizal host plants and the failure to find obvious mycorrhizal structures. However, other features of their biology such as absence or very limited basidiospore germination under a range of conditions (Griffith, unpub. data) and stable carbon and nitrogen isotope ratios unlike those of known saprotrophs (Griffith et al. 2002, 2004; Trudell et al. 2004; Seitzman et al. 2011) suggest more complex nutrient requirements. There are only two confirmed examples of successful axenic culture of species in this group (confirmed by ITS sequencing), namely *G. laetus* (L Deacon, 2003, pers. comm. to Griffith in Roderick 2009) and *C. virgineus* (Roderick 2009), though cultures of the latter are listed in the CBS culture collection, and Griffith retains a subculture.

Other aspects of the biology of *Hygrocybe* spp. also exhibit patterns similar to those found in ectomycorrhizal basidiomycetes, for instance their sensitivity to inorganic forms of nitrogen, and hence their occurrence in nitrogen poor habitats (Seitzman et al. 2011). Their current rarity in most European grasslands is attributed to the widespread application of inorganic fertilizers (Griffith et al. 2002, 2004). Furthermore, examination of the carbon and nitrogen isotopic patterns of these fungi suggests that they are not saprotrophic as all species examined so far exhibited highly elevated ∂15 N and low ∂13C signatures in both European grasslands (Griffith 2002 and unpublished data) and North American woodland habitats (Seitzman et al. 2011). The depletion in ^{13}C has not been fully explained, but Seitzman et al. (2011) postulated that some genera of Hygrophoraceae with unknown nutritional strategies may derive part of their carbon from mosses, algae or cyanobacteria as mutualists, parasites, necrotrophs or perhaps as saprotrophs. Seitzman et al. (2011) found a similar degree of ^{13}C in a collection of *Galerina* sp. resembling *G. paludosum* – a species previously shown to be biotrophic on sphagnum moss (Redhead 1981). Furthermore, species of *Hygrocybe* s.l. and *Cuphophyllus* often occur with mosses in both European grasslands and North American woodlands (Boertmann 2010; Seitzman et al. 2011). Persoh (2013) recovered sequences of *Hygrocybe coccinea* from leaves, suggesting it may be an endophyte.

The abundance of *Hygrocybe* and *Cuphophyllus* spp. in European grasslands in contrast to their woodland distribution elsewhere may be a legacy of the post-glacial history of these habitats. Bakker et al. (2004) dispute the dogma that deforestation and the prehistoric balance between woodlands and grasslands was the result of human influence. They make a

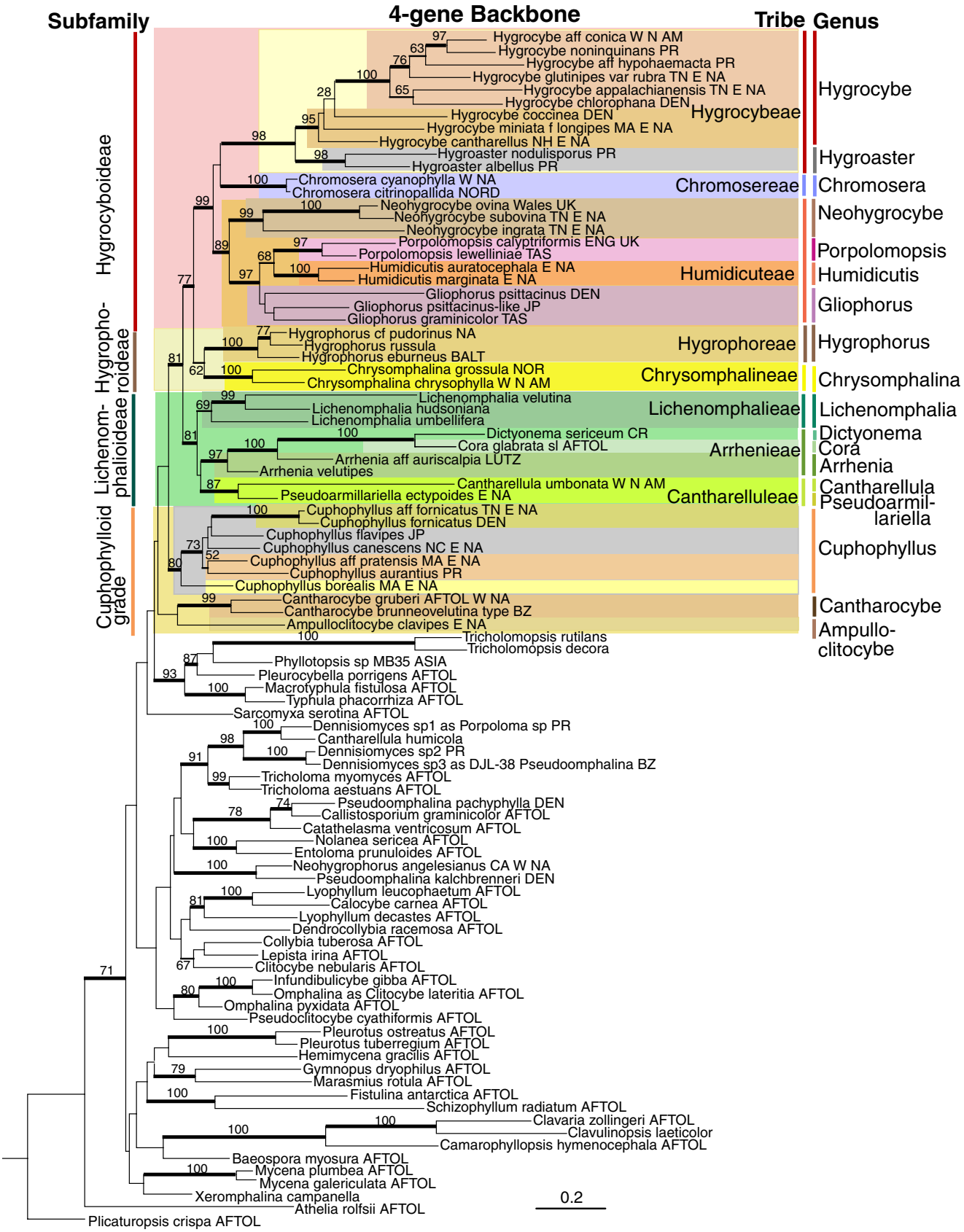
convincing case that fluctuations in numbers of large mammalian herbivores (not necessarily the result of human livestock management) have led to a vegetation cycle as follows: grassland – thorny scrub – woodland establishment – closed canopy woodland – parkland – grassland. If one considers European grasslands as (temporarily) treeless woodlands, then it may be the ability of these *Hygrocybe* and *Cuphophyllus* spp. to survive these cyclical changes in vegetation (in contrast to other macrofungi requiring the presence of live woody hosts or dead woody resources), which explains their present abundance in these habitats. Alternatively, it could be argued that *Hygrocybe* s.l. and *Cuphophyllus* spp. are more tolerant of the harsher climatic conditions of grassland habitats (large diurnal/seasonal fluctuations in temperature and humidity) from which even soil organisms are only partially insulated. This latter factor may explain why these species are often late-fruiting in European grasslands, a feature also found in *Hygrophorus* spp. Young (2005) suggested that shady forests and dense thickets in Australia may provide a humid microclimate close to the ground.

Despite stable isotope ratios that suggest that most Hygrophoraceae are biotrophic, a search of GenBank using BLAST searches of ITS sequences from two species per clade found mainly *Hygrophorus* s.s. sequences from root tips (Online Resource 2). A sequence of an unknown species was obtained from an unidentified bryophyte (GenBank AM999704, Kauserud et al. 2008) and similar ITS sequences were obtained from live *Deschampsia* grass roots (Poaceae) in the boreal zone (GenBank FJ517589— FJ517592, Tejesvi et al. 2010, Online Resource 2). These root and moss associated sequences cluster near *Chromosera* in our ITS analysis (Online Resource 3), but support is low for placement in tribe *Chromosereae* (20 % MLBS in our analysis, Online Resource 3; 33 % MLBS in the analysis by Ercole, pers. com., 16 Nov. 2012). The ecology of the moss-grass root clade is more consistent with tribe *Lichenomphaleae*, and it might eventually be placed there once more gene regions have been sequenced and analyzed. BLAST Searches of GenBank (November 2012) using ITS sequences of two species per clade revealed many *Cuphophyllus* and *Hygrocybe* sequences from soil or litter but not roots, which suggests they are neither mycorrhizal nor endophytic, though Persoh (2013) and Tello et al. (2013) has since presented evidence of *Hygrocybe* and *Cuphophyllus* as endophytes. A study of fungi in the rhizosphere of *Picea glauca* in Canada by Lamarche, Seguin and Hamelin (unpublished, study described in Lamarche and Hamelin 2007, fungal sequences deposited in Genbank 2008), showed 5 clones of *Hygrocybe* cf. *splendidissima* (EU690689 and others), 26 clones of *H.* aff. *punicea* (GenBank EU690689 and others), 33 clones of *H. chlorophana* (EU690793 and others), >23 clones in the *H. ceracea-H. insipida* clade (EU690866 and others), and 39 clones of *H. reidii* (EU690490 and others). Little is known regarding transfer of plant compounds to rhizosphere fungi, though the fungal-specific Mrt gene in *Metarrhizium robertsii* was shown to function in transport of sucrose and raffinose-related oligosaccharides from root exudates (Fang and St. Leger 2010).

Species of *Chrysomphalina* were assumed to be saprotrophic because they grow on wood and are associated with white rot (Norvell et al. 1994). Lignicolous fungi, however, have various nutritional strategies (Huhndorf et al. 2004). Stable isotope analyses would be useful in determining whether the ratios in *Chrysomphalina* match those of wood decomposers or biotrophic fungi. The clade comprising *Cantharellula umbonata* and *Pseudoarmillariella ectypoides* is sister to the *Lichenomphalia-Dictyonema* clade (but without BS support) in our 4-gene backbone and Supermatrix analyses (Figs. 1 and 2). While the trophic nature of *P. ectypoides* is unknown, *C. umbonata* is associated with mosses (Lawrey et al. 2009).

At least two lichenized lineages appear within Hygrophoraceae, if *Lichenomphalia* including *L. umbellifera* is considered monophyletic (Lawrey et al. 2009). *Lichenomphalia* forms omphalinoid fruiting bodies associated with green, eukaryotic photobionts, whereas the *Dictyonema* s.l. clade (including *Cyphellostereum*, *Acantholichen*, *Corella* and *Cora*) features cyphelloid or corticioid basidiocarps and invariably associates with a novel cyanobacterial lineage, *Rhizonema* (Lawrey et al. 2009; Lücking et al. 2009). Both lineages are primarily tropical montane to temperate and often co-occur over soil and between bryophytes on the ground. Seitzman et al. (2011) suggested that biotrophic relationships appear throughout Hygrophoraceae and that nutritional strategies were moderately conserved within lineages. The well documented ectomycorrhizal genus *Hygrophorus* and the lichen and moss symbionts in the genera *Lichenomphalia, Dictyonema, Cora, Corella, Cyphellostereum, Eonema* and *Acantholichen* (Lawrey et al. 2009) fall between *Cuphophyllus* at the base of the Hygrophoraceae and *Hygrocybe*, *Gliophorus* and *Neohygrocybe* in more distal branches of our 4-gene phylogenetic tree (Fig. 1). Categorization of genera by combined nitrogen and carbon isotope ratios in Seitzman et al. (2011) was partly concordant with the molecular phylogeny, pairing *Hygrocybe* with *Gliophorus*, while leaving *Cuphophyllus*, *Hygrophorus* and *Humidicutis* in separate groups. Seitzman et al. (2011, Fig. 4) found that some *Cuphophyllus* and *Humidicutis* species were unlike ectomycorrhizal and

Fig. 1 Four-gene backbone analysis of Hygrophoraceae, representatives of the Hygrophoroid clade (*Phyllotopsis*, *Pleurocybella*, *Macrotyphula*, *Tricholomopsis*, *Typhula* and *Sarcomyxa*), and representatives of outgroups from the Entolomataceae, Marasmiaceae, Mycenaceae, Pleurotaceae and Tricholomataceae ss, rooted with *Plicaturopsis crispa*. Genes analyzed were ITS (ITS1, 5.8S & ITS2), LSU (LROR-LR5), SSU and RPB2 (between domains 6 and 7). ML bootstrap values ≥50 % appear above the branches. Heavily bolded branches have ≥70 % and lightly bolded branches have 50–69 % ML bootstrap support


Subfamily
4-gene Backbone
Tribe
Genus
Hygrocyboideae
Hygrophoroideae
Lichenomphalioideae
Cuphophylloid grade
Hygrocybeae
Chromosereae
Humidicuteae
Hygrophoreae
Chrysomphalineae
Lichenomphalieae
Arrhenieae
Cantharelluleae
Hygrocybe aff conica W N AM
Hygrocybe noninquinans PR
Hygrocybe aff hypohaemacta PR
Hygrocybe glutinipes var rubra TN E NA
Hygrocybe appalachianensis TN E NA
Hygrocybe chlorophana DEN
Hygrocybe coccinea DEN
Hygrocybe miniata f longipes MA E NA
Hygrocybe cantharellus NH E NA
Hygroaster nodulisporus PR
Hygroaster albellus PR
Chromosera cyanophylla W NA
Chromosera citrinopallida NORD
Neohygrocybe ovina Wales UK
Neohygrocybe subovina TN E NA
Neohygrocybe ingrata TN E NA
Porpolomopsis calyptriformis ENG UK
Porpolomopsis lewelliniae TAS
Humidicutis auratocephala E NA
Humidicutis marginata E NA
Gliophorus psittacinus DEN
Gliophorus psittacinus-like JP
Gliophorus graminicolor TAS
Hygrophorus cf pudorinus NA
Hygrophorus russula
Hygrophorus eburneus BALT
Chrysomphalina grossula NOR
Chrysomphalina chrysophylla W N AM
Lichenomphalia velutina
Lichenomphalia hudsoniana
Lichenomphalia umbellifera
Dictyonema sericeum CR
Cora glabrata sl AFTOL
Arrhenia aff auriscalpia LUTZ
Arrhenia velutipes
Cantharellula umbonata W N AM
Pseudoarmillariella ectypoides E NA
Cuphophyllus aff fornicatus TN E NA
Cuphophyllus fornicatus DEN
Cuphophyllus flavipes JP
Cuphophyllus canescens NC E NA
Cuphophyllus aff pratensis MA E NA
Cuphophyllus aurantius PR
Cuphophyllus borealis MA E NA
Cantharocybe gruberi AFTOL W NA
Cantharocybe brunneovelutina type BZ
Ampulloclitocybe clavipes E NA
Tricholomopsis rutilans
Tricholomopsis decora
Phyllotopsis sp MB35 ASIA
Pleurocybella porrigens AFTOL
Macrotyphula fistulosa AFTOL
Typhula phacorrhiza AFTOL
Sarcomyxa serotina AFTOL
Dennisiomyces sp1 as Porpoloma sp PR
Cantharellula humicola
Dennisiomyces sp2 PR
Dennisiomyces sp3 as DJL-38 Pseudoomphalina BZ
Tricholoma myomyces AFTOL
Tricholoma aestuans AFTOL
Pseudoomphalina pachyphylla DEN
Callistosporium graminicolor AFTOL
Catathelasma ventricosum AFTOL
Nolanea sericea AFTOL
Entoloma prunuloides AFTOL
Neohygrophorus angelesianus CA W NA
Pseudoomphalina kalchbrenneri DEN
Lyophyllum leucophaetum AFTOL
Calocybe carnea AFTOL
Lyophyllum decastes AFTOL
Dendrocollybia racemosa AFTOL
Collybia tuberosa AFTOL
Lepista irina AFTOL
Clitocybe nebularis AFTOL
Infundibulicybe gibba AFTOL
Omphalina as Clitocybe lateritia AFTOL
Omphalina pyxidata AFTOL
Pseudoclitocybe cyathiformis AFTOL
Pleurotus ostreatus AFTOL
Pleurotus tuberregium AFTOL
Hemimycena gracilis AFTOL
Gymnopus dryophilus AFTOL
Marasmius rotula AFTOL
Fistulina antarctica AFTOL
Schizophyllum radiatum AFTOL
Clavaria zollingeri AFTOL
Clavulinopsis laeticolor
Camarophyllopsis hymenocephala AFTOL
Baeospora myosura AFTOL
Mycena plumbea AFTOL
Mycena galericulata AFTOL
Xeromphalina campanella
Athelia rolfsii AFTOL
Plicaturopsis crispa AFTOL
0.2
Hygrocybe
Hygroaster
Chromosera
Neohygrocybe
Porpolomopsis
Humidicutis
Gliophorus
Hygrophorus
Chrysomphalina
Lichenomphalia
Dictyonema
Cora
Arrhenia
Cantharellula
Pseudoarmil-lariella
Cuphophyllus
Cantharocybe
Ampullo-clitocybe

saprotrophic species while others were unclassified based on their ∂^{15}N signatures, and all *Cuphophyllus* and *Humidicutis* species were unlike ectomycorrhizal and saprotrophic species based on their ∂^{13} C signatures. *Gliophorus laetus*, *Lichenomphalia, Dictyonema* and all *Hygrocybe* species resembled ectomycorrhizal, but not saprotrophic species based on their ∂^{15}N, but neither ectomycorrhizal nor saprotrophic species based on their ∂^{13} C (Fig. 4 vs 3 in Seitzman et al. 2011). Although ectomycorrhizal associations have evolved independently many times in the Basidiomycota (Hibbett et al. 2000) including at least 11 independent origins in the Agaricales (Matheny et al. 2006), they arose only once in the Hygrophoraceae in the monophyletic genus *Hygrophorus* (Moncalvo et al. 2002; Seitzman et al. 2011, our data). These data support the finding of moderate conservation of nutritional strategies in Hygrophoraceae by Seitzman et al. (2011) though the nutritional mode of many genera remains enigmatic.

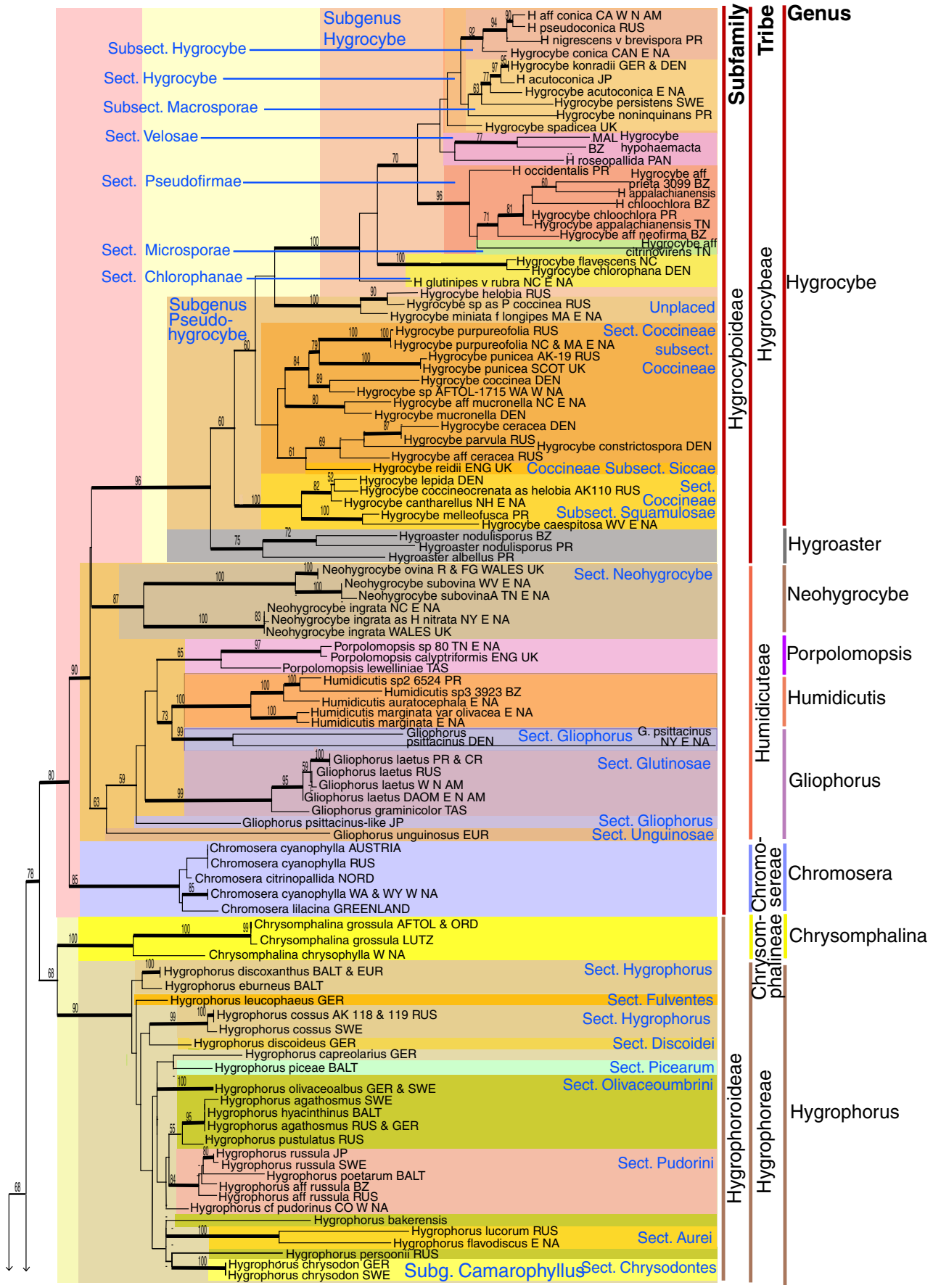
Pigments and other taxonomically informative metabolites The basidiocarp pigments of members of the *Hygrophoraceae* are among the most diverse and striking in fungi. While the adaptive significance of many of these pigments is uncertain, their utility in chemotaxonomy has long been recognized. For example, Singer (1958) noted the contrasting effects of 10 % KOH on the yellow-orange pigments of *Hygrocybe flavescens* and *Humidicutis marginata*, Cibula (1976) and Bresinsky and Kronawitter (1986) found pigment chemistry distinguished major groups in Hygrophoraceae, while Bresinsky (2008) described the genus *Porpolomopsis* based on pigment chemistry. Furthermore, Redhead et al. (2002) used metabolites with other characters in describing *Ampulloclitocybe,* and Norvell et al. (1994) suggested a close relationship between *Haasiella* and *Chrysomphalina* based on shared carotenoid pigments (Arpin and Fiasson 1971) and pachypodial hymenium construction – a relationship supported by our analyses (Online Resource 3). Though carotenoids are widespread in fungi, notably the Cantharellales (Mui et al. 1998), they are infrequent in Hygrophoraceae where instead the yellow-red pigments are mostly tyrosine-derived betalains (Online Resource 4).

Betalain pigments are found elsewhere only among higher plants in the Caryophyllales (except those containing anthocyanins) and a few *Amanita* spp. (*A. muscaria, A. caesaria* and *A. phalloides*, Grotewold 2006). In plants, tyrosinase-mediated hydroxylation of tyrosine to form DOPA by the action of tyrosinase, extradiol ring cleavage catalyzed by a DOPA-dioxygenase leads to the formation of 4,5-seco-DOPA (Online Resource 5). Spontaneous recyclization leads to the formation of betalamic acid (6-membered heterocyclic ring) (Online Resource 5). Conjugation of betalamic acid with either cycloDOPA (formed via the oxidation of DOPA by tyrosinase) to form betanidin or with various amino acids/amines leads to the formation respectively of diverse violet (betacyanin) or yellow (betaxanthine) pigments.

Fig. 2 Supermatrix Maximum Likelihood analysis of Hygrophoraceae ▶ ss. All taxa with LSU sequences were included; ITS (ITS1, 5.8S & ITS2), LSU (LROR-LR5), SSU and RPB2 (between domains 6 and 7) were also included, if available. ML bootstrap values ≥50 % appear above the branches. Heavily bolded branches have ≥70 % and lightly bolded branches have 50–69 % ML bootstrap support

The major yellow water soluble pigment in basidiocarps of many *Hygrocybe* spp. is muscaflavin (Steglich and Strack 1990), an unusual betalain pigment first identified as a minor pigment in *A. muscaria* (Steglich and Preuss 1975; Von Ardenne et al. 1974). Cibula (1976) partially characterized the same pigment calling it flavohygrocybin. Muscaflavin comprises a 7-membered heterocyclic ring, formed by the action of a 2,3- DOPA dioxygenase on DOPA followed by spontaneous recyclization of the resulting 2,3-seco-DOPA intermediate (Steglich and Preuss 1975; Von Ardenne et al. 1974) (Fig. 4). Betalamic acid is also present in *A. muscaria* and *H. conica* (Musso 1979; Terradas and Wyler 1991a, b). Examination of the peptide sequences of the fungal, bacterial and plant DOPA dioxygenases shows little similarity, suggesting that these pathways have all evolved independently (Grotewold 2006; Novotna et al. 2004).

Whilst the major red pigments of *Amanita muscaria* (e.g. muscapurpurin) are derived from betalamic acid, the orange-red pigments of *Hygrocybe* spp. (hygroaurins) are apparently derived from muscaflavin via conjugation with amino acids. Bresinsky and Kronawitter (1986) confirmed the involvement of threonine but the precise nature of the red pigment(s) remains unknown. Cibula (1976) partially characterized a magenta pigment ('rhodohygrocybin', a type of hygroaurin), which was quantitatively correlated with the redness of the pileus, and he also noted its chemical similarity to muscaflavin (with these two pigments accounting for >80 % of the light absorption of pilei). Thus with muscaflavin (flavohygrocybin sensu Cibula) absorbing light below 500 nm (reflecting light at 500–700 nm –i.e., yellow) and 'rhodohygrocybin' absorbing light at 480–590 nm, the combined effect of these pigments is reflection of bright red. Cibula also found that muscaflavin was present at much higher concentrations (ca. 1200 ppm) than 'rhodohygrocybin' (ca 60 ppm) even in species with bright red pilei, with the latter also being less stable (Online Resource 4). The presence of an amino group (ninhydrin positive) in rhodohygrocybin further suggests that it is a hygroaurin, as discovered by Bresinsky and Kronawitter (1986), possibly conjugated with cyclo-DOPA (as found in betanidin) or an aromatic amino acid to achieve absorbance in the 500–600 nm region. The blackening of older or bruised basidiocarps of *H. conica* is also linked to muscaflavin synthesis, probably the result of melanin formation following oxidation of DOPA to DOPA-quinone and ultimately melanin by tyrosinase (Steglich and Preuss 1975).


Subgenus Hygrocybe
Subsect. Hygrocybe
Sect. Hygrocybe
Subsect. Macrosporae
Sect. Velosae
Sect. Pseudofirmae
Sect. Microsporae
Sect. Chlorophanae
H aff conica CA W N AM
H pseudoconica RUS
H nigrescens v brevispora PR
Hygrocybe conica CAN E NA
Hygrocybe konradii GER & DEN
H acutoconica JP
Hygrocybe acutoconica E NA
Hygrocybe persistens SWE
Hygrocybe noninquinans PR
Hygrocybe spadicea UK
MAL Hygrocybe hypohaemacta BZ
H roseopallida PAN
H occidentalis PR
Hygrocybe aff prieta 3099 BZ
H appalachianensis
H chloochlora BZ
Hygrocybe chloochlora PR
Hygrocybe appalachianensis TN
Hygrocybe aff neofirma BZ
Hygrocybe aff citrinovirens TN
Hygrocybe flavescens NC
Hygrocybe chlorophana DEN
H glutinipes v rubra NC E NA
Subgenus Pseudo-hygrocybe
Hygrocybe helobia RUS
Hygrocybe sp as P coccinea RUS
Hygrocybe miniata f longipes MA E NA
Unplaced
Hygrocybe purpureofolia RUS
Hygrocybe purpureofolia NC & MA E NA
Hygrocybe punicea AK-19 RUS
Hygrocybe punicea SCOT UK
Hygrocybe coccinea DEN
Hygrocybe sp AFTOL-1715 WA W NA
Hygrocybe aff mucronella NC E NA
Hygrocybe mucronella DEN
Hygrocybe ceracea DEN
Hygrocybe parvula RUS
Hygrocybe constrictospora DEN
Hygrocybe aff ceracea RUS
Hygrocybe reidii ENG UK
Sect. Coccineae subsect. Coccineae
Coccineae Subsect. Siccae
Hygrocybe lepida DEN
Hygrocybe coccineocrenata as helobia AK110 RUS
Hygrocybe cantharellus NH E NA
Hygrocybe melleofusca PR
Hygrocybe caespitosa WV E NA
Sect. Coccineae
Subsect. Squamulosae
Hygroaster nodulisporus BZ
Hygroaster nodulisporus PR
Hygroaster albellus PR
Neohygrocybe ovina R & FG WALES UK
Neohygrocybe subovina WV E NA
Neohygrocybe subovinaA TN E NA
Neohygrocybe ingrata NC E NA
Neohygrocybe ingrata as H nitrata NY E NA
Neohygrocybe ingrata WALES UK
Sect. Neohygrocybe
Porpolomopsis sp 80 TN E NA
Porpolomopsis calyptriformis ENG UK
Porpolomopsis lewelliniae TAS
Humidicutis sp2 6524 PR
Humidicutis sp3 3923 BZ
Humidicutis auratocephala E NA
Humidicutis marginata var olivacea E NA
Humidicutis marginata E NA
Gliophorus psittacinus DEN
Sect. Gliophorus
G. psittacinus NY E NA
Gliophorus laetus PR & CR
Gliophorus laetus RUS
Gliophorus laetus W N AM
Gliophorus laetus DAOM E N AM
Gliophorus graminicolor TAS
Sect. Glutinosae
Gliophorus psittacinus-like JP
Sect. Gliophorus
Gliophorus unguinosus EUR
Sect. Unguinosae
Chromosera cyanophylla AUSTRIA
Chromosera cyanophylla RUS
Chromosera citrinopallida NORD
Chromosera cyanophylla WA & WY W NA
Chromosera lilacina GREENLAND
Chrysomphalina grossula AFTOL & ORD
Chrysomphalina grossula LUTZ
Chrysomphalina chrysophylla W NA
Hygrophorus discoxanthus BALT & EUR
Hygrophorus eburneus BALT
Sect. Hygrophorus
Hygrophorus leucophaeus GER
Sect. Fulventes
Hygrophorus cossus AK 118 & 119 RUS
Hygrophorus cossus SWE
Sect. Hygrophorus
Hygrophorus discoideus GER
Sect. Discoidei
Hygrophorus capreolarius GER
Hygrophorus piceae BALT
Sect. Picearum
Hygrophorus olivaceoalbus GER & SWE
Hygrophorus agathosmus SWE
Hygrophorus hyacinthinus BALT
Hygrophorus agathosmus RUS & GER
Hygrophorus pustulatus RUS
Sect. Olivaceoumbrini
Hygrophorus russula JP
Hygrophorus russula SWE
Hygrophorus poetarum BALT
Hygrophorus aff russula BZ
Hygrophorus aff russula RUS
Hygrophorus cf pudorinus CO W NA
Sect. Pudorini
Hygrophorus bakerensis
Hygrophorus lucorum RUS
Hygrophorus flavodiscus E NA
Sect. Aurei
Hygrophorus persoonii RUS
Hygrophorus chrysodon GER
Hygrophorus chrysodon SWE
Subg. Camarophyllus
Sect. Chrysodontes
Subfamily
Tribe
Genus
Hygrocyboideae
Hygrocybeae
Hygrocybe
Hygroaster
Humidicuteae
Neohygrocybe
Porpolomopsis
Humidicutis
Gliophorus
Chromo-sereae
Chromosera
Chrysom-phalineae
Chrysomphalina
Hygrophoroideae
Hygrophoreae
Hygrophorus

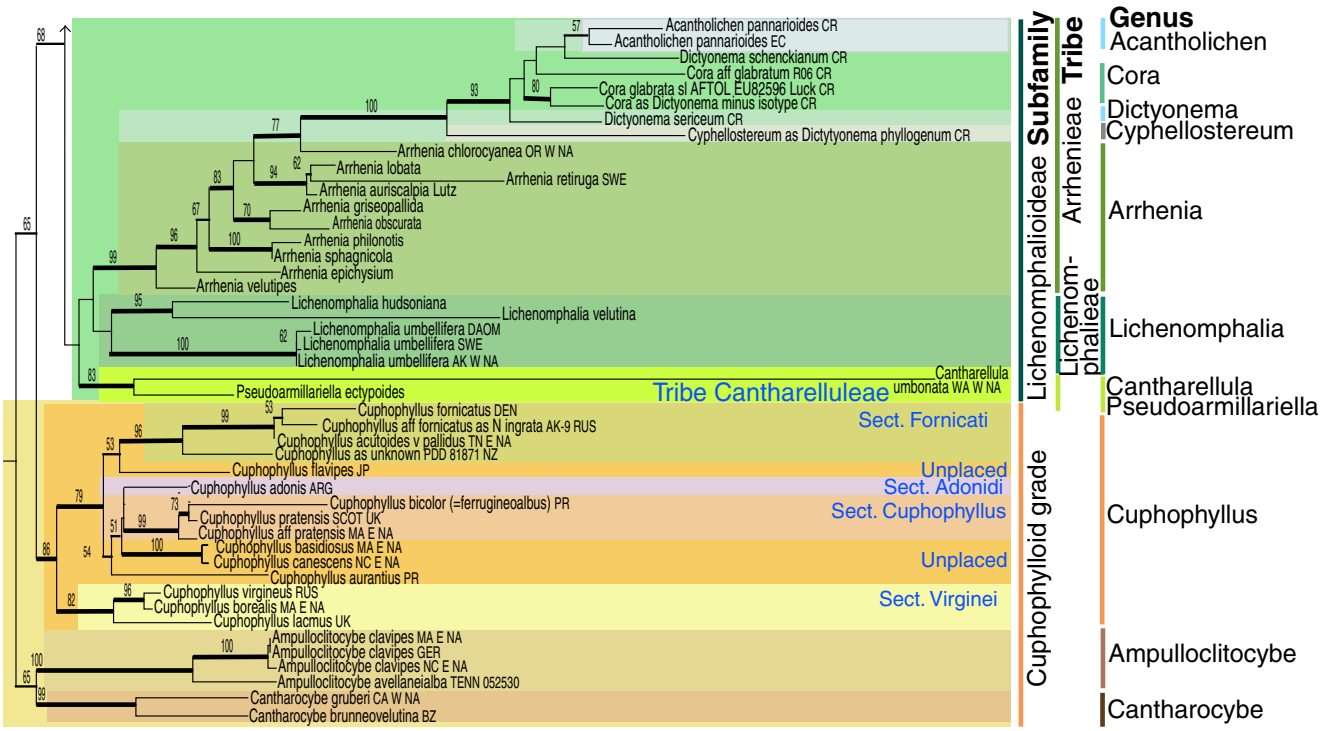


Fig. 2 (continued)

The distribution of the betalain pigments is taxonomically informative, since muscaflavin is the dominant pigment in all of the 30 species of *Hygrocybe* hitherto studied, with hygroaurins also being found in all of these (Bresinsky and Kronawitter 1986; Cibula 1976; Steglich and Strack 1990) (Fig. 4). Muscaflavin and hygroaurins were also detected in *H. ovina* but not other species of *Neohygrocybe* (Bresinsky and Kronawitter 1986), with muscaflavin only being found in a few *Hygrophorus* species (Bresinsky and Kronawitter 1986; Lübken 2006; Steglich and Strack 1990) (Online Resource 4). Equally informative is the absence of betalains in *Chromosera* (2 spp.), *Cuphophyllus* (4 spp.), *Gliophorus* (5 spp.), *Humidicutis marginata* and *Porpolomopsis calyptriformis* (Online Resource 4), differences in the concepts of some species globally (e.g. '*Gliophorus' vitellina*) can cause confusion. The nature of the pigments in these other groups is unknown. Cibula (1976) found that the yellow pigment of *Gliophorus* spp. was a non-carotenoid polyene but was unable to characterize the highly unstable ('fugaceous') cyan pigment of *G. psittacinus*. For several, such as in *C. pratensis*, the insolubility of the pigments in diverse organic solvents hindered further analysis. Muscaflavin is absent from *Cuphophyllus fornicatus*.

Several unpigmented metabolites have been characterized from basidiocarps of *Hygrophoraceae*, including polyacetylenic acids from *Cuphophyllus virginea* (Farrell et al. 1977), hygrophoric acid (a lactone derived from caffeic acid) and hygrophorones (cyclopentone derivatives) from several *Hygrophorus* spp. (Lübken et al. 2006); it is possible that some of these are precursors of pigments. Hygrophorones were shown to have antifungal and antibacterial activity (Lübken 2006) so they likely have adaptive significance. A new type of antifungal compound derived from fatty acids, chrysotrione, was found in *Hygrophorus chrysodon* (Gillardoni et al. 2006). Whilst the basidiocarps of Hygrophoraceae are not noted for their toxicity to humans, both *Cuphophyllus virginea* and *Hygrophorus chrysodon* arrest *Drosophila* development with an LD_{100} of ≤5 mg/ml in growth medium (Mier et al. 1996). *Ampulloclitocybe clavipes* produces an aldehyde dehydrogenase inhibitor (Cochran and Cochran 1978; Yamaura et al. 1986) and a tyrosine kinase inhibitor named clavilactone (Cassinelli et al. 2000).

Molecular analyses The ITS region has high heterozygosity in some Hygrophoraceae, especially *Hygrocybe*, *Gliophorus, Neohygrocybe* and *Porpolomopsis* (personal experiences, Hughes et al. 2009; Babos et al. 2011), which necessitated cloning the ITS region for many collections. There are also many insertions in the LSU and SSU of Hygrophoraceae that disrupt amplification. Especially troublesome are introns inserted close to the primers and secondary structural loops that cause out-of-sequence chimeric reads. Cloning was sometimes used to obtain full sequences. In other cases, 5–15 amplification and sequencing runs were obtained per gene region using different combinations of primers to yield a full sequence. In difficult species only one or two full 3′ to 5′ sequences were obtained. Group I introns inserted 14–15 nt to the right of the NS5 primer

(position 943) in the SSU disrupted amplification or yielded mixtures of amplicons with and without introns. Group I introns were confirmed in *Gliophorus psittacinus, Lichenomphalia umbellifera, Hygrocybe hypohaemacta*, and *H. miniata* f. *longipes*. However, it is likely that introns are more frequent in other members of the group for the following reasons: length polymorphisms were commonly revealed in the PCR gels of other taxa in this study, there is a PCR bias against copies with introns, and primer NS6 anneals across an intron insertion site and therefore, does not amplify intron-containing rDNA repeats (Hibbett 1996; Wang et al. 2009). The introns were 375–444 bp in length and matched other fungal Group I introns (Hibbett 1996; 80–83 % similarity in BLAST searches). The conserved Group I intron regions (P, Q, R and S) defined by Davies et al. (1982) and reported in Wang et al. (2009) were all located, with three changes. In the R region, the last three nt consisted of 5′-AGA instead of 5′-AAA, and one species (*H. hypohaemacta*) had a CW insertion after a 5′-gtt (i.e., GTTCWCAGAGACTAGA). The introns in all species had a single substitution of G for A in the S region (i.e., AAGGUAUAGUCC). None of the intron sequences appeared to code for a functional endonuclease, but a 16 aa protein translation from the 3′ end matched a Rho GTPase activator in two ascomycete fungi, *Trichophyton* and *Arthroderma*. In *Neohygrocybe ovina*, there was a partial tandem repeat of the NS5–6. Some self-chimeric LSU sequences resulted from using the LR5 primer and were likely caused by secondary structure, but no intron sequences were recovered in either *G. psittacinus* or *Hygrocybe* aff. *citrinopallida* DJL05TN10, the two species examined in detail. Reverse reads proceeded to near the LR3, where 31–37 nucleotides were missing, followed by a forward read beginning in or near the LROR.

Group I introns have frequently been reported from mitochondrial genomes of ciliates, green algae, plants, fungi and slime molds, and are transmitted both vertically and horizontally (De Wachter et al. 1992; Gargas et al. 1995; Hibbett 1996; Wang et al. 2009). Group I fungal introns of about 400 bp have previously been found in nuc-rDNA SSU sequences of several basidiomycetes including *Artomyces pyxidatus, Auriscalpium vulgare* and *Lentinellus* and *Panellus stipticus* (Lickey et al. 2003; Hibbett and Donoghue 1995). BLAST searches in the NCBI database using the intron sequence revealed additional basidiomycetes with similar introns, including *Descolea maculata* (Cortinariaceae) AFTOL-1521, DQ440633), *Piloderma fallax* (Atheliaceae, GU187644), *Galerina atkinsoniana* (Strophariaceae, AFTOL-1760, DQ440634), *Tubaria serrulata* (Strophariaceae, AFTOL-1528, DQ462517), *Porotheleum fimbriatum* (MeripilaceaeAFTOL-1725, DQ444854) and *Oudemansiella radicata* (Physalacriaceae, AY654884).

Results of phylogenetic analyses are reported under each taxon and compared to previously published analyses. Maximum Likelihood bootstrap support (MLBS) values >69 % and Bayesian posterior probabilities (BPP) >0.94 are considered significant (strong).

Taxonomy

The following text and tables are arranged according to the branching order of clades in the four-gene backbone and Supermatrix analyses (Figs. 1 and 2, respectively). The synonymy shown is incomplete but includes obligate synonyms that are needed to trace names to their basionym, a few facultative synonyms, synonyms that are invalid or illegitimate and misapplied names.

Hygrophoraceae subfam. *Hygrocyboideae* Padamsee & Lodge, subf. nov.

MycoBank MB804066.

Type genus: *Hygrocybe* (Fr.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871).

≡ *Hygrophorus* subg. *Hygrocybe* Fr., Summa veg. Scand., Section Post. (Stockholm): 308 (1849).

Basidiomes fleshy; colors usually bright, rarely dull; lamellae, usually thick, yielding a waxy substance when crushed, rarely absent; true veils lacking, rarely with false peronate veils formed by fusion of the gelatinous ixocutis of the pileus and stipe, and fibrillose partial veils formed by hyphae emanating from the lamellar edge and stipe apex; basidiospores thin-walled, guttulate, hyaline (though species with black staining basidiomes may have fuscous inclusions), smooth or ornamented by conical spines, inamyloid, acyanophilous; basidia guttulate, mono- or dimorphic, if dimorphic then basidia emanating from the same fascicle differing in length and width; mean ratio of basidia to basidiospore length 3–7; pleurocystidia absent; pseudocystidia sometimes present; true cheilocystidia usually absent but cystidia-like hyphoid elements emanating from the lamellar context or cylindric or strangulated ixo-cheilocystidia embedded in a gelatinous matrix sometimes present; lamellar trama inamyloid, regular or subregular but not highly interwoven, divergent or pachypodial; comprised of long or short hyphal segments with oblique or perpendicular cross walls, often constricted at the septations, usually thin-walled but hyphae of the central mediostratum sometimes slightly thickened. Pileipellis structure a cutis, disrupted cutis, ixocutis, ixotrichodermium or trichodermium, but never hymeniform; clamp connections present or absent; habit terrestrial, rarely on wood or arboreal, often associated with mosses, growing in forests or grasslands; possibly biotrophic but not known to form ectomycorrhizae with woody plants.

Phylogenetic support Support for a monophyletic clade representing subf. *Hygrocyboideae* was high in the 4-gene

backbone (99 % MLBS, Fig. 1; 1.0 B.P. Online Resource 6), and Supermatrix (80 % MLBS, Fig. 2) analyses, but fell below 50 % in the LSU and ITS-LSU analyses (Figs. 3 and 5). The ITS analysis by Dentinger et al. (unpublished) shows 98 % MLBS support for subf. *Hygrocyboideae*. Support for subf. *Hygrocyboideae* as the sister clade to subf. *Hygrophoroideae* was highest in the Bayesian 4-gene backbone analysis (1.0 PP), while bootstrap support was moderately high in all the ML analyses except the LSU (78 % Supermatrix, and 77 % 4-gene backbone). Moncalvo et al. (2002) found Bayesian support for two sister clades, one with *Hygrocybe* and *Chromosera* and another with *Hygrophorus* and *Chrysomphalina*, and Lodge et al. (2006) recovered the same topology without support, but the topology was more complex in the Supermatrix analysis by Matheny et al. (2006).

Tribes included Hygrocybeae, Humidicuteae, stat. nov. and *Chromosereae*, tribe nov.

Hygrophoraceae [subfam. *Hygrocyboideae*] tribe *Hygrocybeae* Kühner, Bull. Soc. Linn. Lyon 48: 621 (1979)

Type genus: *Hygrocybe* (Fr.) P. Kumm., Führ. Pilzk. (Zwickau): 26 (1871).

Emended here by Lodge

Basidiomes lacking carotenoid pigments, typically with betalain, DOPA based compounds that usually appear as bright colors (muscaflavin, flavohygrocybin, rhodohygrocybin), but these sometimes converted to fuscous forms, or as colorless forms (hygroaurin, formed by conjugation of muscaflavin with amino acids) or pigments completely absent; true veils lacking but rarely with false peronate veils formed by fusion of the gelatinous ixocutis of the pileus and stipe, and fibrillose partial veils formed by hyphae emanating from the lamellar edge and stipe apex; lamellae usually present, thick, yielding a waxy substance when crushed; basidiospores thin-walled, guttulate in KOH mounts, hyaline, sometimes with fuscous inclusions in staining species, smooth or rarely ornamented by conical spines, inamyloid, acyanophilous, non-metachromatic; basidia guttulate, mono- or dimorphic, if dimorphic then basidia emanating from the same fascicle differing in length and often width; mean ratio of basidia to basidiospore length 3–7; context not dextrinoid; pleurocystidia absent; pseudocystidia may be present, true cheilocystidia usually absent but cystidia-like hyphoid elements emanating from the lamellar context commonly present, rarely with true cheilocystidia; lamellar trama regular to subregular, never divergent, pachypodial or highly interwoven; clamp connections usually present in context and hymenium unless spores are ornamented with spines or basidia bisporic; clamps normal or medallion type, rarely toruloid; habit terrestrial, bryophilous, rarely on wood or arboreal, growing in forests or grasslands; possibly biotrophic, cloned from the rhizosphere but not plant roots, not forming ectomycorrhizae with woody plants.

Fig. 3 LSU analysis (LROR–LR5) of Hygrophoraceae together with representatives of the hygrophoroid clade (*Sarcomyxa* and *Xeromphalina*) and several outgroups (*Mycena* and *Omphalina*), rooted with *Macrotyphula phacorrhiza*. ML bootstrap values ≥50 % appear above the branches. Heavily bolded branches have ≥70 % and lightly bolded branches have 50–69 % ML bootstrap support

Phylogenetic support Support for Tribe *Hygrocybeae* is strong in our LSU (85 % MLBS, Fig. 3), 4-gene backbone (98 % MLBS & 1.0 B.P. Fig. 1 and Online Resource 6), and Supermatix (96 % MLBS, Fig. 2) analyses. Dentinger et al. (unpublished) show 93 % MLBS support for tribe *Hygrocybeae* in their ITS analysis. Previous studies show similarly high support for a monophyletic *Hygrocybeae* using a maximum parsimony analysis of LSU (98 % MPBS, Moncalvo et al. 2002), ITS (100 % MPBS, Seitzman et al. 2011) and a multigene analysis (100 % MLBS and 1.0 B.P. Matheny et al. 2006) but none of those analyses included *Hygroaster*.

Genera included Hygrocybe and *Hygroaster*.

Comments As noted by Bas (1990), the citation by Arnolds (1990) as tribe *Hygrocybeae* (Kühner) Bas & Arnolds was incorrect because only names at or below genus are recombined (Art. 6.7), so authors of higher taxa remain the same when they are transferred to another position. Bas (1990) and Arnolds (1990) treated tribe *Hygrocybeae* in the Tricholomataceae instead of Hygrophoraceae.

Hygrocybe (Fr.) P. Kumm., Führ., Pilzk. (Zwickau): 26 (1871)

≡ *Hygrophorus* subg. *Hygrocybe* Fr. (1849).

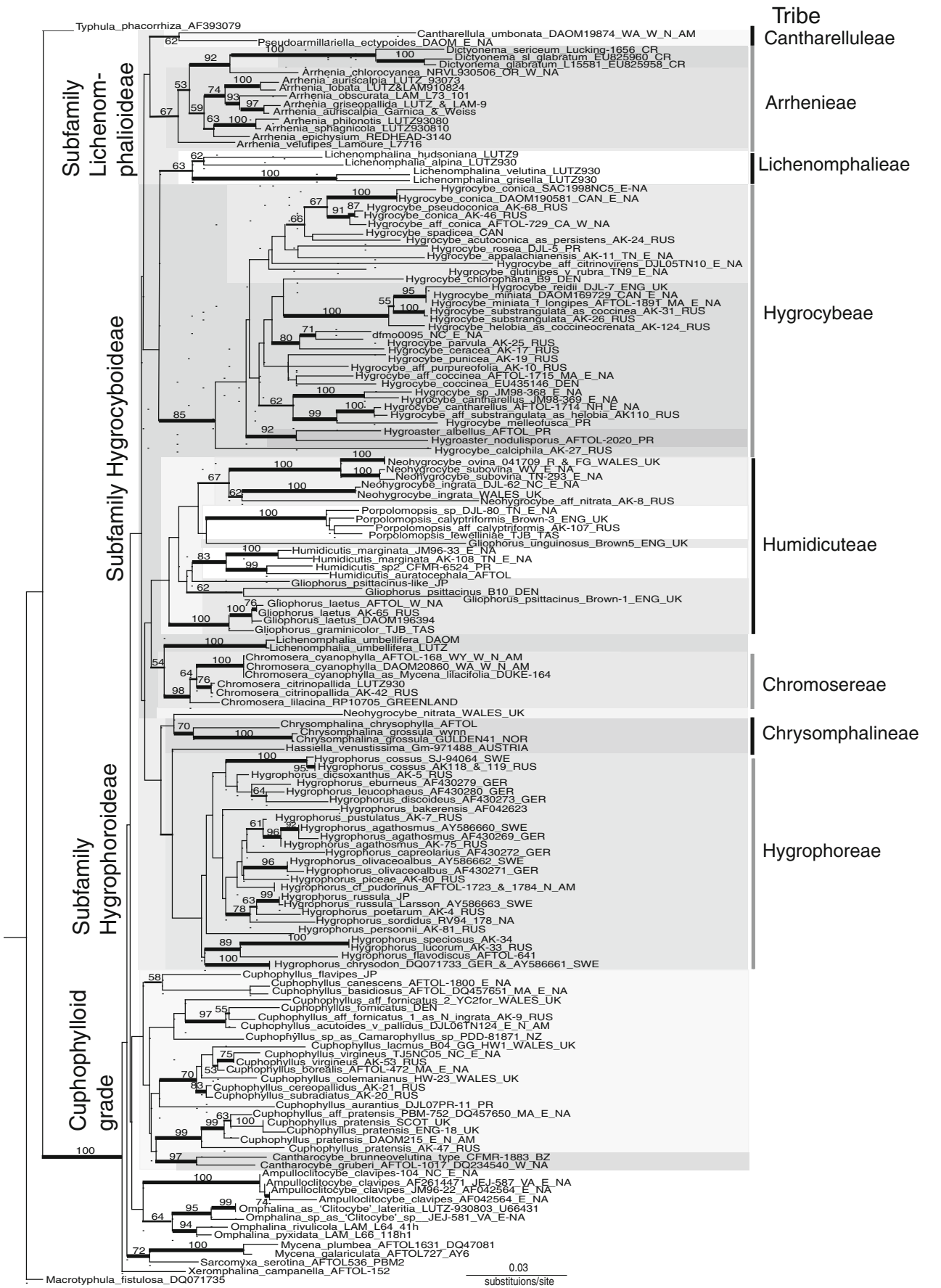
Type species: *Hygrocybe conica* (Schaeff.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871)

≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838) [1836–1838],

≡ *Agaricus conicus* Schaeff., Fung. Bavar. Palat. 4: 2 (1877)].

Characters as in tribe *Hygrocybeae*. Differing from *Hygroaster* in usually having bright pigments, and basidiospores that are typically smooth, but if conical warts are present, the spores are broadly ellipsoid rather than globose or subglobose and the outline is usually subangular.

Phylogenetic support Hygrocybe s.s. is strongly supported as monophyletic in our 4-gene backbone (95 % MLBS, 1.0 B.P. Fig. 1 and Online Resource 6), LSU (87 % MLBS, Online Resource 7) and ITS-LSU analyses (90 % MLBS, Fig. 4); support is lower in our Supermatix analysis (60 % MLBS; Fig. 2). Previously, Moncalvo et al. (2002) found a monophyletic *Hygrocybe* using LSU, but it lacked significant BS support. Others subsequently showed 100 % BS or 1.0 Bayesian PP support for a monophyletic *Hygrocybe* including Binder


Tribe
Cantharelluleae
Arrhenieae
Lichenomphalieae
Hygrocybeae
Humidicuteae
Chromosereae
Chrysomphalineae
Hygrophoreae
Subfamily Lichenom-phalioideae
Subfamily Hygrocyboideae
Subfamily Hygrophoroideae
Cuphophylloid grade
Typhula_phacorrhiza_AF393079
Cantharellula_umbonata_DAOM19874_WA_W_N_AM
Pseudoarmillariella_ectypoides_DAOM_E_NA
Dictyonema_sericeum_Lucking-1656_CR
Dictyonema_sl_glabratum_EU825960_CR
Dictyonema_glabratum_L15581_EU825958_CR
Arrhenia_chlorocyanea_NRVL930506_OR_W_NA
Arrhenia_auriscalpia_LUTZ_93073
Arrhenia_lobata_LUTZ&LAM910824
Arrhenia_obscurata_LAM_L73_101
Arrhenia_griseopallida_LUTZ_&_LAM-9
Arrhenia_auriscalpia_Garnica_&_Weiss
Arrhenia_philonotis_LUTZ93080
Arrhenia_sphagnicola_LUTZ930810
Arrhenia_epichysium_REDHEAD-3140
Arrhenia_velutipes_Lamoure_L7716
Lichenomphalina_hudsoniana_LUTZ9
Lichenomphalia_alpina_LUTZ930
Lichenomphalina_velutina_LUTZ930
Lichenomphalina_grisella_LUTZ930
Hygrocybe_conica_SAC1998NC5_E-NA
Hygrocybe_conica_DAOM190581_CAN_E_NA
Hygrocybe_pseudoconica_AK-68_RUS
Hygrocybe_conica_AK-46_RUS
Hygrocybe_aff_conica_AFTOL-729_CA_W_NA
Hygrocybe_spadicea_CAN
Hygrocybe_acutoconica_as_persistens_AK-24_RUS
Hygrocybe_rosea_DJL-5_PR
Hygrocybe_appalachianensis_AK-11_TN_E_NA
Hygrocybe_aff_citrinovirens_DJL05TN10_E_NA
Hygrocybe_glutinipes_v_rubra_TN9_E_NA
Hygrocybe_chlorophana_B9_DEN
Hygrocybe_reidii_DJL-7_ENG_UK
Hygrocybe_miniata_DAOM169729_CAN_E_NA
Hygrocybe_miniata_f_longipes_AFTOL-1891_MA_E_NA
Hygrocybe_substrangulata_as_coccinea_AK-31_RUS
Hygrocybe_substrangulata_AK-26_RUS
Hygrocybe_helobia_as_coccineocrenata_AK-124_RUS
dfmo0095_NC_E_NA
Hygrocybe_parvula_AK-25_RUS
Hygrocybe_ceracea_AK-17_RUS
Hygrocybe_punicea_AK-19_RUS
Hygrocybe_aff_purpureofolia_AK-10_RUS
Hygrocybe_aff_coccinea_AFTOL-1715_MA_E_NA
Hygrocybe_coccinea_EU435146_DEN
Hygrocybe_sp_JM98-368_E_NA
Hygrocybe_cantharellus_JM98-369_E_NA
Hygrocybe_cantharellus_AFTOL-1714_NH_E_NA
Hygrocybe_aff_substrangulata_as_helobia_AK110_RUS
Hygrocybe_melleofusca_PR
Hygroaster_albellus_AFTOL_PR
Hygroaster_nodulisporus_AFTOL-2020_PR
Hygrocybe_calciphila_AK-27_RUS
Neohygrocybe_ovina_041709_R_&_FG_WALES_UK
Neohygrocybe_subovina_WY_E_NA
Neohygrocybe_subovina_TN-293_E_NA
Neohygrocybe_ingrata_DJL-62_NC_E_NA
Neohygrocybe_ingrata_WALES_UK
Neohygrocybe_aff_nitrata_AK-8_RUS
Porpolomopsis_sp_DJL-80_TN_E_NA
Porpolomopsis_calyptriformis_Brown-3_ENG_UK
Porpolomopsis_aff_calyptriformis_AK-107_RUS
Porpolomopsis_lewelliniae_TJB_TAS
Gliophorus_unguinosus_Brown5_ENG_UK
Humidicutis_marginata_JM96-33_E_NA
Humidicutis_marginata_AK-108_TN_E_NA
Humidicutis_sp2_CFMR-6524_PR
Humidicutis_auratocephala_AFTOL
Gliophorus_psittacinus-like_JP
Gliophorus_psittacinus_B10_DEN
Gliophorus_psittacinus_Brown-1_ENG_UK
Gliophorus_laetus_AFTOL_W_NA
Gliophorus_laetus_AK-65_RUS
Gliophorus_laetus_DAOM196394
Gliophorus_graminicolor_TJB_TAS
Lichenomphalia_umbellifera_DAOM
Lichenomphalia_umbellifera_LUTZ
Chromosera_cyanophylla_AFTOL-168_WY_W_N_AM
Chromosera_cyanophylla_DAOM20860_WA_W_N_AM
Chromosera_cyanophylla_as_Mycena_lilacifolia_DUKE-164
Chromosera_citrinopallida_LUTZ930
Chromosera_citrinopallida_AK-42_RUS
Chromosera_lilacina_RP10705_GREENLAND
Neohygrocybe_nitrata_WALES_UK
Chrysomphalina_chrysophylla_AFTOL
Chrysomphalina_grossula_wynn
Chrysomphalina_grossula_GULDEN41_NOR
Hassiella_venustissima_Gm-971488_AUSTRIA
Hygrophorus_cossus_SJ-94064_SWE
Hygrophorus_cossus_AK118_&_119_RUS
Hygrophorus_dicsoxanthus_AK-5_RUS
Hygrophorus_eburneus_AF430279_GER
Hygrophorus_leucophaeus_AF430280_GER
Hygrophorus_discoideus_AF430273_GER
Hygrophorus_bakerensis_AF042623
Hygrophorus_pustulatus_AK-7_RUS
Hygrophorus_agathosmus_AY586660_SWE
Hygrophorus_agathosmus_AF430269_GER
Hygrophorus_agathosmus_AK-75_RUS
Hygrophorus_capreolarius_AF430272_GER
Hygrophorus_olivaceoalbus_AY586662_SWE
Hygrophorus_olivaceoalbus_AF430271_GER
Hygrophorus_piceae_AK-80_RUS
Hygrophorus_cf_pudorinus_AFTOL-1723_&_1784_N_AM
Hygrophorus_russula_JP
Hygrophorus_russula_Larsson_AY586663_SWE
Hygrophorus_poetarum_AK-4_RUS
Hygrophorus_sordidus_RV94_178_NA
Hygrophorus_persoonii_AK-81_RUS
Hygrophorus_speciosus_AK-34
Hygrophorus_lucorum_AK-33_RUS
Hygrophorus_flavodiscus_AFTOL-641
Hygrophorus_chrysodon_DQ071733_GER_&_AY586661_SWE
Cuphophyllus_flavipes_JP
Cuphophyllus_canescens_AFTOL-1800_E_NA
Cuphophyllus_basidiosus_AFTOL_DQ457651_MA_E_NA
Cuphophyllus_aff_fornicatus_2_YC2for_WALES_UK
Cuphophyllus_fornicatus_DEN
Cuphophyllus_aff_fornicatus_1_as_N_ingrata_AK-9_RUS
Cuphophyllus_acutoides_v_pallidus_DJL06TN124_E_N_AM
Cuphophyllus_sp_as_Camarophyllus_sp_PDD-81871_NZ
Cuphophyllus_lacmus_B04_GG_HW1_WALES_UK
Cuphophyllus_virgineus_TJ5NC05_NC_E_NA
Cuphophyllus_virgineus_AK-53_RUS
Cuphophyllus_borealis_AFTOL-472_MA_E_NA
Cuphophyllus_colemanianus_HW-23_WALES_UK
Cuphophyllus_cereopallidus_AK-21_RUS
Cuphophyllus_subradiatus_AK-20_RUS
Cuphophyllus_aurantius_DJL07PR-11_PR
Cuphophyllus_aff_pratensis_PBM-752_DQ457650_MA_E_NA
Cuphophyllus_pratensis_SCOT_UK
Cuphophyllus_pratensis_ENG-18_UK
Cuphophyllus_pratensis_DAOM215_E_N_AM
Cuphophyllus_pratensis_AK-47_RUS
Cantharocybe_brunneovelutina_type_CFMR-1883_BZ
Cantharocybe_gruberi_AFTOL-1017_DQ234540_W_NA
Ampulloclitocybe_clavipes-104_NC_E_NA
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Ampulloclitocybe_clavipes_JM96-22_AF042564_E_NA
Ampulloclitocybe_clavipes_AF042564_E_NA
Omphalina_as_'Clitocybe'_lateritia_LUTZ-930803_U66431
Omphalina_sp_as_'Clitocybe'_sp__JEJ-581_VA_E-NA
Omphalina_rivulicola_LAM_L64_41h
Omphalina_pyxidata_LAM_L66_118h1
Mycena_plumbea_AFTOL1631_DQ47081
Mycena_galariculata_AFTOL727_AY6
Sarcomyxa_serotina_AFTOL536_PBM2
Xeromphalina_campanella_AFTOL-152
Macrotyphula_fistulosa_DQ071735
0.03
substituions/site

et al.'s (2010) six gene analysis (RAxML and Bayesian), Lawrey et al.'s (2009) ITS-LSU (ML and MP), Matheny et al.'s multigene Supermatrix (MP and Bayesian), Seitzman et al.'s (2011) ITS (MP) and Vizzini et al.'s (2012) ITS-LSU (ML, MP and Bayesian). Babos et al. (2011) found lower support using only ITS (70 % MLBS). We find high support for *Hygrocybe* as the sister clade to *Hygroaster* in the 4-gene backbone (98 % ML BS, 1.0 B.P. and Supermatrix analyses (96 % MLBS).

Subgenera included Hygrocybe s.s. is currently treated as comprising two subgenera, *Hygrocybe* and *Pseudohygrocybe*. Other subgenera that have previously been included in *Hygrocybe* s.l. are treated as segregate genera here but are listed in Table 1.

Comments The name *Hygrocybe* was not validly published in Fries (1821) or (1838), but was validated as *Hygrophorus* subgen. *Hygrocybe* in Fries (1849). Though Rabenhorst (1844) pre-dates this, he did not list *Hygrocybe* among the infrageneric names he accepted, which indicates he rejected them as synonyms of genus *Agaricus,* [unranked] *Hygrophorus,* [unranked] *Hygrocybe* (pers. com. Shaun Pennycook, 28 Oct. 2010 to S.A. Redhead). Kummer (1871) was thus the first to validly use *Hygrocybe* Fr. at genus rank. Kovalenko (1988) treated the current subgenera as separate genera: *Hygrocybe* and *Pseudohygrocybe* (Bon) Kovalenko. Herink (1959) previously attempted to separate the two main *Hygrocybe* groups at genus rank using *Godfrinia* Maire (1902), nom. illeg., with type species *G. conica* (Scop. ex Fr.) R. Maire, and an emended *Hygrocybe*. Except for inclusion of *H. punicea*, Maire's (1902) "*Godfrinia*" illeg. is concordant with the current *Hygrocybe* subg. *Hygrocybe*. Because "*Godfrinia*" (1902) is predated by *Hygrocybe* (Kummer 1871) and shares the same type species, it is superfluous and therefore illegitimate (Art. 52.10). Heim (1936)

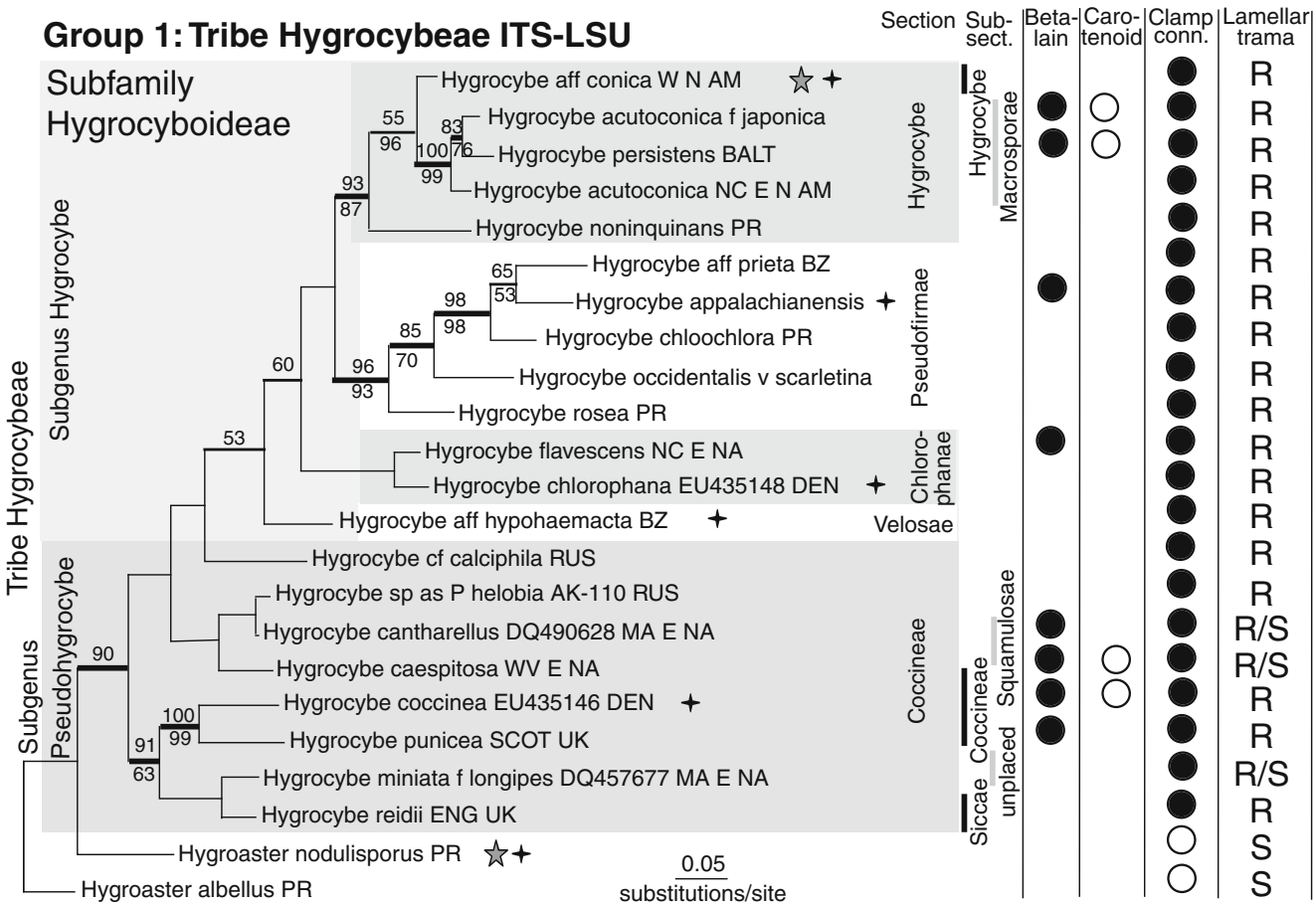


Fig. 4 Tribe *Hygrocybeae* (Group 1) ITS-LSU analysis, rooted with *Hygroaster albellus*. Genes analyzed were ITS (ITS1, 5.8S & ITS2), LSU (LROR-LR5). Presence of betalain (DOPA based) and carotenoid pigments and presence of clamp connections in forms with 4-spored basidia are denoted by filled circles while empty circles denote their absence. Lamellar trama types are: R for regular (parallel) and S for subregular. ML bootstrap values ≥50 % appear above the branches. Heavily bolded branches have ≥70 % and lightly bolded branches have 50–69 % ML bootstrap support

Table 3 Synoptic key to the Hygrophoroid clade. Substrata reported are: bryophytes (b), debris (d), ectomycorrhizal hosts (e), ferns (f), grasses (g), lichenized with chlorophyta (l^{ch}) or cyanobacteria (l^{cy}), soil (s), humus (h), and wood (w). Characters are noted as present (+), absent (−), or if variable the predominant form is presented first (+/− or −/+)

	Veil	Lamellae					Basidiospores				
Genus, Subgenus, Section	Glutinous/ cortina	Absent	Free	Adnexed/ uncinate	Adnatodecurrent	Edge gelatinized	L Basid. >5x spore L	Hyaline	Dimorphic	Amyloid	Ornamented
Hygrocybe	+/−	+/−	+/−	+/−	+/−	+/−	+/−	+	+/−	−	−
subg. *Hygrocybe*	+/−	+/−	+/−	+/−	+/−	+/−	−/+	+	+/−	−	−
sect. *Hygrocybe*	−	−/+	+	−	−	+[a]/−	−	+	−	−	−
sect. *Velosae*	+	−	+	−	−	+	−	+	+	−	−
sect. *Chlorophanae*	−	−	−	+	+[b]/−	−	−/+	+	−	−	−
sect. *Pseudofirmae*	−	+/−	−	+	+	−/+	−/+	+	+	−	−
sect. *Microsporae*	−	−	−	−	+	−	−/+	+	−	−	−
subg. *Pseudohygrocybe*	−	−	−	+	+/−	−	+/−	+	−	−	−/+[c]
sect. Coccineae	−	−	−	+	+	−	+/−	+	−	−	−/+
sect. Firmae	−	−	−	−	+	−	+	+	+	−	−
Hygroaster	−	−	−	−	+	−	+	+	−	−	+
Neohygrocybe	−	−	−	+	−	−	+	+	−	−	−
Humidicutis	−	−	−	+	+	−	+/−	+	−	−	−
Porpolomopsis	−	−	+	+	−	−/+	+/−	+	−	−	−
Gliophorus	−	−	−	+	+	+/−	+/−	+	−	−	−
sect. *Glutinosae*	−	−	−	−	+	+	+/−	+	−	−	−
sect. *Gliophorus*	−	−	−	+	+	−	+/−	+	−	−	−
sect. *Unguinosae*	−	−	−	−	+	−	+	+	−	−	−
Chromosera	−	−	−	−	+	−	−	+	−	−[f]	−
Gloioxanthomyces	−	−	−	−	+	+	−/+	+	−	−	−
Hygrophorus	+/−	−	−	−	+	−	+	+	−	−	−
Chrysomphalina	−	−	−	−	+	−	+	−	−	−	−
Haasiella	−	−	−	−	+	−	+	−	−	−	−
Aeruginospora	−	−	−	−	+	−	+	−	−	−	−
Arrhenia	−	+/−	−	−	+	−	−	+	−	−	−
Eonema	−	−	−	−	−	−	−	+	−	−	−
Dictyonema	−	+					−	+	−	−	−
Lichenomphalia	−	−	−	−	+	−	+	+	−	−	−
Cantharellula	−	−	−	−	+	−	−	+	−	+	−
Pseudoarmillariella	−	−	−	−	+	−	−	+	−	+	−
Cuphophyllus	−	−	−	−	+	−	+	+	−	−	−
sect. *Fornicatae*	−	−	−	+	+	−	+	+	−	−	−
sect. *Cuphophyllus*	−	−	−	−	+	−	+	+	−	−	−
sect. *Adonidae*	−	−	−	−	+	−	+	+	−	−	−
sect. *Virginei*	−	−	−	−	+	−	+	+	−	−	−
Ampulloclitocybe	−	−	−	−	+	−	−	+	−	−	+
Cantharocybe		−	−	−	+	−	+	+	−	−	−
Tricholomopsis	−	−	−	+	+	−	−/+	+	−	−	−
Phyllotopsis	−	−	−	−	+	−	−	+	−	−	−
Pleurocybella	−	−	−	−	+	−	−	+	−	−	−
Macrotyphula	−	+					+	+	−	−	−

Table 3 (continued)

Genus, Subgenus, Section	*Veil*	Lamellae					Basidiospores				
	Glutinous/ cortina	Absent	Free	Adnexed/ uncinate	Adnatodecurrent	Edge gelatinized	L Basid. >5x spore L	Hyaline	Dimorphic	Amyloid	Ornamented
Typhula	−	+					−	+	−	−	−
Sarcomyxa	−	−	−	−	+	−	−	+	−	+	−

Genus, Subgenus, Section	Lamellar Trama					*Clamp*			Pig-ments		Ecol.
	Metachromatic + + +	Hyphae >160 µm	Regular/ subregularr	Interwoven	Pachypodial	Divergent	Trama	Basidia; toruloid:T	Carotenoid	L DOPA Betalains	Substratum
Hygrocybe	−	+/−	+	−	−	−	+	+		+	shbg
subg. *Hygrocybe*	−	+/−	+	−	−	−	+	+	−	+	shbg
sect. *Hygrocybe*	−	+	+	−	−	−	+	+		+	shbg
sect. *Velosae*	−	+	+	−	−	−	+	+			shb
sect. *Chlorophanae*	−	+	+	−	−	−	+	+		+	shbg
sect. *Pseudofirmae*	−	+/−	+	−	−	−	+	+		+	shwb
sect. *Microsporae*	−	+/−	+	−	−	−	+	+			shg
subg. *Pseudohygrocybe*	−	−	+	−	−	−	+	+		+	shbwg
sect. Coccineae	−	−	+	−	−	−	+	+		+	shbwg
sect. Firmae	−	−	+	−	−	−	+	+			shb
Hygroaster	−	−	+	−	−	−	+	+	−		sb
Neohygrocybe	−	−/+	+	−	−	−	+	+		+/−	shg
Humidicutis	−	−/+[d]	+	−	−	−	−	T			shbg
Porpolomopsis	−	+/−[d]	+	−	−	−	+/−	T		−	shbg
Gliophorus	−	−	+	−	−	−	+	+/T		−	shbg
sect. *Glutinosae*	−	−	+	−	−	−	+	T		−	shbg
sect. *Gliophorus*	−	−	+	−	−	−	+	+		−	shbg
sect. *Unguinosae*	−	−	+	−	−	−	−/+	T			shbg
Chromosera	−	−	−	+	−	−	+	+		−	shbw
Gloioxanthomyces	−	−	+	−	−	−	+	+		?[e]	shbg
Hygrophorus	−	−	−	−	−	+	+/−	+		+[e]	e
Chrysomphalina	−	−	−	−	+	+	−	−	+		w
Haasiella	+	−	−	−	+	−	+/−	+/−	+		dw
Aeruginospora	+	−	−	−	+	−	−	−			d[g]
Arrhenia	−	−	−	+	−		+	+/−	−	−	bh

Table 3 (continued)

Genus, Subgenus, Section	Lamellar Trama					*Clamp*			Pig-ments		Ecol.
	Metachromatic + + +	Hyphae >160 µm	Regular/ subregularr	Interwoven	Pachypodial	Divergent	Trama	Basidia; toruloid:T	Carotenoid	L DOPA Betalains	Substratum
Eonema	−	−	−	+	−	−	−	−	−	−	fg
Dictyonema	−	−	−	+	−	−	−	−/+[h]	−	−	l[cy]
Lichenomphalia	−	−	−	+	−	−	−	−	−		l[ch]
Cantharellula	−	−	−	+	−	−	+	+	−		b
Pseudoarmillariella	−	−	−	+	−	−	+	+	−		bw
Cuphophyllus	−	−	−/+	+	−	−	+	+		−	sbg
sect. *Fornicatae*	−	−	−/+[i]	+	−	−	+	+		−	sbg
sect. *Cuphophyllus*	−	−	−/+[i]	+	−	−	+	+			sbg
sect. *Adonidae*	−	−	−	+	−	−	+	+			sbg
sect. *Virginei*	−	−	−	+	−	−	+	+			sbg
Ampulloclitocybe	−	−	−	+	−	−	+	+	−	−	s
Cantharocybe	−	−	+	−	−	−	+	+		−	sh
Tricholomopsis	−	−	+	−	−	−	+	+			w
Phyllotopsis	−	−	+	−	−	−	+	+			w
Pleurocybella	−	−	−	+	−	−	+	+		−	w
Macrotyphula	−	−					−/+	−/+			hw
Typhula	−	−					−/+	−/+			dhwg
Sarcomyxa	−	+	−	−	−	−	+	+			w

[a] Some specimens of *H. acutoconica* and *H. konradii* occasionally have gelatinized lamellar edges (Boertmann 2010)

[b] Placement of *H. glutinipes*, with subdecurrent lamellae, in sect. *Chlorophanae* is ambiguous (Lodge and Ovrebo 2008)

[c] Nodulose basidiospores occur in some *H. anomala, H. insipida* and *H. kuoskosii* (Boertmann 2010; Young 2005)

[d] This could change with additional *Humidicutis* sequences from species of Australasia, Asia and South America

[e] *Hygrophorus* spp. reportedly have muscaflavin but not hygroaurin; positive for *H. vitellina* may be a misapplied name

[f] *Chromosera* has weakly dextrinoid context hyphae and inamyloid spores

[g] *Aeruginospora* is reported from debris under bamboo

[h] *Dictyonema irpicinum* and *D. ligulatum* are reported to have clamp connections (Parmasto (1978) [1977])

[i] *Cuphophyllus* sect. *Fornicatae* and some species in sect. *Cuphophyllus* have a subregular central strand in the lamellar context; *C. aurantius*, which may or may not belong in sect. *Cuphophyllus*, has a regular mediostratum and subregular lateral strata in the lamellar context

named a new genus, *Bertrandia*, to accommodate a conical blackening species from Africa that exudes copious latex when cut, but the type species is now correctly classified as *Hygrocybe astatogala* (Heim) Heinem. (1963) in subg. *Hygrocybe* [sect. *Hygrocybe*] subsect. *Hygrocybe*, rendering *Bertrandia* a synonym of *Hygrocybe*. Although the composition of Herink's (1959) emended *Hygrocybe* (*H. miniata*, *H. coccinea, H. marchii, H. miniato-alba* and *H. turunda*) corresponds to the current subg. *Pseudohygrocybe*, he was incorrect in attempting to replace the type species of *Hygrocybe* (*H. conica*) with *H. miniata*. Babos et al. (2011) erroneously reported that Candusso (1997) transferred *Hygrocybe* to the Agaricaceae, apparently mistaking the early history of the Hygrophoraceae (pp. 33–44), in which all agaric species were first placed in *Agaricus* by Scopoli, Schaeffer and Fries, for the classification accepted by Candusso (pp. 313–323).

As delineated by Fries (1849) and Bataille (1910), *Hygrocybe* included terrestrial species with a pileus that was thin, tender, sometimes striate, with a moist, lubricous or viscid surface; stipe hollow or stuffed, splitting or fibrillose, generally smooth at the apex, with a moist or viscid surface. *Hygrocybe* species are frequently brightly colored, though gray-brown ones also occur. DOPA betalain pigments are found throughout the pigmented *Hygrocybe* ss, but rarely outside this group, while carotenoid pigments are apparently absent from *Hygrocybe* s.s. (Table 3, Online Resource 4). As in other members of the family, the lamellae of *Hygrocybe* are waxy and yield an oily substance when crushed (Young 1997), and they are usually but not always thick (Lodge et al. 2006). The lamellar trama structure is always regular or subregular in *Hygrocybe* s.s. and s.l., differentiating it from the typically interwoven arrangement in *Cuphophyllus*, the divergent trama in *Hygrophorus*, and the pachypodial arrangement in *Chrysomphalina* and *Haasiella* (Norvell et al. 1994) and now *Aeruginospora* (Table 3). The hyphae typically have clamp connections. The basidiospores of *Hygrocybe* s.s. and s.l. are always hyaline, inamyloid, thin-walled, and typically smooth but occasionally with conical warts. While most *Hygrocybe* s.s. and s.l. are terrestrial, often growing in grasslands in Europe and forests in North America and the tropics, a few tropical species are now known to be arboreal (e.g., *H. hapuuae* Desjardin and Hemmes 1997; *H. pseudoadonis* S.A. Cantrell and Lodge 2004; and *H. rosea*, Lodge et al. 2006). Although they appear to be biotrophic based on isotopes, their biotic relationships are enigmatic (Seitzman et al. 2011). *Hygrocybe* have been sequenced from the rhizosphere of plant roots (see Ecology section), which may explain how they obtain plant carbon.

Hygrocybe* subgen. *Hygrocybe [autonym] (1976).

Type species: *Hygrocybe conica* (Schaeff.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871),

≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838) [1836–1838],

≡ *Agaricus conicus* Schaeff., Fung. Bavar. Palat. 4: 2 (1877).

Pileus usually colored red, orange, yellow, green or purple from DOPA based betalain pigments, rarely colorless or fuscous with age or bruising from transformation of DOPA; fibrillose or glutinous partial veils occasionally present; lamellae usually free or narrowly attached, rarely broadly attached by a decurrent tooth; lamellar trama hyphae strictly parallel, usually with tapered ends and exceeding 140 μm (some >1000 μm) in length, unless the basidia and spores are dimorphic; basidia usually 3–5 times the length of their basidiospores, vs >5 times in subg. *Pseudohygrocybe* (Table 3).

Phylogenetic support Subg. *Hygrocybe* is strongly supported as a monophyletic clade in two of our analyses without inclusion of *H. helobia* (100 % MLBS in the Supermatrix, 100 % MLBS and BPP in the 4-gene backbone analyses, Fig. 1 and Online Resource 6), but only weakly supported by analyses of ITS-LSU (53 % MLBS, Fig. 4), and LSU (54 % & 32 % MLBS, Fig. 3 and Online Resource 7). Previous analyses using fewer species found strong support for a monophyletic subg. *Hygrocybe* (100 % MLBS in the multigene analysis by Matheny et al. 2006; 95 % MPBS in the LSU analysis by Moncalvo et al. 2002; 96 % support in the analysis of mostly ITS data by Seitzman et al. 2011). Support for a monophyletic subg. *Hygrocybe* using ITS sequences alone is not significant for the two spp. in Babos et al. (2011), our 24 spp. (37 % MLBS, Online Resource 8) but high for the 18 spp. in Dentinger et al. (unpublished data, 83 % MLBS).

Sections included Type section *Hygrocybe*; includes existing sections *Chlorophanae* and *Microsporae*, and new sections *Pseudofirmae* and *Velosae*.

Comments Our various phylogenetic analyses, as detailed below, reveal six clades or segments of grades of which four are concordant with currently named sections and subsections. These are sect. *Hygrocybe* with subections *Hygrocybe* and *Macrosporae* R. Haller Aar. ex Bon, sect. *Chlorophanae* (Herink) Arnolds ex Candusso, and sect. *Microsporae* Boertm. In addition, we describe two new sections to accommodate monophyletic clades that comprise most of the species with dimorphic spores and basidia, which were previously assigned to sect. *Firmae*. The position of *H. helobia* is unstable among analyses, but it also belongs in subg. *Hygrocybe*.

Hygrocybe* [subgen. *Hygrocybe*] sect. *Hygrocybe. [autonym] (1889).

Type species: *Hygrocybe conica* (Schaeff.) P. Kumm., Führ. Pilzk. (Zwickau): 111 (1871)

≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838) [1836–1838],

≡ *Agaricus conicus* Schaeff., Fung. Bavar. Palat. 4: 2 (1877).

Pileus conical or conico-campanulate; lamellae free or narrowly attached; lamellar trama hyphae parallel, some 200 μm in length, with tapered ends and oblique septa.

Phylogenetic support Sect. *Hygrocybe* support varies from high in our 4-gene backbone analysis (97 % MLBS and 100 % BPP; Fig. 1 and Online Resource 6), ITS-LSU analyses (93 % MLBS and 87 % MPBS including *H. noninquinans* (a replacement name for *H. konradii* var. *antillana*, 55 % MLBS and 87 % MPBS excluding it; Fig. 4) and ITS (77 % MLBS, Online Resource 8) to low in our Supermatrix and *Hygrocybe* LSU and ITS analyses (Fig. 2, Online Resources 8). A previous ITS analysis by Seitzman et al. (2011) shows 96 % MLBS support while the ITS analysis by Babos et al. (2011) shows 83 % neighbor joining (NJ) BS and 79 % MLBS support for sect. *Hygrocybe*.

Subsections included Type sect. *Hygrocybe*; includes subsect. *Macrosporae*.

Hygrocybe* [subg. *Hygrocybe* sect. *Hygrocybe*] subsect. *Hygrocybe [autonym].

[= subsect. "*Nigrescentes*" (Bataille) Arnolds, invalid as the type species of the genus is included (Art. 22.2)].

Type species: *Hygrocybe conica* (Schaeff.) P. Kumm., Für Pilzk. (Zwickau): 111 (1871)

≡ *Hygrophorus conicus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 331 (1838),

≡ *Agaricus conicus* Schaeff., Fung. Bavar. Palat. 4: 2 (1877).

Characters as in sect. *Hygrocybe*; pileus surface sometimes fibrillose. Usually differs from subsect. *Macrosporae* in presence of black staining reactions and fibrillose pileus.

Phylogenetic support This subsection was moderately to highly supported by the various phylogenetic analyses. Support is highest in the Supermatrix (92 % MLBS) and LSU analyses (67 % and 89 % MLBS; Figs. 2 and 3, Online Resource 7), and moderate in our ITS analysis (51 % MBS, Online Resource 8). Dentinger et al. (unpublished data) and Babos et al. (2011) also showmoderate to high support for the *H. conica* species complex (61 % MLBS, respectively and 98 % NJBS) using ITS sequences.

Species included Type species: *Hygrocybe conica* (Schaeff.) P. Kumm. 1871. Species confirmed by molecular phylogenies include *H. conica* varieties, *H. nigrescens* var. *brevispora*, and *H. singeri* (A.H. Sm. & Hesler) Singer. Species placed here based on morphology alone include *H. astatogala* (R. Heim) Heinem., *H. atrosquamosa* Pegler and *H. olivaceonigra* (P.D. Orton) M.M. Moser. The status of other named species is unresolved as this group is in need of revision, including *H. cinereifolia* Court. & Priou, *H. cuspidata* (Peck) Murrill, *H. riparia* Kreisel, *H. conicopalustris* R. Haller Aar., *H. pseudoconica* J.E. Lange and *H. veselsky*i Singer & Kuhtan. *Hygrocybe cortinata* Heinem., described from Africa, closely resembles *H. conica* except for the presence of a cortinoid partial veil, so it likely belongs in subsect. *Hygrocybe*. *Hygrocybe noninquinans* is excluded based on the absence of black staining reactions, a silky-fibrillose pileus surface, and placement at the base of subsect. *Macrosporae* in the Supermatrix analysis; *H. spadicea* may also belong in subsect. *Macrosporae*.

Comments This subsection is often referred to as the staining conica group as all of the confirmed species have blackish staining reactions and a conic or cuspidate pileus, the surface sometimes with coarse fibrils or appressed squamules. *Hygrocybe cuspidata* (Peck) Roody is a blackening species described from eastern North America, but the name has been misapplied to collections from Europe of *H. acutoconica* in the non-staining conica group under the name *H. acutoconica* var. *cuspidata* (Peck) Arnolds (1985a) (see Boertmann 2010). The Japanese *H. conica* sequences comprise a distinct clade in our ITS analysis (88 % MLBS). The type species, *H. conica*, has micromorphology that is typical of subg. *Hygrocybe* including parallel lamellar trama hyphae that are long and tapered at the ends with oblique septa (Fig. 5). The longest hyphae are rare and are best viewed by teasing the trama hyphae apart in smash mounts.

Hygrocybe* [subg. *Hygrocybe* sect. *Hygrocybe*] subsect. *Macrosporae R. Haller Aar. ex Bon, Doc. Mycol. 24(6): 42 (1976).

Type species: *Hygrocybe acutoconica* (Clem.) Singer (1951) [as *H. acuticonica* Clem.]

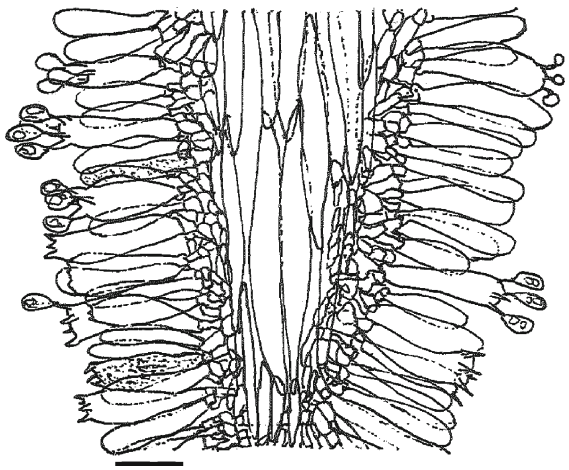


Fig. 5 *Hygrocybe* (subg. *Hygrocybe*) sect. *Hygrocybe*. *Hygrocybe conica* lamellar cross section (DJL05TN89). Scale bar=20 μm

≡ *Mycena acutoconica* Clem., Bot. Surv. Nebraska 2: 38 (1893),

= *Hygrocybe persistens* (Britzelm.) Singer (1940),

≡ *Hygrophorus conicus* var. *persistens* Britzelm. (1890)].

Characters of sect. *Hygrocybe*; lacking dark staining reactions, though the stipe base may slowly stain gray; surface usually radially fibrillose-silky and viscid or glutinous but some with dry surface even when young; some spore lengths exceed 10 μm. Differs from subsect. *Hygrocybe* in absence of dark staining reaction and often a smoother pileus surface texture.

Phylogenetic support Strong support for subsect. *Macrosporae* is shown in our ITS analysis (99 % MLBS, with 77 % support as the sister clade to subsect. *Hygrocybe*; Online Resource 8). Support for this subsection in our other analyses varies depending on whether species in the basal part of the grade are included or excluded. The *Hygrocybe acutoconica* complex, including *H. acutoconica* (Clem.) Singer var. *acutoconica*, collections of this variety from Europe previously referred to as *H. persistens* (Britzelm.) Singer, and *H. acutoconica* f. *japonica* Hongo, form a strongly supported clade (99 % ML and 100 % MPBS in the ITS-LSU; 99 % MLBS in the ITS), but with weaker support in the Supermatrix analysis (63 % MLBS). Placement of *H. spadicea* is ambiguous, with strongest support for inclusion in subsect. *Macrosporae* using ITS (99 % MLBS), ambiguous placement using LSU (Fig. 3 and Online Resource 7) and basal to both subsect. *Hygrocybe* and *Macrosporae* in the Supermatrix analysis (Fig. 2). Similarly, both Babos et al. (2011) and Dentinger et al. (unpublished data) show ambiguous placement of *H. spadicea* lacking significant BS support. In our ITS analysis, *H. noninquinans* is basal to both subsections (69 % ML BS) making subsect. *Macrosporae* paraphyletic if included. Similarly, including *H. noninquinans* makes subsect. *Macrosporae* paraphyletic in our ITS-LSU analysis as a species in the staining conica group (subsect. *Hygrocybe*) falls between *H. noninquinans* and other non-staining spp. with high BS support. The 4-gene backbone analysis places *H. noninquinans* with *H.* aff. *conica* in sect. *Hygrocybe* with high support (97 % ML, 1.0 BPP), while the Supermatrix places it as a basal member in sect. *Macrosporae* but with low support (Supermatrix, 24 % MLBS). In an ITS analysis by Dentinger et al. (unpublished data), however, *H. noninquinans* (as *H. konradii* var. *antillana*) is basal to subsect. *Conica* with low support as part of a paraphyletic grade corresponding to subsect. *Macrosporae*. *Hygrocybe subpapillata* is unplaced in our ITS analysis, but is basal to spp. in sect. *Pseudofirmae* and sect. *Macrosporae* in an ITS analysis by Dentinger et al. (unpublished data).

Species included Type species: *H. acutoconica*. All of the varieties of *H. acutoconica* are included. *Hygrocybe persistens* (Britzelm.) Singer is currently considered a synonym of *H. acutoconica* (Boertmann 2010; Cantrell and Lodge 2000), as is *H. subglobispora* P.D. Orton (Boertmann 2010). *Hygrocybe spadicea* P. Karst. is tentatively included based on high support in our ITS analysis, though support for inclusion is weak or ambiguous in our other analyses and Dentinger et al.' (unpublished) ITS analysis, and the fibrillose pileus surface which fits better in subsect. *Hygrocybe*. *Hygrocybe noninquinans* is included based on its similarities to *H. acutoconica* var. *konradii*, and its placement basal to other species of sect. *Macrosporeae* in our Supermatrix analysis. *Hygrocybe zuluensis* Boertmann is included based on morphology.

Comments This subsection is often referred to as the non-staining conica group. Boertmann (2010) regards *H. konradii* as a wide-spored variety of *H. acutoconica*. The ITS analysis by Dentinger et al. (unpublished), however, suggests that while there are wide-spored collections embedded in the *H. acutoconica* clade, there is also a well-supported sister clade to *H. acutoconica* comprised of *H. konradii* s.s. collections (100 % support for the clade, 77 % MLBS support as sister to *H. acutoconica* var. *acutoconica*). *Hygrocybe noninquinans* was described as *H. konradii* var. *antillana*, but it is raised here to species rank based on phylogenetic analyses that place it apart from *H. konradii*. The name *H. antillana* was occupied, so a new name is provided.

Hygrocybe noninquinans Lodge & S.A. Cantrell, nom. nov., stat. nov.

MycoBank MB804045.

Replaced synonym: *Hygrocybe konradii* var. *antillana* Lodge & Cantrell, Mycol. Res. 104(7): 877–878 (2000).

Type: PUERTO RICO, Mun. Río Grande, El Yunque National Forest (Caribbean National Forest), Caimitillo Trail, 16 Jun 1997, CFMR-PR 4555, CFMR.

Hygrocybe* [subg. *Hygrocybe*] sect. *Velosae Lodge, Ovrebo & Padamsee, sect. nov.

MycoBank MB804047.

Type species: *Hygrophorus hypohaemactus* Corner, Trans. Br. Mycol. Soc. 20(2): 180, Figs. 5, 6, 8a (1936)

≡ *Hygrocybe hypohaemacta* (Corner) Pegler & Fiard, *Kew Bull.* 32(2): 299 (1978).

Pileus and stipe red or pink, covered in a thin to thick glutinous layer, glutinous layer of pileus and stipe surface connected, rupturing when pileus expands leaving an appendiculate gelatinous margin on the pileus and sometimes leaving a glutinous annulus on the stipe, resembling a peronate veil but the glutinous layer not separated from the pileus or stipe surface hyphae by a differentiated layer; lamellar trama hyphae fusiform, with tapered ends and oblique septa, some exceeding 140 μm in length; lamellar edge with pseudocystidia originating in the context, swollen, containing

many vacuoles with oleaginous contents, sometimes with glutinous coating, simple or branched, projecting from the lamellar margin where they intertwine with similar but less vacuolated structures emanating from the stipe apex above the glutinous zone, these structures forming an arachnoid connection between the lamellae and stipe; sometimes hyphal strands connecting the pileus margin and stipe leave a fibrillose layer above the glutinous annulus; annulus sometimes obscure; basidia and spores dimorphic: macrobasidia clavate or somewhat capitate-stipitate, 4-sterigmate, with oleaginous contents and basal clamp connection; microbasidia clavate; basidiospores globose, subglobose to broadly ellipsoid.

Etymology Velo-veil, referring to the fibrillose and glutinous partial veil.

Phylogenetic support Our Supermatrix (Fig. 2) and *Hygrocybe* LSU analyses (Online Resource 7) place *H. roseopallida* in the same clade with *H. hypohaemacta* and *H.* aff. *hypohaemacta* from the neotropics, but with low bootstrap values. Lodge and Ovrebo (2008) show stronger support (76 % MLBS) for a monophyletic *H. roseopallida* – *H. hypohaemacta* clade using ITS and LSU sequences; its inclusion in sect. *Pseudofirmae* has low support (53 %). In the 4-gene backbone analysis there is 100 % MLBS (0.9 B.P. support for placing the *H. hypohaemacta* clade apart from the *Pseudofirmae* clade (*H. appalachianensis)*. In both the ML and Bayesian backbone analyses, *H. hypohaemacta* (sect. *Velosae*) falls between. sect. *Hygrocybe* on one side. and *H. glutinipes* (sect. *Chlorophanae*) and sect. *Pseudofirmae* on the other side. The ITS-LSU analysis (Fig. 4) has a well-supported sect. *Pseudofirmae* clade (96 % MLBS, 93 % MPBS) that excludes *H. hypohaemacta*; instead, *H. hypohaemacta* appears basal to sect. *Chlorophanae*. The Supermatrix analysis has high support for paleotropical *H. hypohaemacta* (LSU only) and neotropical *H.* afn *hypohaemacta* as sister species (77 %) but Dentinger (personal comm.) shows higher support (99 % MLBS) in an LSU analysis. Our *Hygrocybe* LSU analysis has moderate support (62 % MLBS; Online Resource 7) for placing *H.* aff. *hypohaemacta* and *H. hypohaemacta* together. In our 4-gene backbone analyses (Fig. 1 and Online Resource 6) and our ITS analysis, *H. hypohaemacta* appears in a grade with *H. glutinipes*, but *H. glutinipes* is included in sect. *Chlorophana* in our Supermatrix analysis, far from *H. hypohaemacta*.

Species included Type species: *Hygrocybe hypohaemacta*. Inclusion of two neotropical species, *H.* aff. *hypohaemacta* and *H. roseopallida* Ovrebo & Lodge, is phylogenetically and morphologically supported.

Comments Singer (1986) placed *H. hypohaemacta* in subg. *Hygrocybe* owing to the regular lamellar trama composed of long, fusiform elements – a placement confirmed by our molecular phylogenies. Others, including Pegler and Fiard (1978) and Lodge and Pegler (1990) placed *H. hypohaemacta* in subg. *Pseudohygrocybe* sect. *Firmae*, though Cantrell and Lodge (2004) noted the resemblance of trama structure to subg. *Hygrocybe* and suggested that molecular phylogenies were needed to resolve placement. Neotropical collections identified as *H. hypohaemacta* will need a new name as the spores differ somewhat in shape and size and the LSU sequences diverge by 12.6 % from the SE Asian sequence. *Hygrocybe roseopallida* is included in sect. *Velosae* based on moderate molecular support and shared characters, i.e., subglobose to broadly ellipsoid macro- and microspores, a glutinous peronate pseudoveil, cortinoid connections between the lamellar edge and stipe apex partly formed by vacuolated pseudocystidia emanating from the lamellar edge (Lodge and Ovrebo 2008). Although Corner (1936) stated that the glutinous layer of the pileus margin was not connected to the stipe in *H. hypohaemacta*, a projecting glutinous margin is visible on the pileus, a vague glutinous annulus is visible in photos of the *H. hypohaemacta* collection from Malaysia that was sequenced, and a glutinous annulus can be seen in a photo of *H.* aff. *hypohaemacta* from Puerto Rico (Fig. 25 insert). Pseudocystidia emanating from the lamellar edge in both *H.* aff. *hypohaemacta* and *H. roseopallida* that form the inner fibrous portion of the veil are shown in Fig. 6. Inner fibrous and outer glutinous veil elements were clearly visible in the type and other collections of *H. roseopallida* (Lodge and Ovrebo 2008).

Hygrocybe* [subg. *Hygrocybe*] sect. *Pseudofirmae Lodge, Padamsee & S.A. Cantrell, sect. nov.

MycoBank MB804048.

Type species: *Hygrophorus appalachianensis* Hesl. & A.H. Sm. North American Species of *Hygrophorus*: 147 (1963),

≡ *Hygrocybe appalachianensis* (Hesl. & A.H. Sm.) Kronaw. (as '*appalachiensis*'), in Kronawitter & Bresinsky, Regensb. Mykol. Schr. 8: 58 (1998).

Pileus usually viscid or glutinous, often perforated in the center. Basidiospores and basidia dimorphic; ratio of macrobasidia to macrospore length usually <5, macrobasidia expanded in upper part, typically broadly clavate or clavate-stipitate; lamellar trama hyphae parallel, long or short, with or without oblique septa; pileipellis a cutis, disrupted cutis or trichoderm, overlain by a thin to thick ixocutis which if ephemeral then leaves a thin patchy gelatinous coating on the cuticular hyphae.

Etymology Pseudo = false, firmae – referring to sect. *Firmae.*

Phylogenetic support Support for a monophyletic sect. *Pseudofirmae,* including *H. rosea*, is strongest in the ITS-

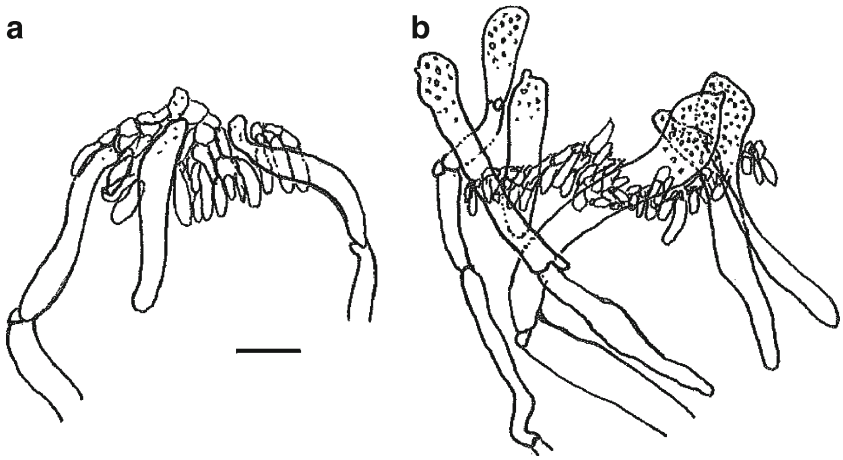


Fig. 6 *Hygrocybe* (subg. *Hygrocybe*) sect. *Velosae*. Pseudocystidia emanating from the lamellar edge, which contributes to an inner, fibrous pseudoveil: **a**. *Hygrocybe* aff. *hypohaemacta* (BZ-1903); **b**. *Hygrocbe roseopallida* (type). Scale bar=20 μm

LSU analysis (96 % MLBS and 93 % MPBS; Fig. 4). ITS support is high (94 % MLBS, not shown) for the clade comprising *H. appalachianensis, H. chloochlora*, *H.* aff. *chloochlora* and *H.* aff. *prieta*, but declines to 42 % MLBS if *H. rosea* is included; *H. occidentalis*, *H.* cf. *neofirma* and *H. trinitensis* are placed in a neighboring clade with low support. A similar paraphyletic grade topology is shown in our ITS analysis (Online Resource 8), but our *Hygrocybe* LSU (Online Resource 7) shows *Pseudofirmae* as monophyletic. Similarly, an LSU analysis by Dentinger (pers. com.) shows sect. *Pseudofirmae* as a single clade comprised of *H. appalachianensis*, *H. occidentalis* and *H. rosea*, but with high support (94 % MLBS). Our Supermatrix analysis also has high support for the *Pseudofirmae* clade (96 % MLBS; Fig. 2), but the type of sect. *Microsporae* (*Hygrocybe* aff. *citrinovirens*) is embedded close to the base, possibly from long-branch attraction though the ITS analysis by Dentinger et al. (unpublished) also shows the same topology; *H. rosea* is not included in Dentinger et al.'s ITS and LSU analyses.

Species included Type species: *Hygrocybe appalachianensis* (Hesler & A.H. Sm.) Kronaw. *Hygrocybe chloochlora, H. occidentalis*, *H.* cf. *neofirma* (MCA-1721), *H.* aff. *neofirma* (BZ-1926), *H.* aff. *prieta, H. rosea* and *H. trinitensis* (Dennis) Pegler are included here based on both molecular and micromorphological data. The following species are included based on macrobasidia morphology: *H. amazonensis* Singer, *H. brunneosquamosa* Lodge & S.A. Cantrell, *H. campinaranae* Singer, *H. chamaeleon* (Cibula) D.P. Lewis & Ovrebo, *H. cheilocystidiata* Courtec., *H. cinereofirma* Lodge, S.A. Cantrell & T.J. Baroni, *H. earlei* (Murrill) Pegler, *H. flavocampanulata* S.A. Cantrell & Lodge, *H. guyanensis Courtec., H. helvolofirma* Pegler, *H. hondurensis* Murrill, *H. laboyi* S.A. Cantrell & Lodge, *H. lutea* (Beeli) Heinem., *H. megistospora* Singer, *H. miniatofirma* S.A. Cantrell & Lodge, *H. mississippiensis* D.P. Lewis & Ovrebo, *H. naranjana* Pegler, *H. neofirma* Lodge & S.A. Cantrell, *H. nouraguensis* Courtec., *H. olivaceofirma* Lodge, S.A. Cantrell & Nieves-Riv. and *Hygrophorus alutaceus* Berk. & Broome.

Comments Species in sect. *Pseudofirmae,* such as *H. appalachianensis,* often have staggered development of the macro- and microbasidia. The holotype of *H. appalachianensis* was not fully mature, and the description of basidia was only for microbasidia while the immature macrobasidia were described as pleurocystidia. There were mature macrobasidia in the holotype on the lamellae close to the juncture of the stipe and pileus, which accounts for the macrospores that were described; the microspores, however, were present but ignored.

Hygrocybe rosea was found upon re-examination to have weakly dimorphic basidia and spores, consistent with phylogenetic placement as a basal species in sect. *Pseudofirmae*. Macrobasidia in all of the species in the *H. appalachianensis* clade are clavate-stipitate (Fig. 7) while those in the *H. occidentalis–H. neofirma* clade are clavate and expand gradually toward the apex (Fig. 8), so they might eventually be accorded status of subsections in *Pseudofirmae*. Macrobasidia of sect. *Pseudofirmae* are clavate or clavate-stipitate whereas those of *H. firma,* which is now placed in subg. *Pseudohygrocybe*, are cylindric to narrowly clavate. Furthermore, the ratio of macrobasidia to macrospore length is generally less than 5 in *Pseudofirmae*, as typical of subg. *Hygrocybe*, and exceeds 5 in *H. firma*, typical of subg. *Pseudohygrocybe*. Further revision of sect. *Pseudofirmae* with greater taxon sampling for molecular analyses is needed. *Hygrophorus alutaceus* was erroneously listed as a synonym of *Hygrocybe firma* by Pegler (1986) because it bears the same collection number (Petch 880) as the type of *H. firma,* but the diagnoses described the pileus as glabrous in *H. alutaceus* whereas the pileus of *H. firma* was described as tomentose. Annotation of the type of *H. alutaceus* by DJL and SAC shows the macrobasidia are broadly clavate (39–46×10.7–18 μm) and the pileipellis is a repent ixocutis, unlike

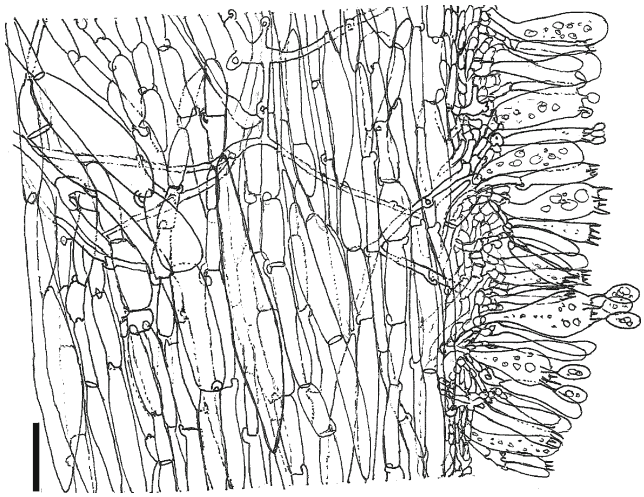


Fig. 7 *Hygrocybe* (subg. *Hygrocybe*) sect. *Pseudofirmae*. *Hygrocybe appalachianensis* lamellar cross section, showing macrobasidia rooted more deeply in the hymenium than the microbasidia (Roody, DMWV00-953). Scale bar=20 μm

the type of *H. firma* with narrowly clavate macrobasidia of (36–60×6.4–7.2 μm), and a disrupted cutis transitioning to a trichodermium that is lacking gelatinization.

Hygrocybe* [subg. *Hygrocybe*] sect. *Microsporae Boertm., The genus *Hygrocybe*. Fungi of Northern Europe (Greve) 1: 16 (1995).

Type species: *Hygrocybe citrinovirens* (J.E. Lange) Jul. Schäff., Ber. bayer. bot. Ges. 27: 222 (1947) [≡ *Camarophyllus citrinovirens* J.E. Lange, Dansk Botanisk Arkiv 4(4): 20 (1923)].

Pileus conical or conico-campanulate, surface dry and appressed tomentose, squamulose or loosely fibrillose, red, orange or yellow; basidiospores mostly less than 10 μm long; pileipellis a trichoderm at least in the center.

Phylogenetic support Support for a monophyletic sect. *Microsporae* (*H. citrinovirens, H. intermedia* and an *H. intermedia*-like collection from Tennessee labeled *H.* aff. *citrinovirens*) is strong in our ITS analysis (73 % MLBS, Online Resource 8). These species plus *H. helobia* appear as a paraphyletic grade in the ITS analysis by Dentinger et al. (unpublished data). Support for placing *H. helobia* in subg. *Hygrocybe* using ITS sequences is strong in Dentinger et al. (unpublished), weak in our analysis (Online Resource 8), its position is unstable among analyses and it has decurrent rather than adnexed to free lamellae, so we leave it unplaced.

Species included Type species: *H. citrinovirens*. *Hygrocybe intermedia* and *H.* aff. *citrinovirens* from Tennessee are included based on molecular and morphological data and *H. virescens* (Hesler & A.H. Smith) Montoya & Bandala is included based on morphological data.

Comments Though some spores in *H. intermedia* are up to 13 μm long, most are less than 10 μm long, the pileipellis is similar to that of the type, and phylogenetic support for the clade is strong so it is included here. *Hygrocybe* aff. *citrinovirens* differs from *H. intermedia* only in having a smooth instead of a fibrillose stipe, but ITS sequences places it closer to *H. citrinovirens*.

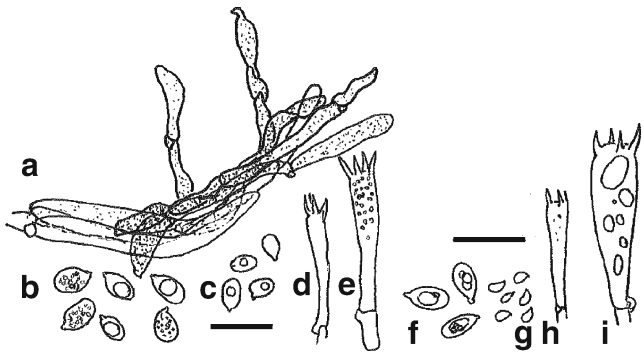


Fig. 8 *Hygrocybe* (subg. *Hygrocybe*) sect. *Pseudofirmae*. *Hygrocybe neofirma* (M.C. Aime, Guyana): **a**. pileipellis; **b**. macrospores; **c**. microspores; **d**. microbasidium; **e**. macrobasidium. *Hygrocybe occidentalis* (E. Cancerel, Puerto Rico): **f**. macrospores; **g**. microspores; **h**. microbasidium; **i**. macrobasidium. Scale bar=20 μm

Hygrocybe* [subg. *Hygrocybe*] sect. *Chlorophanae (Herink) Arnolds ex Candusso, *Hygrophorus*. Fungi europ. (Alassio) 6: 464 (1997),

= *Godfrinia* R. Maire em. Herink, sect. *Ceraceae* Herink, subsect. *Chlorophaninae* Herink, Acta. Mus. Bot. Sept. Lib. 1: 66 (1959).

Type species: *Hygrocybe chlorophana* (Fr. : Fr.) Wünsche, Die Pilze: 112 (1877)

≡ *Agaricus chlorophanus* Fr. : Fr., Syst. mycol. (Lundae) 1: 103 (1821).

Pileus viscid or glutinous, red, orange or yellow, stipe viscid or not, hymenophoral trama hyphae parallel, exceeding 200 μm in length, with tapered ends and oblique septa; pileipellis an ixocutis or ixotrichodermium.

Phylogenetic support Support for the *H. chlorophana* – *H. flavescens* clade is strong in the Supermatrix, ITS and LSU analyses (100 % MLBS; Figs. 2 and 3). The 4-gene analyses place *H. chlorophana* as sister to the clade containing *H. hypohaemacta* (100 % MLBS and 1.0 BPP). *Hygrocybe glutinipes* appears as part of a grade near *H. chlorophana* in the Supermatrix, one of our LSU analyses (Fig. 3) and ours and Dentinger et al.'s (unpublished) ITS analyses with varying levels of support. Lodge and Ovrebo (2008) found different topologies for placing *H. glutinipes* with or apart from *H. chlorophana*, and bootstrap support for the two together of <50 % up to 86 %.

Species included Type species: *H. chlorophana*. Possibly *H. flavescens*, if distinct from *H. chlorophana*; placement of *H. glutinipes* is ambiguous but it is tentatively included.

Comments *Hygrocybe flavescens* (Kauffman) Singer was described from Michigan, and may be a distinct species, especially if it corresponds to the eastern North American clade labeled *H. flavescens*. In fact, one of the soil clones from Michigan (GU174284) matched the ITS sequences of specimens identified as *H. flavescens*. *Hygrocybe flavescens* is said to have a viscid stipe whereas *H. chlorophana* has a moist or dry stipe, but this character is not always reliable. A hybrid ITS sequence was found in a collection with a viscid stipe from the Great Smoky Mountain National Park despite a 9–12 % divergence in ITS sequences between the two clades (Hughes et al. 2010; in press). *Hygrocybe glutinipes* may be part of a grade within subg. *Hygrocybe* near *H. chlorophana* but is unstable in its position; it could be retained in sect. *Chlorophanae* based on morphology.

Species unplaced in subgen. *Hygrocybe*.

Hygrocybe glutinipes appears in a grade near *H. hypohaemacta* in the 4-gene backbone analyses, suggesting a relationship with sect. *Velosae*. Unlike spp. in sect. *Velosae, H. glutinipes* lacks a partial veil and has spores that are narrow and strangulated, so we regard it as unplaced.

Hygrocybe helobia resembles species in subg. *Pseudohygrocybe*, sect. *Squamulosae*, except that the long lamellar trama hyphae exceeding 400 μm indicate placement in subg. *Hygrocybe* (Boertmann 1995, 2010). Support for placing *H. helobia* in subg. *Hygrocybe* is strong in the ITS analysis by Dentinger et al., confirming Boertmann's placement (1995, 2010). The position of *H. helobia* is unstable, however. Our ITS analysis places *H. helobia* as sister to sect. *Microsporae,* Dentinger et al.'s (unpublished) places it sister to *H. intermedia* and near *H. citrinovirens*, whereas our Supermatrix and LSU analyses place it with high support (90 %–100 % ML BS) in the *H. miniata* clade in subg. *Pseudohygrocybe*. The *H. helobia* clade appears to be a species complex that is strongly supported in our ITS analysis (91 % MLBS, Online Resource 8) as well as in the ITS analysis by Dentinger et al. (unpublished, 100 % MLBS).

Hygrocybe* subgen. *Pseudohygrocybe Bon, Doc. Mycol. 6 (24): 42 (1976).

Type species: *Hygrocybe coccinea* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 330 (1838) [1836–1838],

≡ *Agaricus coccineus* Schaeff. Fung. Bavar. Palat. 4: 70 (1774),

≡ *Pseudohygrocybe coccinea* (Schaeff.: Fr.) Kovalenko (1988).

[NOT *Agaricus coccineus* Scop., Fl. carniol., (Wein) Edn. 2: 436 (1772), an earlier homonym of a sanctioned name]

Lamellar trama typically subregular, hyphal elements generally <140 μm long, frequently <80 μm long, mostly with right-angled septations. Basidia and spores mostly monomorphic in size in one section and dimorphic in length in the other section, spore walls hyaline, usually smooth, rarely with spines; mean ratio of basidiospore to basidia length usually >5. Basidiomes typically with bright DOPA based pigments, rarely colorless or with browning reactions from conversion of DOPA pigments.

Phylogenetic support Subg. *Pseudohygrocybe* appears as a paraphyletic grade with the monophyletic subg. *Hygrocybe* clade on a long branch in our 4-gene backbone, Supermatrix, ITS-LSU analysis and ours and Seitzman et al.'s (2011) ITS analyses. Our LSU analysis of tribe *Hygrocybeae* (not shown), however, has strong support (87 % MLBS) for subg. *Pseudohygrocybe* as sister to subg. *Hygrocybe*. Similarly strong support for a monophyletic *Pseudohygrocybe* as sister to subg. *Hygrocybe* was previously found in a multigene Supermatrix analysis by Matheny et al. (2006, 100 % MLBS, 1.0 BPP). While the same sister-clade topology appears in our full LSU and our *Hygrocybe* LSU analyses, as well as in an LSU analysis by Moncalvo et al. (2002) and an ITS analysis by Babos et al. (2011), bootstrap support is lacking in those analyses.

Sections included *Coccineae* and *Firmae*.

Comments The basionym of the type species, *H. coccinea*, has sometimes been confused with *Agaricus coccineus* Scop. (a diminutive species of *Mycena*), which is an earlier homonym of a conserved name. In pers. comm. from S. Pennycook (13 Apr 2012), he explained: "In the sanctioning work (p. 105), Fries referred (indirectly) the name to "Pers Obs. Myc. 2. p. 49. Syn. 334. Wulf. In Jacq. Coll. 2. p. 106. [etc.]". Wulfen is the earliest of the numerous references. However, Wulfen (Misc. Austriac. 2: 106. 1781) explicitly referred the name to Schaeffer, and so did Persoon (Syn. Meth. Fung.: 334. 1801). In the 1821 volume index (p. 508), Fries cited the name as "coccineus Wulf."; and in Syst. Mycol. Index Alphabeticus (1832, p. 13; also part of the sanctioning works) he cited the sanctioned *A. coccineus* as "Wulf. Pers." (along with four unsanctioned *A. coccineus* homonyms), but in Epicrisis (1838, p. 330) and Hymen. Eur. (1874, pp. 417–418), he made the indirect reference explicit, citing the basionym of *Hygrophorus coccineus* as *Agaricus coccineus* Shaeff. [Fung. Bavar. Palat. Nasc. 4: 70. 1774]."

Hygrocybe species in subg. *Pseudeudohygrocybe* typically differ from those in subg. *Hygrocybe* in having relatively short lamellar trama hyphae with right-angled septa and long basidia relative to spore length (Fig. 9). Currently, subg. *Pseudohygrocybe* s.s. has one widely recognized section – *Coccineae,* while sect. *Firmae* Heinem. with dimorphic spores and basidia has been recognized by some tropical agaricologists (Cantrell and Lodge 2001, Courtecuisse 1989, Heim 1967, Pegler 1983), but not others (Horak 1971, Singer 1986, Young 2005). Our *Hygrocybe* LSU analysis (Online Resource 7) strongly recovers a sister relationship with subg.

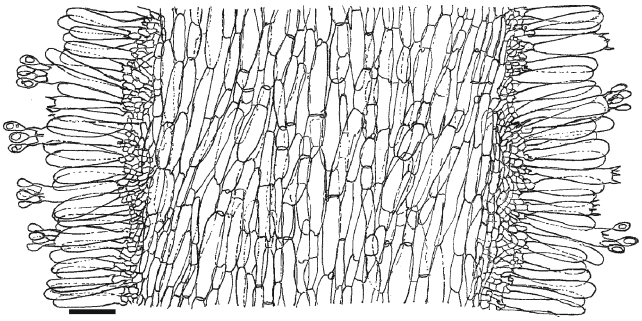


Fig. 9 *Hygrocybe* (subg. *Pseudohygrocybe*) sect. *Coccineae*, *Hygrocybe purpureofolia* lamellar cross section (NC-64, DJL05NC64). Scale bar=20 μm

Hygrocybe, albeit without bootstrap support. Though *H. miniata* is universally regarded as belonging to the same section as *H. coccinea* (i.e., in sect. *Coccineae*), our LSU analysis of tribe *Hygrocybeae* instead places *H. miniata* in a strongly supported clade that is sister to sect. *Firmae* s.s. (100 % MLBS). We have retained sect. *Firmae* and leave the unnamed *H. miniata* clade unplaced. The remaining former sections of subg. *Pseudohygrocybe* are treated here as segregate genera. The genus *Hygroaster* could be reduced to a subgenus or to section rank in subg. *Pseudohygrocybe* to keep the genus *Hygrocybe* s.l. monophyletic (i.e., including the segregate genera *Hygroaster*, *Neohygrocybe, Humidicutis, Gliophorus, Porpolomopsis* and *Chromosera* in *Hygrocybe*). Sect. *Coccineae* s.s. currently has three subsections: *Puniceae*, *Siccae* and *Squamulosae*. Additional sections and subsections will likely be named in *Hygrocybe* subg. *Pseudohygrocybe* with further sampling of gene regions and taxa.

Hygrocybe* sect. *Coccineae Fayod, Proc. Hist. Nat. Agar. Ann. Scient. Nat. 7(9): 309 (1889).

Lectotype species: *Hygrocybe coccinea* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 330 (1838) [1836–1838], designated by Singer (1951) [1949],

≡ *Agaricus coccineus* Schaeff. Fung. Bavar. Palat. 4: 70 (1774),

≡ *Pseudohygrocybe coccinea* (Schaeff.: Fr.) Kovalenko (1988)].

[= *Hygrocybe* sect. *Puniceae* Fayod (1889), superfluous, illegit.],

[= *Hygrocybe* sect. "*Inopodes*" Singer (1943), nom. invalid].

Characters as in subg. *Pseudohygrocybe* except basidia and spores always monomorphic.

Phylogenetic support There are too few species in our 4-gene backbone analyses to draw conclusions regarding subg. *Pseudohygrocybe* sections. The ITS-LSU analysis shows strong (91 % MLBS) support for a branch connecting subsects. *Coccineae* and *Siccae,* while subsect. *Squamulosae* appears as a separate clade. The grade in our Supermatrix analysis has a branch with low support (44 % MLBS) subtending subsects. *Coccineae* and *Siccae*, while subsect. *Squamulosae* is basal (60 % MLBS). Our *Hygrocybe* LSU analysis (Online Resource 7) shows sect. *Coccineae* as a grade with strong support for subsect. *Squamulosae* (97 % MLBS).

Subsections included There are currently three validly named subsections in sect. *Coccineae*, namely *Coccineae, Siccae* and *Squamulosae*.

Comments Both *Hygrocybe* sects *Coccineae* and *Puniceae* were first validly published by Fayod (1889) in the same publication. Singer [(1949) 1951, p. 152] recognized that the type species of these two sections, *H. coccinea* and *H. punicea*, belonged in the same section, and between the two competing names he selected *Coccineae* over *Puniceae*. Thus sect. *Coccineae* is the correct name for this group. Previously, Singer (1943) had erected sect. "*Inopodes*", nom. invalid, which contained *H. punicea* (lacking a Latin description, Art. 36.1).

Hygrocybe* [subg. *Pseudohygrocybe* sect. *Coccinea*] subsect. *Coccineae (Bataille) Singer, Agar. Mod. Tax., Lilloa 22: 152 (1951)[1949].

[= *Hygrocybe* subsect. *Puniceae* (Fayod) Arnolds ex Candusso (1997), superfluous, illeg. = *Hygrocybe* subsect. "*Inopodes*" Singer (1952), nom. invalid].

Type species: *Hygrocybe coccinea* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 330 (1838) [1836–1838]] [≡ *Agaricus coccineus* Schaeff. Fung. Bavar. Palat. 4: 70 (1774), ≡ *Pseudohygrocybe coccinea* (Schaeff.: Fr.) Kovalenko (1988)].

Pileus brightly colored, lubricous or viscid at least when young. Lamellae broadly adnate or slightly sinuate, sometimes with a decurrent tooth. Basidiospores usually narrow (mean Q 1.5–2.4), often constricted; mean ratio of basidia to basidiospore length >5. Pileipellis a persistent or ephemeral ixocutis or mixed ixocutis-ixotrichodermium with narrow hyphae (2–5 μm wide) embedded in gel over hyphae of moderate diameter (6–12 μm wide). Chains of ellipsoid to subglobose hyphal elements generally absent from the hypodermium.

Phylogenetic support Our ITS-LSU analysis strongly supports subsect. *Coccineae* as a monophyletic clade comprising *H. coccinea* and *H. punicea* (100 % MLBS, Fig. 4). Our Supermatrix strongly supports subsect. *Coccineae* (*H. coccinea, H. punicea* and *H. purpureofolia*) if *H. mucronella* is excluded (84 % MLBS), but support drops to 46 % MLBS if the *H. mucronella* complex is included. Our large LSU analysis has 100 % MLBS support for a monophyletic clade comprising the *H. coccinea* species complex, our LSU analysis of tribe *Hygrocybeae* has modest support (50 % ML BS)

for a clade comprising *H. coccinea, H. punicea* and *H. purpureofolia*, and our ITS analysis has only weak support for the subsect. *Coccineae* clade. Support for including *H. ceracea* and *H. constrictospora* in *Coccineae* is low in the Supermatrix analysis (44 % MLBS), absent in our LSU analysis of tribe *Hygrocybeae* (Online Resource 7) and absent in ITS analyses (ours and Dentinger et al., unpublished data). Dentinger et al. (unpublished data) shows moderate support (61 % MLBS) for a clade comprising *H. coccinea, H. punicea* and *H. splendidissima*.

Species included Type: *Hygrocybe coccinea*. *Hygrocybe punicea* and *H. purpureofolia* are included in subsect. *Coccineae* based on molecular and morphological data. *H. aurantiosplendens* is similar to species in sect. *Coccineae*, and an ITS analysis by Dentinger et al. (unpublished data) places this species near *H. coccinea*, so we include it in subsect. *Coccineae*. There is some molecular support for including *H. splendidissima,* but we exclude it based on the dry pileus surface, narrowly attached lamellae and broader spores, which are all deviating characters. *Hygrocybe ceracea, H. constrictospora, H. insipida, H. miniata, H. mucronella, H. salicis-herbaceae* and *H. subminutula* are tentatively excluded, though the morphology of *H. salicis-herbaceae* matches the diagnosis of *H.* subsect. *Coccineae*.

Comments In 1943 Singer erected *Hygrocybe* subsect. "*Inopodes*", nom. invalid, then reduced the rank to subsect. in 1951 (1949) and designated *H. punicea* as the type species. The name is invalid because neither it nor its basionym had a Latin description (Art. 36.1). Thus subsect. *Coccineae* (Bataille) Singer (1951) is the only validly published subsection name for this group in *Hygrocybe*. The type of *H.* subsect. *Puniceae* (Fayod) Arnolds ex Candusso (1997) falls into this subsection, making it superfluous, thus a nom. illegitimate.

Boertmann (1995, 2010) included *H. aurantiosplendens, H. ceracea, H. insipida, H. punicea* and *H. salicis-herbacea* in subsect. *Coccineae*. Only *H. ceracea, H. coccinea* and *H. punicea* are included in our Supermatrix analysis, which provides only weak support for them as comprising the same clade with *H. constrictospora, H. purpureofolia, H. subminutula* and *H. mucronella*. All of these species, however, share the diagnostic characters of subsect. *Coccineae*. Arnolds (1986a), however, placed *H. constrictospora* in subsect. *Squamulosae* instead of subsect. *Coccineae* based on pileipellis structure. Our Supermatrix and ITS analyses (< 50 % ML BS support), and the ITS analysis by Dentinger et al. (7 % MLBS) place *H. mucronella* near *H. ceracea* and *H. insipida* (plus *H. quieta* and *H. salicis-herbacea* in Dentinger et al., unpublished). Kovalenko (1989), Arnolds (1990) and Bon (1990) regarded *H. insipida* as closely related to *H. mucronella*, but Boertmann thought it was related to *H. coccinea* and *H. ceracea.* If all these species belong to the same group, then all are in agreement. Alternatively, *H. mucronella*, *H. ceracea, H. insipida* and *H. subminutula* may be best regarded as unplaced (see Online Resource 8). Although our Supermatrix analysis weakly supports (61 % MLBS) inclusion of *H. reidii* as basal in the *H. ceracea – H. constrictospora* clade, *H. reidii* differs in having a dry pileipellis with a mixture of vertical and horizontal elements, and is the type of subsect. *Siccae* (see below).

Hygrocybe* [subg. *Pseudohygrocybe* sect. *Coccineae*] subsect. *Siccae Boertm., The genus *Hygrocybe*, Fungi of Northern Europe (Greve) 1:15 (1995).

Type species: *Hygrocybe reidii* Kühner, Bull. trimest. Soc. mycol. Fr. 92: 463 (1976).

Pileus smooth, matt, dry or slightly greasy when young from an ephemeral ixicutis. Stipe dry and smooth. Pileipellis hyphae of intermediate diameter (3–9 μm wide), with interwoven horizontal and vertical elements; ovoid to subglobose elements absent from the hypodermium. Basidiospores constricted and rather narrow, mean Q 1.6–2.1; mean ratio of basidia to basidiospore length >5. Some species have characteristic odors.

Phylogenetic support Elements of subsect. *Siccae* are weakly supported in ITS analyses (27 % MLBS for *H. reidii* and *H. constrictospora* in our analysis, Online Resource 8, and 34 % MLBS in Dentinger et al., unpublished). These two species appear in the same clade in our Supermatrix analysis (61 % MLBS) but together with *H. parvula* and *H. ceracea*. Using ITS analyses, *H. quieta* appears on a separate branch emerging from the backbone in our analysis, while it appears near *H. ceracea* and *H. mucronella* in the analysis by Dentinger et al. (unpublished data). In our ITS-LSU analysis, *H. reidii* is recovered as sister to *H. miniata* (Fig. 4). We have tentatively retained sect. *Siccae* because the type species is not included with strong support in other clades.

Species included Type species: *H. reidii* Kühner. There is morphological and some phylogenetic support for including *H. constrictospora* in this subsection.

Comments Boertmann (1995) included *H. constrictospora, H. quieta, H. splendidissima, H. phaeococcinea,* and *H. aurantia* in subsect. *Siccae*. The position of *H. quieta* is unresolved. Candusso (1997, p. 532) and Arnolds (1990) have used *Hygrocybe obrussea* (Fr.) Wünsche (1877) is an earlier name for *Hygrophorus quietus* Kühner (1947), but as noted by Bon (1990) and Boertmann (1995, 2010), the diagnosis in Fries (1821) of *Agaricus obrusseus* is too vague to be sure of what species was intended, and therefore a nomem dubium. As it is not the intent of this paper to resolve such issues when they do not involve type species of genera or infrageneric taxa, we have used the name *H. quieta* as we are certain that our DNA sequences represent that species. While *H.*

phaeococcinea fits subsect. *Siccae* morphologically, it is allied with *H. miniata* in ITS analyses by us and Dentinger et al. (unpublished). ITS analyses (ours and Dentinger et al., unpublished data) place *H. splendidissima* as sister to *H. punicea* with strong support, but the morphological characters fit subsect. *Siccae* and not *Coccineae*. Our molecular phylogenies show *H. aurantia* belongs in *Cuphophyllus*.

Hygrocybe* [subg. *Pseudohygrocybe* sect. *Coccineae*] subsect. *Squamulosae (Bataille) Singer, Lilloa 22: 152 (1951) [1949]

[≡ *Hygrocybe* subsect. *Turundae* (Herink) Bon, Doc. Mycol. 19(75): 56 (1989), superfluous, nom. illeg.].

Type species: *Hygrocybe turunda* (Fr.) P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 235 (1879)

≡ *Hygrophorus turundus* (Fr.: Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 330 (1838),

≡ *Agaricus turundus* Fr., Observationes mycologicae 2: 199 (1818).

Pileus subglobose at first, depressed in center, often deeply depressed or infundibuliform at maturity; surface dry, squamulose or minutely tomentose; stipe dry and smooth. Lamellae often arcuate-decurrent. Pileipellis a trichoderm at the center, of broad hyphae (6–8–25 μm wide), typically with subglobose to ovoid elements in the hypoderm. Basidiospores relatively broad, Q 1.2–1.7 (−1.8); mean ratio of basidia to basidiospore length >5, constricted or not.

Phylogenetic support The core of subsect. *Squamulosae* is strongly supported as a monophyletic clade in our Supermatrix, full LSU, *Hygrocybe* LSU and ITS analyses (100 %, 99 %, 97 % and 84 % MLBS, respectively). The *Squamulosae* clade in our Supermatrix analysis comprises *H. caespitosa*, *H. cantharellus* and *H. melleofusca*. Support for this branch falls below 50 % in our ITS-LSU ML analysis. Babos et al. (2011), show 98 % BS support for the clade comprising *H. turundus* and *H. lepida* (as *H. cantharellus*; see Arnolds 1986b), while Dentinger et al. (unpublished data) show 100 % MLBS support for the clade comprising *H. cantharellus* s.s., *H. lepida* (as *H. cantharellus*), *H. caespitosa*, *H. coccineocrenata*, *H. melleofusca* and *H. turunda* using ITS alone. The ITS analsysis by Babos et al. (2011) shows moderately high support for including *H. quieta* in this clade (74 %), but the analysis by Dentinger et al. (unpublished) does not support inclusion of *H. quieta* in subsect. Squamulosae. In our ITS analysis, the subsect. Squamulosae clade comprises *H. caespitosa*, *H. cantharellus*, *H. lepida*, *H. melleofusca*, *H. papillata* and *H. turunda* with 84 % MLBS support, but *H. quieta* appears on a long branch in a separate clade. Although *H. miniata* is traditionally treated in subsect. *Squamulosae*, which is consistent with the micromorphology and an ITS analysis by Babos et al. (2011) that places *H. miniata* in a sister clade to subsect. *Squamulosae* s.s. (78 % MLBS). Our ITS analysis (Online Resource 8) places the clade containing *H. miniata* and *H. phaeococcinea* near sect. *Firmae*, and the ITS analysis by Dentinger et al. shows strong support (93 % MLBS) for sect. *Firmae* as sister to the *H. miniata*—*H. phaeococcinea* clade, but not near subsect. *Squamulosae*.

Species included Type species: *Hygrocybe turunda* (Fr.) P. Karst. *Hygrocybe cantharellus* (Schwein.) P. Karst. *H. caespitosa* Murrill, *H. coccineocrenata* (P.D. Orton) M.M. Moser, *H. lepida* Arnolds, *H. melleofusca* Lodge & Pegler (if different from *H. caespitosa*), *H. substrangulata* (Peck) P.D. Orton & Watling, and *H. turunda* (Fr.) P. Karst. are included based on molecular and morphological data. Although the *H. miniata* complex has similar morphology, we tentatively exclude it from subsect. *Squamulosae* because it appears in a clade with sect. *Firmae* (*H. firma, H. martinicensis*), *H. andersonii,* and *H. phaeococcinea* in our ITS analysis, and as a strongly supported sister to sect. *Firmae* in our LSU analysis and the ITS analysis by Dentinger et al. (unpublished data).

Comments Singer [1949 (1951)] inadvertently combined Bataille's *Hygrophorus* [unranked] *Squamulosi* at subsection rank in the genus *Hygrocybe*. Konrad and Maublanc (1953) combined Bataille's *Squamulosae* at higher (section) rank (neither with a designated type species) and Herink published a different name, *Turundae*, for this group in the genus *Hygrocybe* with the same type (*H. turundua*) as Singer's subsection and he included a Latin diagnosis; Herink included *H. cantharellus* and an ambiguous species, *H. marchii* sensu Karsten. Excluding *H. marchii,* Herink's section refers to the same clade as *Hygrocybe* subsect. *Squamulosae.* Bon (1989) reduced *Turundae* to subsect. rank and included only the type species, which is characterized by having a pileus with darkening squamules. *Hygrocybe turunda* is in subsect. *Squamulosae* Singer (1951), making subsect. *Turundae* (Herink) Bon (1989) superfluous (nom. illeg.). If this clade is recognized at section rank, the correct name is *Hygrocybe* sect. *Squamulosae* (Bataille) Konrad and Maubl. (1953) based on priority.

Our Supermatrix and ITS analyses strongly support inclusion of *H. caespitosa*, *H. coccineocrenata*, *H. lepida*, *H. melleofusca*, *H. substrangulata*, and *H. turunda* in subsect. *Squamulosae*. Lodge and Pegler (1990) and Cantrell and Lodge (2004) incorrectly placed *H. melleofusca* in *Hygrocybe* sect. *Neohygrocybe* based on the brown staining reactions while Arnolds (1995) had correctly placed its sister species, *H. caespitosa*, in subsect. Squamulosae based on micromorphology of the pileus trama and pellis. Although Singer [(1949) 1951)], Bon (1990) and Boertmann (1995, 2010) all treated *H. miniata* in subsect. *Squamulosae*, and we have not found characters that would separate them,

phylogenetic support for retaining *H. miniata* in subsect. *Squamulosae* is lacking so we have tentatively excluded it along with other species in that clade.

Hygrocybe* [subg. *Pseudohygrocybe*] sect. *Firmae Heinem., Bull. Jard. bot. État Brux. 33: 441 (1963).

Type species: *Hygrocybe firma* (Berk. & Broome) Singer, Sydowia 11: 355 (1958)

≡ *Hygrophorus firmus* Berk. & Broome, J. Linn. Soc., Bot. 11: 563 (1871).

Emended here by Lodge to exclude species with macrobasidia broader than the microbasidia and basidia less than 5 times the length of their basidiospores.

Characters as in *Hygrocybe*, sect. *Coccineae*, subsect. *Squamulosae* but differing in presence of dimorphic basidiospores and basidia. Shares dimorphic basidia and spores with *Hygrocybe*, subg. *Hygrocybe*, sect. *Pseudofirmae* but differs in having basidia exceeding 5 times the length of their basidiospores, narrow macrobasidia that differ from the microbasidia primarily in length (not width), presence of chains of subglobose elements in the pileus hypoderm, often a trichodermial pileipellis rather than an interrupted cutis, and long lamellar trama hyphal elements always absent.

Phylogenetic support Sect. *Firmae* appears in a separate, strongly supported clade in our *Hygrocybe* LSU analyses (85 % MLBS, Online Resource 7), and ITS analyses of Dentinger et al. (82 % MLBS, unpublished data), but it appears as a grade in our ITS analysis (Online Resource 8). Our LSU (100 % MLBS, Online Resource 7) and Dentinger et al.'s ITS (93 % MLBS) analyses strongly support placing sect. *Firmae* as sister to the *H. miniata* clade, and we show only weak ITS support (47 % ML BS) for including the type of sect. *Firmae* in the *H. miniata* clade. The sect. *Firmae* – *H. miniata* clade is weakly (39 % MLBS) supported as sister to subsect. *Squamulosae* in our LSU analysis of tribe *Hygrocybeae* (Online Resource 7), (but these clades are apart in our ITS-LSU analysis. The ITS analysis by Dentinger et al. (unpublished data) does not place sect. *Firmae* near subsect. *Squamulosae*.

Species included Type species: *Hygrocybe firma*. *Hygrocybe martinicensis* Pegler & Fiard is included based on phylogenetic and morphological data. Based on morphology of the pileipellis and mean ratios of basidia to basidiospore lengths, *H. anisa* (Berk. & Broome) Pegler and possibly *H. batistae* Singer are tentatively included.

Comments Sect. *Firmae* was delineated by Heinemann (1963) based on presence of dimorphic basidiospores and basidia, and has been recognized by some tropical agaricologists (Cantrell and Lodge 2001, Courtecuisse 1989, Heim 1967; Pegler 1983), but not others (Horak 1971, Singer 1986, Young 2005). It is now apparent based on our phylogenetic analyses that dimorphic basidiospores and basidia arose several times, appearing in two clades of subg. *Hygrocybe* (sects. *Pseudohygrocybe* and *Velosae*) and one strongly supported monophyletic clade (sect. *Firmae* ss, Dentinger et al., unpublished data) in subg. *Pseudohygrocybe*. Species in sect. *Firmae* can be differentiated from those with dimorphic spores and basidia in subg. *Hygrocybe* based on the micromorphological features noted in the emended diagnosis above. Species in sect. *Firmae* have narrow macrobasidia, broad hyphae in the pileipellis and globose mixed with stipitate-capitate elements in the hypodermium, similar to the globose to subglobose elements in the hypoderm of *H. cantharellus* and related species in subsect. *Squamulosae* (Fig. 10). Other than the presence of dimorphic basidiospores and basidia, sect. *Firmae* micromorphologically resembles species in subsect. Squamulosae, where Singer (1986) placed it, and the *H. miniata* species complex, which Singer and others also placed in subsect. *Squamulosae*. Despite the micromorphological similarities, phylogenetic analyses by us and by Dentinger et al. (unpublished data) suggest a strong relationship between sect. *Firmae* and the *H. miniata* complex, but a weak or absent relationship between that combined clade and subsect. *Squamulosae*. Additional analyses including more species and gene regions will be needed to resolve relationships among these clades. In keeping with making minimal changes in classification unless strongly justified by phylogenetic analyses, we have retained sect. *Firmae* and left the *H. miniata* clade unplaced.

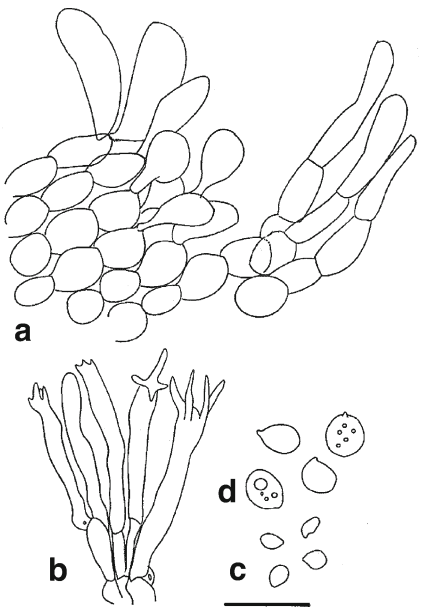


Fig. 10 *Hygrocybe* (subg. *Pseudohygrocybe*) sect. *Firmae*. *Hygrocybe firma* (type): **a**. pileipellis; **b**. hymenium showing macro- and microbasidia; **c**. microspores; **d**. macrospores. Scale bar=20 μm

Species unplaced subgen. *Pseudohygrocybe*.

Hygrocybe miniata, H. miniata f. longipes, and *H. phaeococcinea* appear in a well supported clade that is sister to sect. *Firmae* in our ITS analysis of *Hygrocybe* s.s. Similarly, the *H. miniata* species complex falls in a strongly supported (85 % MLBS) sister clade to sect. *Firmae* (*H. firma* s.s. and *H. martinicensis*) in our LSU analysis of tribe *Hygrocybeae* (Online Resource 7). *Hygrocybe miniata* shares with subsect. *Squamulosae* large diameter pileipellis hyphae (5–18 μm), presence of subglobose elements in the pileus hypoderm and small mean spore Q (1.3–1.6). Consequently, Singer [(1949) 1951), Bon (1990) and Boertmann (1995, 2010)] all treated *H. miniata* in subsect. *Squamulosae*. The *H. miniata* – sect. *Firmae* clade (100 % MLBS) appears as sister to subsect. *Squamulosae* (97 % MLBS) with low support (39 % MLBS) in our LSU analysis of tribe *Hygrocybeae* while the *H. miniata* complex and sect. *Squamulosae* appeared in sister clades with strong support (77 % MLBS) in the ITS analysis by Babos et al. (2011). In our Supermatrix analysis, *H. miniata* f. *longipes* is included in the basal clade of subgen. *Hygrocybe* with *H. helobia*, but without significant bootstrap support (32 % ML); the short lamellar trama hyphae in *H. miniata* argues against that placement. Inclusion of *H. firma*, the type of sect. *Firmae*, as sister to the *H. miniata* clade, and these together as sister to sect. *Coccineae* subsect. *Squamulosae* is problematical on several levels. Species in sect. *Firmae* have dimorphic spores and basidia, but otherwise they have all the diagnostic characters of subsect. *Squamulosae* and species in the *H. miniata* clade. Singer (1986), Horak (1990) and Young (2005) treated *Hygrocybe* with dimorphic basidia as members of subg. *Pseudohygrocybe*, and the phylogenetic placement and micromorphology of the basidiomes of *H. firma* are concordant with that placement. Singer (1986) frequently included dimorphic basidiospores and basidia in his description of *Hygrocybe* sect. *Coccineae*, subsect. *Squamulosae*, but the phylogenetic analyses presented here and the analysis by Dentinger et al. (unpublished) place the sect. *Firmae* – *H. miniata* clade either weakly together with or apart from subsect. *Squamulosae*. Placing the *H. miniata* complex as a new subsection of sect. *Firmae* is one possible solution, but it would neccesitate emending the description of sect. *Firmae* to include species with monomorphic basidia and spores. There is currently no valid name for a subsection typified by *H. miniata*. Recognizing the *H. miniata* clade at section rank is another option, but sect. *Miniatae* Singer (1943) was not validly published (Art. 36.1). Raising subsect. *Squamulosae* to section rank also needs to be considered. We have refrained from making such changes, leaving the *H. miniata* clade unplaced, and sect. *Firmae* and sect. *Coccineae*, subsect. *Squamulosae* at their present ranks.

Hygrocybe calciphila has all the characters of sect. *Coccineae* subsect. *Squamulosae*, but its position is unstable between ITS and paired ITS-LSU analyses. In our ITS-LSU analysis and Dentinger et al.'s (unpublished) ITS analysis, *H. calciphila* falls between subg. *Hygrocybe* and *Pseudohygrocybe* without support.

Hygroaster Singer, Sydowia 9(1–6): 370 (1955).

Type species: *Hygroaster nodulisporus* (Dennis) Singer, Sydowia 9(1–6): 370 (1955)

≡ *Hygrophorus nodulisporus* Dennis, Kew Bull. 8(2): 259 (1953).

Emended here by Lodge to exclude temperate species, basidiomes with bright pigments and basidiospores that are subangular or are not globose or subglobose.

Pileus indented, not viscid, fuscous or white, lacking bright pigments. Lamellae thick, decurrent, distant or subdistant. Basidiospores subglobose or globose, not polygonal in outline; spines long conical with blunt or acute apices, hyaline, inamyloid, not cyanophilous; ratio of basidia to basidiospore lengths (excluding ornaments) >5; lamellar trama subregular, hyphal elements short, central strand pigmented in pigmented species; clamp connections usually absent throughout the basidiomes; pigments mostly vacuolar, but pileipellis hyphae may be lightly encrusted; habit terrestrial in wet tropical forests, so far confined to the neotropics. Differing from *Omphaliaster* in lacking heavily encrusting pigments, if pigmented, absence of pseudocystidia in the hymenium, subregular rather than regular lamellar trama, absence of clamp connections, growing on mineral soil or humus rather than with mosses on small shrubs and rotting wood, and tropical rather than primarily temperate-boreal in distribution.

Phylogenetic support Support for a monophyletic clade represented by *H. nodulisporus* and *H. albellus* is strong in the 4-gene backbone analysis (98 % MLBS and 100 % BPP), LSU analysis (92 %), and Supermatrix (75 % MLBS). Support for *Hygroaster* as sister to *Hygrocybe* is strong (98 %, and 96 %, MLBS in our 4-gene backbone and Supermatrix, analyses, respectively).

Species included Type species: *H. nodulisporus*. Placement of *H. albellus* Singer in *Hygroaster* is confirmed by molecular phylogeny. It is ambiguous as to whether *H. cleefii* Franco-Molano & López-Quintero belongs in *Hygroaster* as the presence of clamp connections, broadly ellipsoid rather than globose spore shape and viscid pileus are deviating characters.

Comments Hygroaster was originally described as a monotypic genus by Singer (1955) to accommodate *Hygrophorus nodulisporus* Dennis (1953) from Trinidad. Singer then added *H. albellus* in 1989. While both of Singer's species lack the bright pigments that are typically found in *Hygrocybe* s.s., the morphology of the lamellar trama and subhymenium are typical of *Hygrocybe* (Fig. 11), and the molecular phylogenies strongly support it as the sister clade to *Hygrocybe*. It is

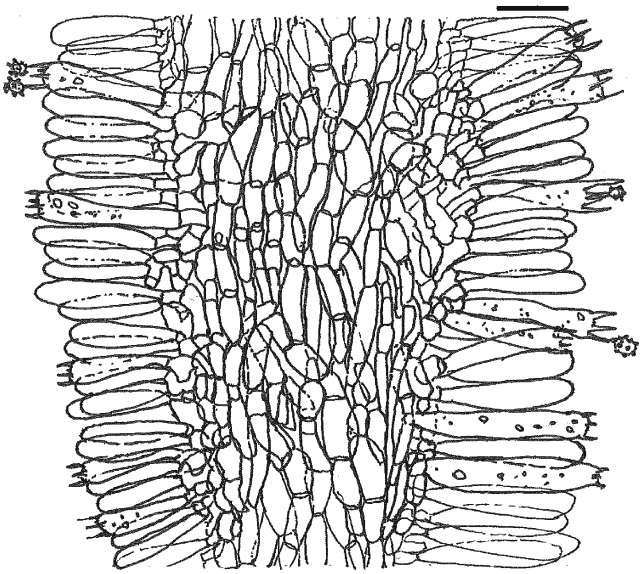


Fig. 11 *Hygroaster nodulisporus* lamellar cross section (PR-6378, Puerto Rico). Scale bar=20 μm

unknown if the dark pigment in *H. nodulisporus* is a betalain, as in *Hygrocybe*. If the segregate genera (e.g., *Gliophorus, Humidicutis, Neohygrocybe* and *Porpolomopsis*) are treated as sections within the genus *Hygrocybe*, *Hygroaster* would need to be reduced in rank to keep *Hygrocybe* from being polyphyletic. Hesler and Smith (1963) reduced the rank of *Hygroaster* to a section, but in the genus *Hygrophorus* rather than *Hygrocybe*. Treatment of nodulose-spored species of *Hygroaster* among the smooth spored *Hygrocybe* is not unreasonable. Several species of *Hygrocybe* have variants that produce spores with conical spines, such as *H. anomala*, *H. insipida* and *H. kula* (Boertmann 1995; Young 2005). It is therefore likely that the presence or absence of spines on spores in Tribe *Hygrocybeae* results from mutation or repression/derepression a single gene. It is unkown if the fuscous pigment in *H. nodulisporus* is a DOPA betalaine, as in *Hygrocybe*, or another type (Online Resource 4).

In the original description by Singer, the lamellar trama of the type species, *H. nodulisporus*, was bilateral with a central slightly interwoven strand and divergent hyphae in a gelatinous matrix in the lateral strands. Neither we nor Hesler and Smith (1963) found evidence of gelatinization or bilateral structure in the type, and we have not seen these characters in subsequent collections of *H. nodulisporus* (Fig. 11), though the central part of the trama is darkly pigmented. In 1986, Singer changed the diagnosis of the trama to subbilateral with pigmented central strand in pigmented species.

Singer's (1986) tribe *Hygroastreae* comprises *Hygroaster* and *Omphaliaster*, but is polyphyletic, as is Ludwig's (1997) concept of *Hygroaster* in which he combined species of *Omphaliaster* in the genus *Hygroaster*. As noted by Franco-Molano and López-Quintero, most of the species placed in *Hygroaster* belong elsewhere. The European species described in *Hygroaster* by Horak (1966, *H. kyrtosporus* and *H. nauseodulcis*) were transferred by Noordeloos (1983) to *Omphaliaster* (between Tricholomataceae tribe *Lyophylleae* and the Tricholomatoid clade in Moncalvo et al. 2002; in the Tricholomatoid clade in Matheny et al. 2006). Kühner (pers. com. to EH) suggested that *H. kyrtosporus* did not belong with *H. asterosporus* and *H. borealis* (both now in *Omphaliaster*). The caulocystidia and the small, smooth ovoid spores attached to basidia in *H. kyrtosporus* are consistant with *Omphalina* spp., while the very large nodulose spores might be chlamedospores of a parasite as they closely resemble those of *Nyctalis parasitica*. Singer (1962) [1961] transferred *Omphalia asterospora* into *Hygroaster*, but Lamoure (1971) transferred it to *Omphaliaster*. The transfer of *Rhodocybe ianthinocystis* into *Hygroaster* by Ludwig (1997) is rejected in favor of placement by Baroni (1981) in *Omphaliaster* based on the presence of pseudocystidia in the hymenium, parallel lamellar trama hyphae and lower ratio of basidia to basidiospore lengths (4–4.5 according to Baroni, but up to 5.2 according to Singer, versus 5.5–7 in *Hygroaster*). Singer (1986) suggested an alternative placement of this species in *Asproinocybe*. While *Hygroaster lacteus* E. Ludw. and Ryberg (Ludwig 1997) described from Europe has nodulose spores, it deviates from *Hygroaster* s.s. in having prominent pseudocystidia and clamp connections. The nodulose spore ornamentation in *H. lacteus* is unlike the ornaments on *Omphaliaster* spores, and DNA sequencing will likely be needed to resolve its affinities. Placement of several tropical species assigned to *Hygroaster* is also complex. The South American *H. iguazuensis* Lechner & J.E. Wright is bright orange and has spores that are more elongated and polygonal in outline, resembling nodulose-spored forms in *Hygrocybe anomala*, and it likely belongs in *Hygrocybe* s.s. (Franco-Molano and López-Quintero 2007). It is uncertain where the Asian *H. sulcatus* (Z.S. Bi) T.H. Li & Z.S. Bi and *H. trachysporus* Bi belong, but presence of pleurocystidia in the former, a glutinous pileus in the latter, and presence of bright pigments, clamp connections and small *Lepista*-like ornamentation on broadly ellipsoid spores in both species argue against placement in *Hygroaster*. *Hygroaster fucatus* Vrinda & Pradeep. described from India (Vrinda et al. 2012) deviates from *Hygroaster* in having orange pigments in the pileus, lamellae that are adnexed rather than decurrent and tinted lilac, ellipsoid spores with inocyboid ornamentation, and presence of clamp connections and pleuro- and cheilocystidia; *H. fucatus* is likely conspecific with or close to *Asprinoinocybe russuloides* that was described from Africa. The data on *H. agumbensis* Sathe & S.M. Kulk from India are insufficient to place this species.

Tribe *Humidicuteae* Padamsee & Lodge, tribe nov.
MycoBank MB804050.

Type genus: *Humidicutis* (Singer) Singer, Sydowia 12(1–6): 225 (1959) [1958].

Basidiomes brightly colored or gray brown, differing from *Hygrocybe* in absence of DOPA based pigments except for in a few species of *Neohygrocybe*. Clamp connections at the base of basidia and basidioles often toruloid and then differing from those in *Chromosera*. Also differing from *Chromosera* in having regular or subregular but not interwoven lamellar context, inamyloid pileus context, and strong odors in some species.

Phylogenetic support The tribe comprising *Neohygrocybe, Gliophorus, Humidicutis,* and *Porpolomopsis* consistently appears either as a single clade that is sister to *Hygroaster* (with *Hygroaster* basal to *Hygrocybe*) (4-gene backbone and LSU analyses) or in adjacent clades (ITS-LSU and Supermatrix analyses). Support for a monophyletic tribe *Humidicutae* comprising all four genera is 89 % MLBS in the 4-gene backbone analysis (99 % MLBS for it being a sister to tribes *Hygrocybeae* and *Chromosereae*), but support falls below 50 % in our LSU analysis. In the ITS-LSU analysis, *Neohygrocybe* appears as sister to the *Humidicutis – Porpolomopsis* clade. These four genera are usually basal to *Hygroaster—Hygrocybe* s.s. (tribe *Hygrocybeae*) and distal to *Hygrophorus* and other genera of Hygrophoraceae. Based on the strongly supported placement of *Hygroaster—Hygrocybe* s.s. as sister to the *Gliophorus – Humidicutis – Neohygrocybe – Porpolomopsis* clade, it is untenable to treat these groups as sections within subg. *Pseudohygrocybe*, where the first three have traditionally been placed. Prior to Horak (1990), Young (2005) and Boertmann (2010), who placed *Porpolomopsis* species in *Humidicutis*, *Porpolomopsis* was treated in subg. *Hygrocybe* because it has long, tapered lamellar trama hyphae – an untenable placement that would render subg. *Hygrocybe* polyphyletic.

Genera included Comprising the type genus, *Humidicutis,* together with *Gliophorus, Gloioxanthomyces, Neohygrocybe* and *Porpolomopsis*.

Comments These segregate genera are often treated at subgenus or section rank within the genus *Hygrocybe* (Table 1), which is justifiable as long as the genus *Hygroaster* is reduced to a subgenus so it doesn't render *Hygrocybe* polyphyletic. We have selected subgeneric over section ranks for recommended names when using *Hygrocybe* s.l. (Table 1) because they are strongly divergent, and there are more validly published names available when they are treated at this rank.

Neohygrocybe Herink, Sb., Severocesk. Mus., Prír. Vedy 1: 71 (1959).

Type species: *Neohygrocbye ovina* (Bull. : Fr.) Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 72 (1959)

≡ *Hygrophorus ovinus* (Bull. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 328 (1838) [1836–1838],

≡ *Agaricus ovinus* Bull., Herbier de la France 13: 592 and plate 580 (1793)] **Lectotype here designated as fig. M** in Bulliard, Herbier de la France 13: plate 580 (1793)]; **Epitype here designated GEDC0877**, coll. Griffith, Ffriddoedd Garndolbenmaen, Wales, UK, 19 Oct 2006, K(M)187568, GenBank sequences KF291228, KF291229, KF291230.

Pileus hemispherical or campanulate, center usually umbonate and margin incurved when young, often plane or convex or with depressed center and margin lobed with age; surface dry or moist, minutely tomentose, appressed squamulose or fibrillose, often rimose; pigments grayish brown, mostly with oxidation reactions that produce red, then fuscous colors upon bruising, DOPA pigments present or absent; lamellae adnexed sinuate or broadly adnate, thick, waxy, distant and fragile; stipe central, often compressed or channeled, surface smooth, context stuffed or hollow; flesh usually with distinct odors (nitrous, chlorine or fruity); basidiospores hyaline, thin-walled, ellipsoid, oblong or broadly ellipsoid, rarely broadly ovoid or subglobose, not strangulated, guttulate in KOH, guttules with oily contents, inamyloid; basidia 2- or 4-sterigmate, with modest basal clamp connections; basidia more than 5 times the length of the spores; lamellar trama subregular or regular, hyphae up to 200–400 μm in length, with clamp connections; pseudocystidia absent or present, emanating from the context and protruding from the lamellar edge or sides, sometimes with dissolved fuscous pigment; pileipellis a loose cutis, disrupted cutis or trichoderm, often with dissolved fuscous pigment. Differs from *Humidicutis, Porpolomopsis* and most *Gliophorus* species in lacking bright pigments and clamp connections at the base of the basidia and basidioles not toruloid; differs from *Gliophorus* in absence of glutinous surfaces; differs from *Porpolomopsis* in having subregular rather than regular lamellar trama, and fuscous rather than purple pigments.

Phylogenetic support Support for a monophyletic *Neohygrocybe* is strong in our 4-gene backbone, Supermatrix and ITS-LSU analyses (99 %, 87 % and 76 %, respectively), and moderate in our ITS analysis (Online Resource 3, 61 % MLBS); *N. nitrata* was dropped from these analyses, however, because it caused instability. Support is moderate (67 % MLBS) in our LSU analysis, excluding *N. nitrata* from Turlogh Hill in North Wales, UK but including *N.* aff. *nitrata* from Russia (there is no significant backbone support separating the two representatives identified as *N. nitrata*). The ITS analysis of subf. *Humidicutae* by Dentinger et al. (unpublished) places *N. nitrata* apart from the other *Neohygrocybe* species along the backbone.

Sections included Neohygrocybe and *Tristes.*

Comments The genus *Neohygrocybe* was described by Herink (1959) to accommodate the gray-brown species formerly treated in *Hygrocybe* that lacked viscid surfaces, had

strong odors and usually had tissues that bruised red and then fuscous. It has previously been accepted at genus rank by Kovalenko (1989), or treated within the genus *Hygrocybe* at the rank of either subgenus (Bon, 1990) or section (Boertmann 2010; Candusso 1997; Cantrell and Lodge 2004; Lodge and Pegler 1990, Pegler and Fiard 1978). Bon (1989) validly combined it in *Hygrocybe* as subg. *Neohygrocybe* (Herink) Bon (citing the basionym and source publication, and indirectly inferring the type species, *H. ovina*, was the same as the type of *Neohygrocybe*, as allowed in Art. 37.3). We recognize two sections in *Neohygrocybe*: sects. *Neohygrocybe* (the correct name for sect. "*Ovinae*" Herink, nom. invalid, Art. 22.1), and sect. *Tristes* (Bataille) Singer, which replaces the superfluous sect. *Nitratae* Herink (illeg., Art. 52.1). We have emended the diagnosis of sect. *Tristes* to match the narrower limits of Herink' sect. *Nitratae* rather than Singer's broader sect *Tristes*.

Herink (1959) made an attempt to erect a provisional section, "*Metapodiae*"nom. invalid, in *Neohygrocybe* for a fuscous, red-staining species with smooth, amyloid spores, *Porpoloma metapodium*. Singer (1986) later placed *Porpoloma* in the Tricholomataceae, Tribe *Leucopaxilleae* – a placement supported by molecular phylogenetic analysis of LSU sequences (Moncalvo et al. 2002) (see excluded genera).

Herink designated *N. ovina* as type of *Neohygrocybe*, mentioning both Bulliard and Fries. Thus the type of the generic name is *N. ovina* (Bull. : Fr.) Herink (basionym *Agaricus ovinus* Bull. : Fr.) and it is the type of this species epithet that is the type of the genus. The nomenclatural history of *Agaricus ovinus* Bull. : Fr. is complex. Fries (1821) placed *Agaricus metapodius* Fr. (1818) in synonymy with *A. ovinus* Bull. : Fr., and the figures in Bulliard's plate 580 (Herb. Fr., 1793) that Fries cited (excluding figs. a and b = *Dermoloma*) indeed represent a mixture of *A. ovinus* and *A. metapodium* (the latter species now in *Porpoloma,* Tricholomataceae), though Fries later clearly distinguished these two species (1838: 328). *Agaricus ovinus* Bull.: Fr., however, is a sanctioned name (Systema Mycol. 1: 109, 1821) and is thus protected against competing synonyms and homonyms (including *A. metapodium*); moreover, *H. ovinus* (1793/1801) has priority over *A. metapodius* (1818), regardless of protected status (S. Pennycook, pers. comm. 27 June 2013). Thus the use of 'type *Hygrocybe ingrata'* by Candusso (1997: 323) and recognition by Della Maggiora and Matteucci (2010) of *H. nitiosa* (A. Blytt) M.M. Moser (1967), with *Hygrocybe ovina* (Bull.: Fr.) Kühner ss Kühner (1926) as a facultative synonym, and exclusion of *Agaricus ovinus* Bull. is problematic on many levels. As Fries did not designate a type, the material cited by Fries represents a mixture of species (and collections) and we have not found a subsequent lectotype designation for *A. ovinus* Bull. : Fr., we have instead chosen to stabilize its concept according to Art. 9.2, 9.10, and 9.11 by designating figure M in Bulliard plate 580 (Herb. Fr., 1793) as the lectotype of *Agaricus ovinus* Bull. : Fr., and by designating a photo documented and sequenced collection from Wales (GEDC0877, K(M)187568) as an epitype. The designated lectotype and epitype closely resemble each other and conform to the original diagnosis (both have an innately scaly pileus with split margins, a compressed stipe which indicates they are stuffed or hollow, and a slight flush of pink in the gray lamellae (but neither shows a distinct red staining, which is a character not included in the original diagnosis). The absence of characters from the diagnosis (e.g., pink staining reaction and nitrous odor, as noted by Candusso, 1997) are ignored as it is the characters that are present in a diagnosis that must match the selected lectotype and epitype. We have instead selected the lectotype and epitype based on the following characters that were included in the original diagnosis (Bull., Herb. Fr., 1793: 592) of *A. ovinus* Bull.: stipe swollen, stuffed, becoming hollow; pileus 2–6 cm diam., hemispherical, becoming umbonate, smooth to scaly, margin becoming fissured, brick colored to fuscous-cinereous; lamellae few, sublunate, uncinate, broad, venose, white at first, becoming cinerous. *Porpoloma metapodium* has a solid, non-compressed stipe and lamellae that are not veined.

Neohygrocybe* sect. *Neohygrocybe. [autonym]

[≡ *Neohygrocybe* sect. "*Ovinae*" Herink (1959), nom. invalid and illeg.]

Type species: *Neohygrocybe ovina* (Bull.: Fr.) Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 72 (1959)

[≡ *Hygrocybe ovina* (Bull.: Fr.) Kühner, Le Botaniste 17: 43 (1926), ≡ *Hygrophorus ovinus* (Bull. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 328 (1838) [1836–1838],

≡ *Agaricus ovinus* Bull., Herbier de la France 13: t. 580 (1793)].

Characters as in genus *Neohygrocybe*, some part of the flesh always bruising red, then fuscous; most with a distinctive nitrous, ammonia or fruity odor.

Phylogenetic support Support for a monophyletic sect. *Neohygrocybe* is strong in our 4-gene backbone, LSU, Supermatrix and ITS-LSU analyses (99 %, 67 %, 87 % and 76 % MLBS, respectively). Support is moderate in our ITS analysis (61 %, Online Resource 3).

Species included Type species: *Neohygrocybe ovina*. Additional species included based on molecular phylogenies and morphology are *N. ingrata* and *N. subovina* (Hesl. & A.H. Sm.) Lodge & Padamsee, comb. nov. (below). *Neohygrocybe lawsonensis* (A.M. Young) Lodge & Padamsee, comb. nov. (below) is included based on morphology.

Comments This section contains most of the species known in *Neohygrocybe* including the type, but it has previously been called *Neohygrocybe* sect. "*Ovinae*" Herink (nom. invalid), and *Hygrocybe* [unranked] *Ovinae* Bataille. Herink (1959)

supplied a Latin diagnosis for the unranked group, *Ovini* Bataille (1910), but Herink failed to cite the basionym and its place of publication as required beginning in 1953 (nom. invalid, Art. 33.4). Regardless, sect. *Ovinae* is invalid because the section contains the type of the genus so the name has to repeat the genus name exactly (Art. 22.1), making sect. *Neohygrocybe* the correct name for this group. The combinations in *Hygrocybe,* sect. *Neohygrocybe* (Herink) Bon, and immediately below it, *N.* subsect. *Neohygrocybe* (Herink) Bon (1989), were both validly published making *Hygrocybe* sect. *Neohygrocybe* (Herink) Candusso (1997) superfluous, nom. illeg. (Candusso, 1997: 323, was also incorrect in stating the type species of the section was *H. ingrata*; see Art. 7.4).

Neohygrocybe subovina (Hesl. & A. H. Sm.) Lodge & Padamsee, comb. nov.

MycoBank MB804063.

Basionym: *Hygrophorus subovinus* Hesler & A. H. Sm., North American species of *Hygrophorus*: 162 (1963).

Type: TENNESSEE, Cade's Cove, Great Smoky Mt. National Park, 8 Jun 1957, on soil in deciduous woods, *Hesler 22583*, TENN.

Neohygrocybe lawsonensis (A. M. Young) Lodge & Padamsee, comb. nov.

MycoBank MB804064.

Basionym: *Hygrocybe lawsonensis* A. M. Young in A. M. Young & A. E. Wood, Austral. Syst. Bot. 10(6):981 (1997).

Type: AUSTRALIA, New South Wales, on soil in sclerophyll forest, *T. Lawson*, 30 May 1992, UNSW 92/211.

Neohygrocybe* sect. *Tristes (Bataille) Lodge & Padamsee, comb. nov.

MycoBank MB804067.

Basionym: *Hygrophorus* [unranked] *Tristes* Bataille, Mém. Soc. émul. Doubs, sér. 8 4:183 (1910).

≡ *Hygrocybe* sect. *Tristes* (Bataille) Singer, Lilloa 22: 151 (1951) [1949]

[≡ *Neohygrocybe* sect. "*Nitratae*" Herink, superfluous, nom. illeg., Art. 52.1],

Lectoype designated by Singer (1951): *Hygrocybe nitrata* (Pers.) Wünsche, Die Pilze: 112 (1877),

≡ *Agaricus nitratus* Pers., Syn. meth. fung. (Göttingen) 2: 356 (1801),

≡ *Neohygrocybe nitrata* (Pers.) Kovalenko, Opredelitel' Gribov SSSR (Leningrad): 40 (1989),

[≡ "*Neohygrocybe nitrata*" (Pers.) Herink (1959), nom. invalid., Art. 33.2].

N. Sect. *Tristes* is **emended here by Lodge** to include only the type species.

Odor nitrous. Differs from sect. *Neohygrocybe* in flesh not staining red when bruised.

Phylogenetic support The collection sequenced from North Wales (as *H. nitrata*) matches the type description, so we assume that the collection sequenced from Russia is an unnamed cryptic species in sect. *Nitratae*. The collection identified as *N. nitrata* from N.Y. in the Supermatrix analysis is apparently *N. ingrata*. Inclusion of species of sect. *Nitratae* in phylogenetic analyses caused instability, but we retained them in the LSU analysis. *N. nitrata* and *N.* aff. *nitrata* appeared in separate clades in the LSU analysis. The LSU sequence from the Russian collection appears on a long branch near the base of sect. *Neohygrocybe* while the sequence from the Welsh Turlogh Hill collection appears on a long branch from the backbone. The ambiguous support for this group indicates a need for further revision with greater taxon sampling, so we have tentatively retained the section.

Species included Type species: *Neohygrocybe nitrata*. An unnamed taxon from Russia resembling *N. nitrata* likely also belongs here based on morophology and molecular sequences.

Comments Sect. *Tristes* (Bataille) Singer (1951) replaces the superfluous sect. *Nitratae* Herink (1959) based on priority, but we retained Herink's narrower circumscription for this group. Some collections of *N. nitrata* reportedly have faint staining reactions, (DMB) and the placement of these needs to be verified with DNA sequencing.

Porpolomopsis Bresinsky, Regensb. Mykol. Schr. 15: 145 (2008).

Type species: *Porpolomopsis calyptriformis* (Berk.) Bresinsky, Regensb. Mykol. Schr. 15: 145 (2008)

≡ *Hygrocybe calyptriformis* (Berk.) Fayod, Annls. Sci. Nat. Bot., sér. 7 9: 309 (1889),

≡ *Agaricus calyptriformis* Berk., Ann. Mag. Nat. Hist., Ser. 1 1: 198 (1838).

Pileus conic, conico-campanulate, convex-umbonate or cuspidate, frequently splitting through the pileus and lamellar context near the pileus margin; pigments nonencrusting and insoluble in alkali, salmon, pink, lilac, vinaceous or absent (white); lamellae narrowly attached (adnexed, narrowly sinuate) or free; pileipellis hyphae radially arranged, fusiform; basidia usually 5 or more times longer than the spore length; basidiospores hyaline, thin-walled, inamyloid, not metachromatic, ellipsoid or broadly ellipsoid, not stangulated; lamellar trama strictly regular, of long, fusiform hyphae often exceeding 140 μm in length, with right-angled septa; clamp connections typically absent or rare in context and the pellis, but toruloid clamps present at base of basidia and/or basidioles. Differing from *Humidicutis* in narrowly attached or free lamellae, splitting of the context through the pileus and lamellae, and long, parallel, fusiform trama hyphae.

Phylogenetic support Support for a monophyletic *Porpolomopsis* is strong in our ITS-LSU, ITS and 4-gene

backbone analyses (100 % MLBS, 100 % MLBS, and 97 % MLBS and 100 % BPP), but weaker in our Supermatrix analysis (65 % ML BS). The ITS analysis by Vizzini and Ercole (2012) [2011] shows a single representative of *Porpolomopis* (as *Humidicutis calyptriformis*) on a separate, long branch emanating from the backbone that also gave rise to the *Gliophorus* clade.

Species included Type: *Porpolomopsis calyptriformis*. Species included based on molecular data are *Porpolomopsis lewelliniae* (Kalchbr.) Lodge, Padamsee and Cantrell, comb. nov. (below), and three unnamed species from the USA, UK and Russia. *Hygrocybe pura* (Peck) Murrill) is included based on morphology.

Comments Porpolomopsis was segregated from *Hygrocybe* by Bresinsky (2008) based on the color and absence of DOPA pigments. Most previous authors placed the type and related species in groups corresponding to *Hygrocybe* subg. *Hygrocybe* because of the conic pileus and the long lamellar trama hyphae with tapered ends (Fig. 12; Bon 1990; Candusso 1997; Kovalenko 1989, and tentatively by Singer 1986; Hesler and Smith 1963 as *Hygrophorus* sect. *Hygrocybe*, subsect. *Hygrocybe*; Herink 1959 as *Godfrinia*). Exceptions were Horak (1990) and Young (2005) who placed these species in *Humidicutis*, and Boertmann (2010) who placed *H. calyptriformis* in *Hygrocybe* subg. *Humidicutis* based on the pigments, absence or rarity of clamp connections in the context and pellis, and presence of spectacular toruloid clamp connections at the base of the basidia and basidioles. The molecular phylogenies detailed below place this clade as sister to *Humidicutis*.

Porpolomopsis lewelliniae (Kalchbr.) Lodge, Padamsee & S.A. Cantrell, comb. nov.

MycoBank MB MB804065.

Basionyn: *Hygrophorus lewelliniae* Kalchbr. (as '*lewellinae*'), *Proc. Linn. Soc. N.S.W.* 7(1–2): 105 (1882)

≡ *Humidicutis lewelliniae* (Kalchbr.) A.M. Young, Fungi of Australia: 159, (2005).

Type: AUSTRALIA, Western Port, Victoria, 14 June 1880, M.M.R. Lewellin, holotype RB MSS A11 (MEL).

Humidicutis (Singer) Singer, Sydowia 12(1–6): 225, 1959 [1958].

Type species: *Humidicutis marginata* (Peck) Singer (1959),

≡ *Hygrocybe marginata* (Peck) Murrill [as '*Hydrocybe*'], *N. Amer. Fl.* (New York) 9(6): 378 (1916),

≡ *Hygrophorus marginatus* Peck, Ann. Rpt. N.Y. State Mus. Nat. Hist. 28: 50 (1876).

Basionym: *Tricholoma* subg. *Humidicutis* Singer, Sydowia 2(1–6): 28 (1948).

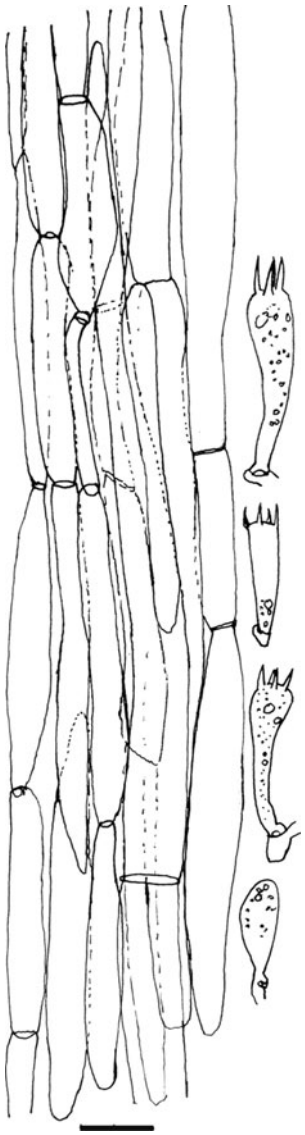


Fig. 12 *Porpolomopsis* aff. *calyptriformis* lamellar cross section (DJL05TN80). Scale bar=20 μm

Humidicutis is **emend. here by Lodge** to include species with a viscid pileipellis.

Pileus convex, convex-umbonate or conic, margin rarely and not deeply splitting; surface subhygrophanous, moist, rarely viscid (e.g., *Humidicutis arcohastata* and *H. auratocephala*), colors usually bright orange, yellow, pink, reddish purple or green but can be dull olivaceous or absent; lamellae thick, sinuate or broadly adnate, often with a decurrent tooth; odor absent or disagreeable; carotenoid pigments usually present, encrusting pigments may also be present on cuticular hyphae, not soluble in alkaline solutions; pileipellis hyphae parallel, prostrate, cylindric; basidia usually 5 or more times longer than the spore length; basidiospores hyaline, thin-walled, inamyloid, not metachromatic, ellipsoid or

broadly ellipsoid, not constricted; lamellar trama subregular or regular, of hyphae <150 μm long, rarely tapered, with right-angled septa; clamp connections absent in context and pellis, but toruloid clamps present at the base of basidia and/or basidioles.

Phylogenetic support There is 100 % ML BS support for a monophyletic *Humidicutis* in the 4-gene backbone (Fig. 1; 1.0 B.P. Online Resource 6), and Supermatrix analyses (Fig. 2), 96 % MLBS support in the ITS-LSU analysis (Fig. 6), 77 % MLBS in the ITS analysis (Online Resource 3) and 83 % MLBS support in the LSU analysis (Fig. 3).

Species included Type species: *Humidicutis marginatus*. Species included based on molecular phylogeny and morphology are *Humidicutis auratocephalus* (Ellis) Vizzini and Ercole (2012) [2011], two undescribed species from Puerto Rico and one from Belize. Species included based on morphology alone include *H. arcohastata* (A.M. Young) A.M. Young, *H. bagleyi* (A.M. Young) A.M. Young, *H. helicoides* (A.M. Young) A.M. Young, *H. lilacinoviridis* (A.M. Young) A.M. Young, *H. luteovirens* (Horak) Horak, *H. multicolor* (Horak) Horak, *H. peleae* Desjardin & Hemmes, *H. poilena* Desjardin & Hemmes and *H. viridimagentea* A.M. Young & Syme. It is uncertain whether *H. taekeri* (A.M. Young) A.M. Young and *H. woodii* (A.M. Young) A.M. Young belong here as their lamellar trama hyphae are fusiform and exceed 140 μm in length. Some species placed by Horak (1990) in *Humidicutis* cannot be verified without analysis of the lamellar trama and molecular sequence data.

Comments Humidicutis was first described as a subgenus of *Tricholoma* by Singer (1948), then raised to generic rank by Singer in 1959 [1958]. It encompasses mostly brightly colored species that lack alkaline soluble pigments and lack clamp connections, except for toruloid clamps in the hymenium. Species of *Humidicutis* typically have rather short lamellar trama hyphae (Fig. 13) as compared to *Porpolomopsis*. While these appear as sister genera in the ITS-LSU and 4-gene backbone analyses, support for the branch that subtends both genera is lacking in the former and moderate (66 % MLBS and 0.67 B.P. in the latter. We retain separate genera here as they represent two strongly supported clades, and they can be separated morphologically by the lamellae which are broadly attached in *Humidicutis* versus adnexed to free in *Porpolomopsis*, and the long, parallel tramal hyphae which corresponds to a tendency for the pileus to split down through the lamellae in *Porpolomopsis* versus shorter, subregular trama hyphae and rarely splitting context in *Humidicutis*. Nevertheless, when treated within the genus *Hygrocybe*, Boertmann's combination of subgen. *Humidicutis* in *Hygrocybe*

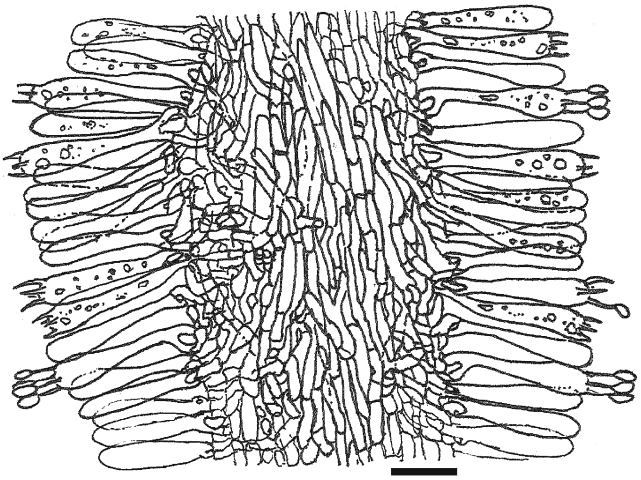


Fig. 13 *Humidicutis auratocephalus* lamellar cross section (DJL05TN81, Tennessee, Great Smoky Mt. Nat. Park, USA). Scale bar=20 μm

(2010, Fungi of Northern Europe 1 (2nd ed): 17) is useful as it reflects the close relationship between these genera. Indeed, Young (2005) included species of *Porpolomopsis* in *Humidicutis*. If using the aggregate genus *Hygrocybe* s.l., the diagnosis of *Hygrocybe* subg. *Humidicutis* (Singer) Boertm. will need emending to include basidiomes with either splitting or non-splitting margins and regular or subregular lamellar context composed of either short or long trama hyphae.

Humidicutis auratocephala (Ellis) Vizzini & Ercole, Micol. Veg. Medit. 16(2): 99 (2012) [2011],

≡ *Hygrophorus auratocephalus* (Ellis) Murrill, Mycologia 9(1): 40 (1917),

≡ *Agaricus auratocephalus* Ellis, Bull. Torrey Bot. Club 6: 75(1876).

Neotype of *Agaricus auratocephalus* designated here, USA: New Jersey, Newfield, in swamp, 28 July 1876, Ellis 3033, NY 774739.

Comments Murrill (1916, 1917) did not find the type among Ellis's collections. Hesler's annotation of Ellis' two collections of *A. auratocephalus* at NY says that while they are authentic, they were apparently collected after the species was described. Ellis 3033 was collected in July 1876, while the journal cover date was February 1876 (released December 1876). The Ellis & Everhart North American Fungi exsiccatti No. 1911 noted by Hesler and Smith (1963) was collected in Aug. 1887, also after the publication date. We selected Ellis 3033 as the neotype as it was authentic material from the topotype location, and Hesler and Smith (1963) found that it matched the protologue in spore dimensions and habitat.

Gliophorus Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 72 (1959).

Type species: *Gliophorus psittacinus* (Schaeff. : Fr.) Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 72 (1959),

≡ *Hygrocybe psittacina* (Schaeff. : Fr.) P. Kumm., Führ. Pilzk. (Zwickau): 112 (1871),

≡ *Hygrophorus psittacinus* (Schaeff.: Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 332 (1838),

≡ *Agaricus psittacinus* Schaeff. : Fr., Fung. Bavar. Palat. 4: 704: 70, t. 301 (1774).

Pileus and stipe glutinous; DOPA based pigments absent, colors include blue, violet, pink, salmon, green, ochre yellow, yellow, brick red, gray-brown or mixtures of these, not bright red; lamellae narrowly or broadly attached, sinuate or decurrent, sometimes with a gelatinized edge; odor absent or of burned rubber; basidiospores ellipsoid, ovoid or obovoid, rarely constricted, hyaline, thin-walled, inamyloid, not metachromatic; ixocheilocystidia present or absent; basidia mostly 4-sterigmate, these and/or basidioles often with toruloid clamp connections, about five times the length of the basidiospores; lamellar trama subregular, of short elements <140 μm long; subhymenium sometimes gelatinized; clamp connections present but sometimes rare in the trama; ixotrichoderm of the pileipellis with toruloid clamps.

Phylogenetic support *Gliophorus* appears as a monophyletic clade only in our 4-gene backbone ML analysis (18 % MLBS, Fig. 1). Similarly, Vizzini and Ercole (2012) [2011] analysis of ITS shows a monophyletic clade lacking MLBS and Bayesian support. Our ML Supermatrix, LSU, ITS-LSU, ITS and Bayesian 4-gene analyses all show *Gliophorus* as a grade that is basal or sister to *Porpolomopsis* and *Humidicutis*. Support for *Gliophorus* as sister to the *Humidicutis – Porpolomopsis* clade is weak, except in our 4-gene backbone ML analysis (97 % BS).

Sections included *Gliophorus*, *Glutinosae* comb. nov. and *Unguinosae*.

Comments Herink (1959) erected the genus *Gliophorus* for species of *Hygrocybe* that had glutinous surfaces and usually bright pigments. The group was validly recombined as *Hygrocybe* subg. *Gliophorus* (Herink) Heinem. (1963). Bon (1990) noted the spectacular basal clamp connections on basidia in this group (termed toruloid by Young 2005) – a character shared with *Humidicutis*. Herink described sect. *Insipidae* in *Gliophorus*, but our molecular phylogenies placed the viscid yellow type species, *H. insipida*, in *Hygrocybe* subg. *Pseudohygrocybe*. The three remaining sections delineated by Herink (1959) are concordant with *Gliophorus* clades or grades in all of our phylogenetic analyses: *Gliophorus* (replaces *G.* sect. *Psittacinae*), *Glutinosae* (replaces *G.* sect. *Laetae*) and *Unguinosae*. In *Hygrocybe* subg. *Gliophorus*, we avoided making new combinaitions for sections as the topology of this group is unstable and may change with greater taxon sampling. *Gliophorus* sect. *Glutinosae* Kühner (1926) is valid, but would need a new combination as *H*ygrocybe sect. *Gliophorus* because Herink's basionym (1959) has priority at section rank over sect. *Psittacinae* (Bataille) Arnolds ex Candusso (1997). Unranked names such as Bataille's (1910) *Psittacinae* do not have a date for priority until they are validly combined at a designated rank (e.g., 1997 in this example). Bon (1990) treated the *H. unguinosae—H. irrigata* group and the *H. psittacina* complex together as stirps within *H.* sect. *Psittacinae*, which is concordant with the topology in our ITS-LSU analysis. These two groups could also be treated as subsections of *Hygrocybe* sect. *Gliophorus*, in which case, *H.* subsect. *Psittacinae* (Bataille) Arnolds ex Candusso (1997) is available, but *G.* sect. *Unguinosae* would need to be recombined in *Hygrocybe* at subsection rank (Table 1).

Gliophorus*, sect. *Gliophorus [autonym]

[= *Gliophorus* sect. "*Psittacinae*" (Bataille) Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 81 (1959), nom. invalid, Art. 22.1, 22.2].

Type species: *Gliophorus psittacinus* (Schaeff.) Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 82 (1959),

≡ *Hygrocybe psittacina* (Schaeff.) P. Kumm. (1871),

≡ *Hygrophorus psittacinus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 332 (1838),

≡ *Agaricus psittacinus* Schaeff., Fung. Bavar. Palat. 4: 301 (1774)].

Characters as in sect. *Gliophorus*, but pileus conico-campanulate or convex, some plano-convex with or without an umbo; colors typically green, purple, salmon or brick red, not gray-brown as in sect. *Unguinosae*; differs from sect. *Glutinosae* in usually having a pileus that is conico-campanulate or convex instead of plano-convex or indented, sinuate rather than decurrent lamellae, uninucleate spores, absence of gelatinization in the lamellar edge and subhymenium, and absence of ixocheilocystidia; differing from sects. *Glutinosae* and *Unguinosae* in form of basal clamp connections on basidia and basidioles (not toruloid).

Phylogenetic support There is no phylogenetic support for a monophyletic sect. *Gliophorus* in our analyses. Similarly, the ITS analysis by Dentinger et al. (unpublished data) shows that *G. psittacinus* is polyphyletic. Additional analyses with greater taxon sampling and genes are needed in this group. While this section may be polyphyletic, the long branches in this group likely contribute to topological instability and there is little or no support for separating the two putative *G. psittacinus* collections from Denmark and Sweden. It is not clear which, if either, of our two sequenced reference collections represents the type species, *G. psittacinus,* as both match

the protolog and type painting. Nevertheless, they are 42.7 % divergent in their ITS and 24.8 % divergent in their LSU sequences. Based on ITS sequences, the collection from Denmark is only 6.2 % divergent from a Hungarian collection but 18 % divergent from an eastern N. American collection, while the collection from S. Sweden is conspecific (1.3 % divergence) with a collection from Japan.

Species included Type species: *Gliophorus psittacinus*. Additional species included based phylogeny and morphology: *Gliophorus perplexus* (A.H. Sm. & Hesler) Kovalenko, plus *G. europerplexus* Dentinger, A.M. Ainsw., & P.F. Cannon and *G. reginae* Dentinger, A.M. Ainsw., & P.F. Cannon (Ainsworth et al., 2013) *Hygrocybe stevensoniae* T.W. May & A.E. Wood is included based on morphology.

Comments Herink (1959) described this as sect. "*Psittacinae*", nom. invalid (Art. 22.2) and Kovalenko (1989) corrected the name to *Gliophorus* because this section contains the type species of the genus so it must repeat the genus name exactly but without author (Art. 22.1). We have retained Herink's (1959) and Kovalenko's (1989) narrow circumscription for this group in *Gliophorus* but Bon's (1990) broader circumscription in *Hygrocybe* (latter combination unpublished) to avoid making changes that are not strongly supported by phylogentic analyses. The extraordinarily high sequence divergence among collections identified as *H. psittacinus* indicates this is a species complex and is in need of further study. Specifically, an epitype needs to be selected and sequenced from the Austrian Alps or Bavarian Forest to stabilize the concept of the genus and sect. *Gliophorus*.

Gliophorus* sect. *Glutinosae (Kühner) Lodge & Padamsee, comb. nov.

MycoBank MB804064.

Basionym: *Hygrocybe* sect. *Glutinosae* Kühner, *Botaniste* 17: 53 (1926).

Lectotype: *Gliophorus laetus* (Pers.: Fr.) Herink (1959) [1958], Sb. Severocesk. Mus., Prír. Vedy 1: 84, selected by Candusso, *Hygrophorus*. Fungi europ. (Alassio) 6: 591 (1997).

≡ *Hygrocybe laeta* (Pers. : Fr.) P. Kumm. (1871),

≡ *Hygrophorus laetus* (Pers. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 328 (1838) [1836–1838,

≡ *Agaricus laetus* Pers., Observ. Mycol. (Lipsiae) 2: 48 (1800) [1779] : Fr.].

[≡ *Gliophorus* sect. *Laetae* (Bataille) Kovalenko 1989, based on *Hygrocybe* sect. *Laetae* (Bataille) Singer (1949) 1951, is superfluous, nom. illeg.].

G. sect. *Glutinosae* is **emended here by Lodge** to exclude *Gliophorus unguinosus* (Fr. : Fr.) Kovalenko.

Characters as in *Gliophorus*; pileus plano-convex and often indented in center; colors green, olive, blue, violet, pink, salmon, yellow, buff, orange or orangish brown; differs from the other sections in having decurrent lamellae and a subhymenium that is gelatinized, at least near the lamellar edge in age, and ixocheilocystidia embedded in a gelatinous matrix; differs from sect. *Gliophorus* in having a flatter pileus that lacks an umbo and is often indented, spores that are often bi- rather than uninucleate, according to Kühner, and basidia with toruloid clamp connections; differs from sect. *Unguinosae* in usually having bright pigments and a gelatinized lamellar edge.

Phylogenetic support There is strong support for a monophyletic sect. *Glutinosae* in all of our phylogenetic analyses. ML bootstrap support is 100 % in our ITS-LSU, 100 % in our LSU and 99 % in our Supermatrix and ITS analyses. Dentinger et al. (unpublished data) also show strong support (100 % MLBS) for sect. *Glutinosae* in their ITS analysis, after correcting misdeterminations.

Species included Type species: *Gliophorus laetus* (Pers.) Herink. *Gliophorus graminicolor* E. Horak is included based on molecular analyses and morphology. Species included based on morphology alone are *G. lilacipes* E. Horak, *G. pallidus* E. Horak, *H. pseudograminicolor* A.M. Young, *G. versicolor* E. Horak, *Hygrocybe chromolimonea* (G. Stev.) T.W. May & A.E. Wood, *H. flava* (Boertm.) F. Rune, *H. noelokelani* Desjardin & Hemmes and *H. viscidobrunnea* Bougher & A.M. Young.

Comments Sect. *Glutinosae* was described by Kühner in 1926 and has priority over the unranked name '*Laetae'* Bataille that was combined in *Hygrocybe* at section rank by Singer in 1951 (superfluous, nom. illeg.). Kühner indicated that since he showed that *H. punicea* was not in the same group as *H. laeta* Pers., he renamed Fayod's sect. *Puniceae* as *Glutinosae* (placing *H. punicea* in section *Coccineae*). Kühner included two species, *H. laeta* and *H. unguinosa*. Apparently Candusso (1997) interpreted Kühner's wording to indicate that the type species was *H. laeta*, but since Kühner's wording did not meet the criteria for designating a type, Candusso (1997) inadvertently designated *H. laeta* as the lectotype. We use Singer's (1951) concept, which excludes *H. unguinosa* and other gray-brown species that lack a gelatinized lamellar margin. Sect. *Glutinosae* is readily recognized by the decurrent lamellae that have a gelatinized edge, and this monophyletic clade is strongly supported by all molecular phylogenies.

Gliophorus* sect. *Unguinosae Herink., Sb. Severocesk. Mus., Prír. Vedy 1: 81,

Type species: *Agaricus unguinosus* Fr. : Fr., Syst. mycol. (Lundae) 1: 101 (1821),

≡ *Gliophorus unguinosus* (Fr. : Fr.) Kovalenko, Mikol. Fitopatol. 22(3): 209 (1988),

[≡ "*Gliophorus unguinosus*" Herink, Sb. Severocesk. Mus., Prír. Vedy 1: 81 (1959), nom. invalid, Art. 41.5],

≡ *Hygrocybe unguinosa* (Fr. : Fr.) P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 237 (1879),

= *Hygrocybe irrigata* (Pers. : Fr.) Bon, Doc. Mycol. 6(24): 4 (1976).

Characters as in *Gliophorus* but gray-brown in color, bright pigments absent; pileus broadly campanulate or convex, often umbonate; lamellae broadly attached, sinuate or adnate with a decurrent tooth or short-decurrent, edge not gelatinized; clamp connections infrequent in the context, toruloid in form at the base of basidia; basidia 5.5–6.5 times the length of the basidiospores; differs from most species in sects. *Gliophorus* and *Glutinosae* in absence of bright pigments; differs from sect. *Gliophorus* in having toruloid rather than modest medallion clamp connections in the hymenium; differs from sect. *Glutinosae* in having a convex or campanulate (not plane or indented) pileus shape and lacking a gelatinized lamellar edge with ixocheilocystidia.

Phylogenetic support Only one representative of this section, *H. irrigata*, is included in our analyses, so we cannot determine support values for this section. However, Ercole (Online Resource 3) shows 100 % MLBS support for a clade comprising two collections of *H. irrigata*, from Europe and a related species from the SE USA (DJL05NC50). In our Supermatrix analysis (Fig. 2), *H. irrigata* is the most basal branch in the *Gliophorus* clade.

Type species: *G. unguinosus* (Fr. : Fr.) Kovalenko. Two unnamed species in the southeastern USA are included based on phylogenetic and morphological data. Arnolds (1990) and Bon (1990) recognized both *G. unguinosus* (Fr.) Kovalenko and *G. irrigatus,* but Boertmann (1995, 2010) and Candusso (1997) treat them as synonyms. Dentinger et al. (unpublished data) show a tight clade on a long branch for six collections from the UK and one each from Hungary and Denmark, which is consistent with the synonomy given in Boertmann (1995, 2010) and Candusso (1997).

Comments Herink (1959) described sect. *Unguinosae* for gray-brown species of *Gliophorus* lacking a gelatinized lamellar edge, citing as type "*Gliophorus unguinosus* (Fr.) comb. n.". The binomial combination was not validly published (Art. 41.5) as it lacked any citation (Art. 41.6) and accompanying description (Art. 41.8), but the fact that the genus *Gliophorus* was stated to be based on *Hygrocybe* (Fr.) Karsten p.p., and that he indicated an earilier name via citation of "(Fr.)" in that pool plus the fact that there is only one species with the validly published epithet '*unguinosa*' in that limited pool, namely *Agaricus unguinosus*/*Hygrocybe unguinosa*, we believe he fulfilled the requirements for valid publication of the subgeneric sectional name by indicating the identity of the type (Art. 40.1). Singer (1986) recognized Herink's section, but his attempt to combine it in *Hygrocybe* was invalid because he failed to cite the original publication (Art. 33.4). Arnolds (1990), Bon (1990), Boertmann (1995, 2010) and Candusso (1997) placed *H. unguinosa* in sect. *Glutinosae*, and included the type species of *Gliophorus, H. psittacina*, in the section. The name, *Gliophorus* (1958), however, has priority over *Psittacinae* (Bataille) Arnolds ex Candusso (1997) at section rank, but that combination has not yet been made in *Hygrocybe* (Table 1).

Tribe *Chromosereae* Vizzini, Lodge, Norvell & Redhead, tribe nov.

MycoBank MB804054.

Type genus: *Chromosera* Redhead, Ammirati & Norvell, Beih. Sydowia 10: 161 (1995).

Emended by Vizzini & Ercole, Micol. Veget. Medit. 26(2): 97 (2012) [2011].

Basidiomes omphalioid (small, with indented pileus and decurrent or arcuate-decurrent lamellae), sometimes with a gelatinized lamellar edge; pigments yellow and/or lilac; surfaces usually viscid; clamps present throughout (sometimes rare in the trama), may be medallion form but not toruloid at the basidial bases; basidia short relative to basidiospore lengths (ratio 3.6–5); basidiospores hyaline, thin-walled, inamyloid, not cyanophilic; cheilocystidia present if lamellar edge is gelatinized; lamellar trama subregular or interwoven, with or without a central subregular strand; ephemeral dextrinoid reactions occasionally present in context; pileipellis an ixotrichoderm when young, often an ixocutis with age (rarely a cutis), sometimes with ephemeral pigment bodies just below the epicutis; stipitipellis an ixocutis (rarely a cutis); mostly growing on ground in arctic-alpine habitats or on conifer wood, possibly associated with grasses and bryophytes.

Phylogenetic support Tribe *Chromosereae* is supported by all molecular phylogenies. Support is strong in our 4-gene backbone analysis (100 % MLBS, 1.0 BPP), Supermatrix (85 % MLBS), LSU (98 %), ITS-LSU (100 % MLBS) and moderate in Dentinger et al.'s ITS analysis (unpublished data, 63 % MLBS). Support for this clade is lower in our ITS analysis (54 % MLBS, Online Resource 3). Previous studies also support tribe *Chromosereae* (represented by *C. cyanophylla* and *C. citrinopallida*). Support shown is 90 % MPBS in Moncalvo et al. (2002; LSU), 100 % MLBS in Lawrey et al. (2009; ITS-LSU), and 1.0 BPP and 96 % MLBS in Vizzini and Ercole (2012; ITS, with addition of *C. viola* and *C. xanthochroa*). The Supermatrix and ITS-LSU analyses place this group near *Gliophorus*, supporting Kühner (1980).

Genera included Tribe *Chromosereae* currently is comprised of the type genus, *Chromosera*, and a new genus, *Gloioxanthomyces*, erected for *Hygrocybe nitida* and *H. vitellina*.

Chromosera Redhead, Ammirati &Norvell, Beih. Sydowia 10: 161 (1995), Vizzini & Ercole, Micol. Veget. Medit. 26(1): 97 (2012).

Type species: *Agaricus cyanophyllus* Fr., Öfvers. Kongl. Svensk Vet.-Akad. Förh. 18(1): 23 (1861)

≡ *Chromosera cyanophylla* (Fr.) Redhead, Ammirati & Norvell, Mycotaxon 118: 456 (2012) [2011].

Emended by Vizzini & Ercole, Micol. Veget. Medit. 26(2): 97 (2012) [2011].

Characters as in Tribe *Chromosereae* except for absence of gelatinization of lamellar edge and cheilocystidia; ephemeral dextrinoid reactions in the context, ephemeral pigment bodies in the pileipellis and lilac pigments sometimes present.

Phylogenetic support Except for our ITS analysis by Ercole which shows 62 % MLBS support for *Chromosera*, support for this clade is the same as noted above for tribe *Chromosereae*. Greater taxon and gene sampling are needed to refine this group.

Subgenera included Comprising three subgenera: *Chromosera*, *Subomphalia* Vizzini, Lodge & Padamsee, subg. nov. and subg. *Oreocybe* (Boertm.) Vizzini & Lodge, comb. nov.

Comments *Chromosera* was proposed for what was believed a single amphi-Atlantic species, *C. cyanophylla* (Redhead et al. 1995, 2012) based on *Agaricus cyanophyllus* Fr. from Europe and *A. lilacifolius* Peck from the eastern USA. These species were originally classified among the omphalioid spp. in *Agaricus* (Omphalia), *Omphalia,* or *Omphalina* (Fries 1861; Peck 1872; Peck 1878; Quélet 1886; Murrill 1916). In the 20th century, some authors retained *C. cyanophylla* in *Omphalina* (Courtecuisse 1986; Krieglsteiner and Enderle 1987). Singer (1942) transferred *A. lilacifolius* to *Clitocybe* (a placement rejected by Bigelow, 1970), while Smith (1947) placed it in *Mycena* based on the dextrinoid hyphae in the stipe and pileus context and viscid stipe. While Singer (1949) [1951] accepted Smith's classification of *A. lilacifolius* in *Mycena*, Kühner (1980) placed *A. cyanophyllus* in *Hygrocybe* subg. *Gliophorus* but his new combination was not validly published. Maas Geesteranus (1992) subsequently excluded *A. lilacifolius* from *Mycena* based on its inamyloid spores, (erroneously) an absence of dextrinoid reaction in the lamellar context, and absence of cheilocystidia. Redhead et al. (1995) synonymized *A. lilacifolius* with *A. cyanophylla* and erected the genus *Chromosera* to accommodate this enigmatic taxon, believing it to be most closely allied with *Mycena* based on the dextrinoid context. While the genus *Chromosera* was validly published in 1995, an incorrect citation was used in recombining the type species as *C. cyanophylla* (Art. 33.5, 33.7, 33.8, MB563787), and the combination was made correctly in 2011 [2012]. Maximum parsimony analyses by Moncalvo et al. (2002) support placement of '*C. cyanophylla*' from western North America in the Hygrophoraceae.

Based on morphological and phylogenetic analyses, Vizzini and Ercole (2012 expanded *Chromosera* from a monotypic genus to include *Hygrocybe viola* and species formerly in *Hygrocybe* subg. *Oreocybe* Boertm. Unlike *C. cyanophylla,* dextrinoid reactions are absent from the context in subg. *Oreocybe* and *C. viola* (subg. *Subomphalia*). The characteristic but ephemeral pigment bodies found in the pileipellis *C. cyanophylla* are also present in subg. *Oreocybe* (DMB), but not in *C. viola* (verified in fresh material by AV). The combination of characters separating *C. cyanophylla, C. viola,* and subg. *Oreocybe* are so striking that we recognize them below as subgenera: *Chromosera*, *Oreocybe*, and *Subomphalia*.

Chromosera* subg. *Chromosera [autonym].

Type species: *Agaricus cyanophyllus* Fr., Öfvers. K. Svensk. Vetensk.-Akad. Förhandl. 18(1): 23 (1861),

≡ *Chromosera cyanophylla* Redhead, Ammirati & Norvell in Redhead, Ammirati, Norvell, Vizzini & Contu, Mycotaxon 118: 456 (2012) [2011].

Pileus and stipe surfaces viscid, pale yellow, sometimes with rosy vinaceous tints; lamellae arcuate-decurrent, bluish or rosy lilac; tramal tissues weakly dextrinoid, only demonstrable in fresh or recently dried collections; lamellar context regular or subregular, becoming more disorganized with age; basidiospores amygdaliform or ellipsoid, not strangulated, mean spore Q 2.3, hyaline, thin-walled, inamyloid, not cyanophilous; cheilocystidia absent; basidia short (20–25 (−29) μm long), basidium to basidiospore length ratio 3.6–5; pileipellis an ixotrichoderm, with extracellular (possibly also intracellular) pigment globules demonstrable only in fresh or recently dried collections; clamp connections throughout the basidiomes, none toruloid; lignicolous, growing on white-rotted conifer wood.

Subg. *Chromosera* differs from subg. *Oreocybe* in lignicolous habit, dextrinoid tramal tissues, regular rather than interwoven lamellar trama, and non-constricted spores. Subg. *Chromosera* shares non-constricted spores with *C. viola* (subg. *Subomphalia*) but differs in lignicolous habit rather than terrestrial among mosses, viscid pileus and stipe surfaces, dextrinoid reactions in tramal tissues, and a (sub)regular lamellar trama that lacks a subregular core of highly inflated elements flanked by strata of highly interwoven slender hyphae.

Phylogenetic support Our ITS-LSU analysis shows 100 % ML BS support for a monophyletic clade on a relatively long branch comprising European and western North American '*C. cyanophylla*' taxa. Subg. *Chromosera* is sister to members of subg. *Oreocybe* (*C. citrinopallida*, *C. xanthochroa* and/or *C. lilacina*) in our 4-gene backbone analyses (100 % MLBS, 1.0 B.P. Fig. 1 and Online Resource 6). Dentinger et al.

(unpublished) show subg. *Chromosera* as a strongly supported terminal clade (96 % MLBS) emerging from a paraphyletic subg. *Oreocybe* grade in their ITS analysis. Others previously found high support for a sister relationship between *C. cyanophylla* and *H. citrinopallida* in analyses of LSU (90 % MPBS, Moncalvo et al. 2002), and ITS sequences (100 % BPP and 79 % MLBS, Vizzini and Ercole 2012). Our Supermatrix analysis, however, places the European and western North American variants on separate branches, with *H. citrinopallida* making *C. cyanophylla* polyphyletic, but the only supported internal branch had representatives from two western US states, Washington and Wyoming. Low variation in the ITS region in *Chromosera* and removal of some ITS bases to align sequences across the entire Hygrophoraceae may have affected the Supermatrix analysis, and the western North American taxon may represent a separate species.

Species included Type species: *Chromosera cyanophylla*, currently monotypic, but likely a species complex.

Comments Subg. *Chromosera* was originally described as a monotypic genus for the presumed amphi-Atlantic species, *C. cyanophylla*. The type species of *Chromosera*, *Agaricus cyanophyllus* Fr., was described from Europe while *Agaricus lilacifolius* Peck (a replacement name for *A. lilacinus* Peck, illeg.) was described from eastern North America. While these two taxa were thought to be conspecific (Redhead et al. 1995), our ITS sequences from Europe and western North America are 5 % divergent, and there are some morphological differences (SR) suggesting they likely represent different species. We were unsuccessful in sequencing collections of *A. lilacifolius* from eastern North America for comparison, so we are uncertain as to whether it is conspecific with the western North American taxon. Greater sampling of taxa, gene regions and geographic areas are needed in this group. A new species to be described from China may prove critical to future molecular analyses.

Chromosera* subg. *Oreocybe (Boertm.) Vizzini, Lodge & Padamsee, comb. nov.

MycoBank MB804070.

Basionym: *Hygrocybe* sect. *Oreocybe* Boertm., Nordic Jl Bot. 10(3): 315 (1990),

Type species: *Chromosera citrinopallida* (A.H. Sm. & Hesler) Vizzini & Ercole, Micol. Veget. Medit. 26(2): 97 (2012) [2011]

≡ *Gliophorus citrinopallidus* (A.H. Sm. & Hesler) Kovalenko (1999),

≡ *Hygrocybe citrinopallida* (A.H. Sm. & Hesler) Kobayasi, Bull. natn. Sci. Mus., Tokyo 14(1): 62 (1971),

≡ *Cuphophyllus citrinopallidus* (A.H. Sm. & Hesler) Bon, Docums. Mycol. 21(no. 81): 56 (1991),

≡ *Hygrophorus citrinopallidus* A.H. Sm. & Hesler, Sydowia (1–6): 327 (1954)].

≡ *Hygrocybe* subg. *Oreocybe* (Boertm.) Beis., Regensburger Mykologische Schriften 10: 11 (2002).

Basidiomes omphalioid (small, with indented pileus and decurrent or arcuate-decurrent lamellae); pigments yellow, buff, orange, and/or lilac to purple; surfaces viscid; lamellar context interwoven, some with a central strand of parallel hyphae; clamps present throughout and not toruloid at the basidial bases; basidia short relative to basidiospore lengths (ratio 3.6–5); some basidiospores constricted, Q 1–2.7; ephemeral greenish yellow extracellular pigment bodies present in the pileipellis; growing in soil among grasses, mosses and arctic-alpine plants. Differing from subg. *Chromosera* in having interwoven lamellar trama and some constricted spores, and terrestrial rather than lignicolous habit. Differing from *C. viola* in subg. *Subomphalia* by having viscid pileus and stipe surfaces, yellow to orange pigments, some constricted spores, an interwoven lamellar context lacking a differentiated central strand, presence of extracellular pigment bodies in the pileipellis, and growing in the arctic-alpine zone. Differing from subg. *Chromosera* in terrestrial rather than lignicolous habit, lacking dextrinoid reactions in context tissues, and having interwoven lamellar trama and some constricted spores. Differing from *Glioxanthomyces nitidus* and *G. vitellinus* in lamellar trama being interwoven rather than subregular with subglobose elements and absence of a gelatinized lamellar margin and cheilocystidia.

Phylogenetic support Subg. *Oreocybe* appears as a well-supported, short-branched grade that is paraphyletic to the long-branched subg. *Chromosera* in our LSU, ITS-LSU and ITS analyses. MLBS support for the *Oreocybe* branch is 76 % in our ITS-LSU, 64 % in our LSU, and 68 % in our ITS analysis by Ercole (Online Resource 3). Subg. *Oreocybe* has similar topology and support in the ITS analysis by Dentinger et al. (79 % MLBS support for the subtending branch, and 93 % MLBS support for it as sister to subg. *Subomphalia*, unpublished data). In our Supermatrix analysis and Vizzini & Ercole's ITS analysis, *C. citrinopallida* and *C. xanthochroa* are intermixed with *C. cyanophylla*, but without support for the internal branches. This may be an artifact of including the ITS region, which varies little in this group, and editing out variation in order to align sequences across the family.

Species included Type species: *Chromosera citrinopallida*. Species included based on molecular phylogenies and morphology are *C. xanthochroa* (P.D. Orton) Vizzini & Ercole, and *C. lilacina* (P. Karst.) Vizzini & Ercole.

Comments Subgen. *Oreocybe* was originally described by Boertmann (1990) as a section in *Hygrocybe* subg. *Cuphophyllus* because of the interwoven lamellar trama and

decurrent lamellae – a placement retained by Candusso (1997). *Oreocybe* was then raised to subgenus rank in *Hygrocybe* by Beisenherz (2002). Kovalenko (1999) placed these species in *Gliophorus*. There is a disagreement in ITS sequences between Boertmann's Danish and other Scandinavian collections deposited at O versus collections from the UK deposited at Kew with regard to determinations as *C. citrinopallida* and *C. xanthochroa* (they are reversed); here we use sequences of the Kew collections for reference as their determinations were verified by matching to sequences of the types and to facilitate comparisons with Dentinger et al. (unpublished). The Scandinavian collections were renamed by matching them to the Kew reference sequences. Boertmann has examined the Kew collections and agrees with their determinations, so the characters used to distinguish these two species need to be re-examined as they may not be reliable across the entire geographic range.

Chromosera* subg. *Subomphalia Vizzini, Lodge & Padamsee, subg. nov.

MycoBank MB804071.

Type species: *Chromosera viola* (J. Geesink & Bas) Vizzini & Ercole, Micol. Veget. Medit. 26(2): 97 (2012) [2011].

≡ *Hygrocybe viola* J. Geesink & Bas, in Arnolds, Persoonia 12(4): 478 (1985a),

≡ *Cuphophyllus viola* (J. Geesink & Bas) Bon, Doc. Mycol. 19(76): 73 (1989).

Omphalioid, pileus indented in center, basidiomes purple or lilac, yellow pigments absent; surfaces dry; dextrinoid reactions absent from all context tissues; clamp connections rare in the trama, some medallion clamps present at base of basidia; basidiospores hyaline, thin-walled, inamyloid, not cyanophilic, broad, Q 1.0-1.9 (mean Q 1.5), not constricted; basidia short relative to the length of the basidiospores (ratio 3.6-5); lamellar context heterogeneous with a central, subregular strand composed of short, highly inflated elements, flanked by lateral strata with highly interwoven slender hyphae. Terrestrial, often among mosses, not in arctic-alpine habitats. Differing from subg. *Chromosera* in dry basidiome surfaces; absence of yellow pigments, extracellular pigment bodies in the pileipellis and dextrinoid reactions in tramal tissues; presence of a heterogeneous lamellar trama; and a terricolous (possibly moss-associated) rather than lignicolous habit. Differing from subg. *Oreocybe* in dry rather than viscid surfaces, absence of yellow pigments, absence of extracellular pigment bodies in the pileipellis, presence of a heterogeneous rather than interwoven lamellar trama, and broad non-constricted basidiospores. Differing from *Glioxanthomyces* in dry rather than viscid surfaces, absence of gelatinization of the lamellar edge, absence of yellow pigments, and presence of a heterogeneous rather than interwoven lamellar trama.

Phylogenetic support Subg. *Subomphalia* appears on a basal branch that is long relative to others in the *Chromosera* clade. The branch placing the monotypic species, *C. viola*, as sister to subgenera *Oreocybe* and *Chromosera* has strong support: 96 % MLBS and 1.0 BPP in ITS analyses by Vizzini and Ercole (Vizzini and Ercole 2012), and moderate support (62 % MLBS) in our ITS analysis (Online Resource 3) and 100 % MLBS in Dentinger et al.'s (unpublished) ITS analysis.

Species included Type species: *Chromosera viola.*

Comments This new, currently monotypic subgenus in *Chromosera* is erected for *C. viola*. It was originally described in *Hygrocybe* by Geesink & Bas, then transferred to *Cuphophyllus* by Bon because of the highly interwoven hyphae in the lateral strands of the lamellar context.

Glioxanthomyces Lodge, Vizzini, Ercole & Boertm., gen. nov.

MycoBank MB804073

Type species: *Hygrophorus vitellinus* Fr., Monogr. Hymenomyc. Suec. (Upsaliae) 2(2): 312 (1863),

≡ *Glioxanthomyces vitellinus* (Fr.) Lodge, Vizzini, Ercole & Boertm.

Lectotype here designated for *Hygrophorus vitellinus* Fr. is an illustration cited in Fries, Monogr. Hymenomyc. Suec. (Upsaliae) 2(2): 312 (1863): Icon. t. 167, f. 3.

Pileus and stipe yellow or orangish yellow, viscid; lamellae arcuate-decurrent, yellow, with a gelatinized or subgelatinized edge, edged often darker (translucent). Basidiospores ellipsoid or subglobose, Q 1.0—1.6, mean Q 1.2—1.3, guttulate in KOH, with a wide hilar appendix, inamyloid, acyanophilic, hyaline, smooth; basidia usually 4-sterigmate, with basal clamp connection occasionally a moderate medallion type, short, 30—40 μm long, ratio of basidia to basidiospore length 4–5; pileipellis and stipitipellis an ixotrichodermium or ixocutis; trama not dextrinoid; lamellar trama subregular, central strand not differentiated, elements cylindric to subglobose, some subglobose cells highly inflated to 10—30 μm diam., subhymenium of tightly interwoven small diameter hyphae, not gelatinized except at the lamellar edge; edge gelatinized or subgelatinized; cheilocystidia clavate, simple or slightly lobed. Clamp connections present throughout, occasionally a modest medallion type, not toruloid. It differs from *Chromosera* subg. *Oreocybe* in presence of a gelatinized lamellar edge and cheilocystidia, and basidiospores with smaller Q (1.2–1.3 vs. 1.4–1.8) and never constricted. It differs from *Chromosera* subg. *Chromosera* in absence of dextrinoid reactions in the context, absence of pigment globules in the pileipellis and lamellar edge gelatinized with cheilocystidia present. It differs from *Chromosera* subg.

Subomphalia in absence of violaceous pigments, viscid rather than dry surfaces, and absence of a central strand in the lamellar trama.

Etymology Gloio — glutinous, xantho —yellow, myces — fungus.

Gloioxanthomyces vitellinus (Fr.) Lodge, Vizzini, Ercole & Boertm., comb. nov.

MycoBank MB804074

Basionym: *Hygrophorus vitellinus* Fr., Monogr. Hymenomyc. Suec. (Upsaliae) 2(2): 312 (1863),

≡ *Gliophorus vitellinus* (Fr.) Kovalenko (1988),

[=?*Hygrocybe luteolaeta* Arnolds].

Lectotype for *Hygrophorus vitellinus* Fr. is an illustration cited by Fries in Monogr. Hymenomyc. Suec. (Upsaliae) 2(2): 312 (1863): Hym. Eur. p. 417, Icon. T. 167, f. 3. Epitype designated by Lodge, Vizzini, Ercole & Boertmann): SWEDEN: RT 90: 6139700; 1336190, in swampy coastal chalk pasture, coll. K. Bergelin, 8 Oct. 2011, LD 1617064. (Berlgin 2012, Svensk Mykologisk Tidskrift 33: 2–8)

Gloioxanthomyces nitidus (Berk. & M.A. Curtis) Lodge, Vizzini, Ercole & Boertm., comb. nov.,

MycoBank MB804075

Type: USA, South Carolina, on earth in damp swamp, M.A. Curtis no. 2893, coll. H.W. Ravanel, Esq., ex herb. Berkeley 1605, K(M) 181764.

Basionym: *Hygrophorus nitidus* Berk. & M.A. Curtis, Ann. Mag. nat. Hist., Ser. 2, 12: 424 (1853),

≡ *Hygrocybe nitida* (Berk. & M.A. Curtis) Murrill [as '*Hydrocybe*'], *N. Amer. Fl.* (New York) 9(6): 378 (1916),

[≡ *Hygrocybe nitida* (Berk. & M.A. Curtis) Malloch (2010), superfluous],

≡ *Gliophorus nitidus* (Berk. & M.A. Curtis) Kovalenko, *Mikol. Fitopatol.* 22(3): 209 (1988)].

[Not "*Hygrophorus nitidus* Fr." (1863) ≡ *Hygrophorus friesii* Sacc. (1887)].

Phylogenetic support As only ITS sequences are available for *G. vitellinus* and *G. nitidus, Gloioxanthomyces* is included only in our ITS analysis. The clade representing *Gloioxanthomyces* has 97 % MLBS support in our ITS analysis by Ercole (Online Resource 3). Both Ercole's and Zhang's (in Boertmann 2012) ITS phylogenies place *Gloioxanthomyces* as sister to *Chromosera citrinopallida* (54 % MLBS and significant BS, respectively). In ITS analyses by Dentinger et al. (unpublished data), *G. vitellinus* and *G. nitidus* appear in clade with 99 % and 100 % MLBS support (entire Hygrophoraceae, and tribe *Chromosereae*, respectively) that is sister to *Chromosera* (63 % MLBS).

Species included Type: *Gloioxanthomyces vitellinus* is European, while its sister species, *G. nitidus* is known from continental North America and Newfoundland (Boertmann 2012).

Comments Gloioxanthomyces falls between *Gliophorus* sect. *Glutinosae* and *Chromosera* based on morphology (Table 3) and ITS sequence divergences. *Gloioxanthomyces* sequences diverge more from *Gliophorus* sect. *Glutinosae* (30 %) than from *Chromosera* (17 % divergent), which is concordant with placement of *Gloioxanthomyces* as sister to *Chromosera* in phylogenetic analyses by Ercole (Online Resource 3) and Zhang (in Boertmann 2012). Those results are concordant with the ITS analyses by Dentinger et al. (unpublished). Morphologically, *G. vitellinus* and *G. nitidus* share with *Gliophorus* sect. *Glutinosae* an indented pileus, gelatinized lamellar edge, subregular lamellar trama and presence of cheilocystidia, but they differ from sect. *Glutinosae* in having modest rather than toruloid clamps in the hymenium, absence of a gelatinized subhymenium, having cheilocystidia that are cylindric or clavate rather than undulating and forked, and mean ratio of basidia to basidiospore lengths of 4.3–5.5 rather than 5–7 (Fig. 14). *Gloioxanthomyces vitellinus* and *G. nitidus* share with *Chromosera* an indented pileus, yellow pigments, absence of toruloid clamp connections in the hymenium, and mean ratio of basidia to basidiospore lengths of 3.5–5.5, but they differ in having a gelatinized lamellar edge, and presence of cheilocystidia. While further analyses with more gene regions are needed, we place *G. nitidus* and *G. vitellinus* in tribe *Chromosereae* based on a combination of molecular, phylogenetic and morphological data.

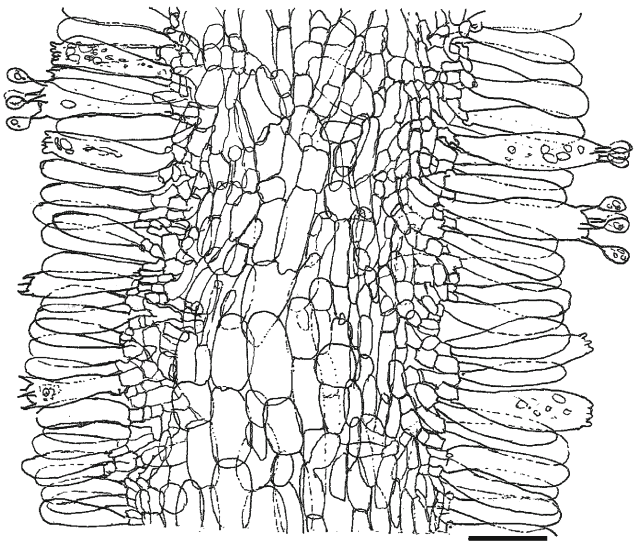


Fig. 14 Subf. *Hygrocyboideae*, tribe *Chromosereae*. *Gloioxanthomyces nitidus* (DJL06NC87, North Carolina, Great Smoky Mt. Nat. Park, USA). Scale bar=20 μm

Subfam. *Hygrophoroideae* E. Larss., Lodge, Vizzini, Norvell & Redhead, subf. nov.

Mycobank 804083.

Type genus *Hygrophorus* Fr., Fl. Scan.: 339 (1836) [1835].

Basidiomes gymnocarpous or secondarily mixangiocarpous; lamellae subdecurrent to deeply decurrent; trama inamyloid; lamellar trama 1) divergent, hyphae diverging from a central strand, or 2) bidirectional, horizontal hyphae that are parallel to the lamellar edge present, sometimes woven through vertically oriented, regular or subregular generative hyphae that are confined or not to a central strand; subhymenium lacking, cells giving rise to basidia originating from hyphae that diverge from the vertical generative hyphae, pachypodial hymenial palisade sometimes present, comprising buried hymenia, thickening over time via proliferation of candelabra-like branches that give rise to new basidia or subhymenial cells; basidiospores thin- or thick-walled, inamyloid, metachromatic or not, hyaline or lightly pigmented (ochraceous, salmon, green); pigments muscaflavin or carotenoids; habit ectomycorrhizal or xylophagous, rarely terricolous.

Phylogenetic support Our 4-gene backbone, Supermatrix and ITS-LSU analyses consistently place *Chrysomphalina* as sister to *Hygrophorus* with moderate support (62 %, 68 % and 62 % MLBS, respectively), with stronger MLBS support for placing the *Hygrophoroideae* as sister to the *Neohygrocybe-Chromosera* clade or the entire *Humidicuteae* clade (*Neohygrocybe, Gliophorus, Humidicutis, Porpolomopsis, Chromosera*) (79 % for ITS-LSU; 77 % for the 4-gene backbone). Matheny et al. (2006) shows the strongest support (1.0 B.P. for *Chrysomphalina* as sister to *Hygrophorus* ss using a 5-gene Supermatrix analysis. Similarly, using ITS alone, Vizzini and Ercole (2012) [2011] show moderate BPP support (0.91) for the clade comprising four *Hygrophorus* species with *C. chrysophylla*, *C. grossula,* and *Haasiella splendidissima*. An ITS-LSU analysis by Vizzini et al. (2012) shows the same topology, but with lower support. Although LSU sequence analyses by Moncalvo et al. (2002) do not show significant MP support for the *Chrysomphalina–Hygrophorus* clade, this clade is found in all their most parsimonious weighted and unweighted MP trees and all bootstrap trees (Moncalvo et al. 2000, 2002).

Comments Molecular phylogenetic support for placing *Chrysomphalina* in a new subfamily with *Hygrophorus* is based on the consistency of this pairing in all current and previous analyses together with moderate to strong BPP values and moderate MLBS support. ITS-LSU sequence analyses by Vizzini and Ercole (2012 and Vizzini et al. (2012) show moderate to strong Bayesian support for placement of *Haasiella* in subf. *Hygrophoroideae* — a placement consistent with our ITS-LSU and ITS phylogenies (Fig. 15, Online Resource 3).

Phylogenetic support. subf. *Hygrophoroideae* is concordant with the suggestion by Redhead et al. (2002) and Clémençon et al. (2004, Fig. caption 9.38) that the pachypodial structure in *Chrysomphalina* may be homologous to the divergent trama in *Hygrophorus* (Figs. 17 and 19). In both, cells that produce basidia arise directly from hyphae that diverge from vertical generative hyphae, without a specialized subhymenium. Although *Chrysomphalina, Haasiella,* and *Aeruginospora* all have bidirectional trama and a pachypodial structure below the active hymenium (Figs. 17 and 18), authors have described these differently as they vary depending on the species, specimen age, and whether sections were taken close to the lamellar edge or pileus flesh (Clémençon et al. 2004; Redhead et al. 2002, Reijnders and Stalpers 1992). The pachypodial structure in this group was interpreted variously as a broad subhymenium (Kühner 1980: 847; Clémençon 1997: 656), a hymenial palisade (Reijnders and Stalpers 1992), or a trama (Clémençon 1982; Clémençon et al. 2004: 305). While Clémençon's term 'pachypodial' is a descriptive adjective, and the most widely used term in the literature, Reijnders and Stalpers (1992) 'hymenial palisade' accurately reflects the origin of this structure, which comprises old basidia and subhymenial cells that have given rise to basidia and thus buried through successive generation of new basidia and subhymenial cells. Here we use pachypodial structure as an adjective and refer to the tissue according to its origin as either a pachypodial hymenial palisade or buried hymenia. Knudsen and Vesterholt (Funga Nordica, 2007) accepted both *Chrysomphalina* and *Haasiella* in the Hygrophoraceae based on shared morphology and pigment chemistries (Vizzini and Ercole 2012). Support for placing *Aeruginospora* near *Haasiella* is based entirely on the shared characters of basidiome form, bidirectional lamellar trama, a thickening hymenium forming a pachypodial structure, and spores that are thick-walled, pigmented, and with a red metachromatic endosporium (not included in the molecular phylogenies, as we could not obtain molecular sequences from the 80–90 year-old collections stored in alcohol.) In *Hygrophoroideae* we recognize tribe *Hygrophoreae* P. Henn. and transfer tribe *Chrysomphalineae* Romagn. to the Hygrophoraceae.

Tribe *Chrysomphalineae* Romag., Doc. Mycol. 112: 135 (1996).

Type genus: *Chrysomphalina* Clémençon, Z. Mykol. 48(2): 202 (1982).

[≡ Cantharellaceae tribe "*Paracantharelleae*" Romagn., Doc. Mycol. 25(98–100): 418, nom. invalid, Art. 18.1].

Tribe *Chrysomphalineae* **emended here by Lodge, Padamsee, Norvell, Vizzini & Redhead** by transferring it from Cantharellaceae to Hygrophoraceae and to exclude *Phyllotopsis*.

Trama monomitic, inamyloid; bidirectional, with horizontal hyphae (parallel to the lamellar edge) woven through vertically oriented, regular or subregular hyphae that are

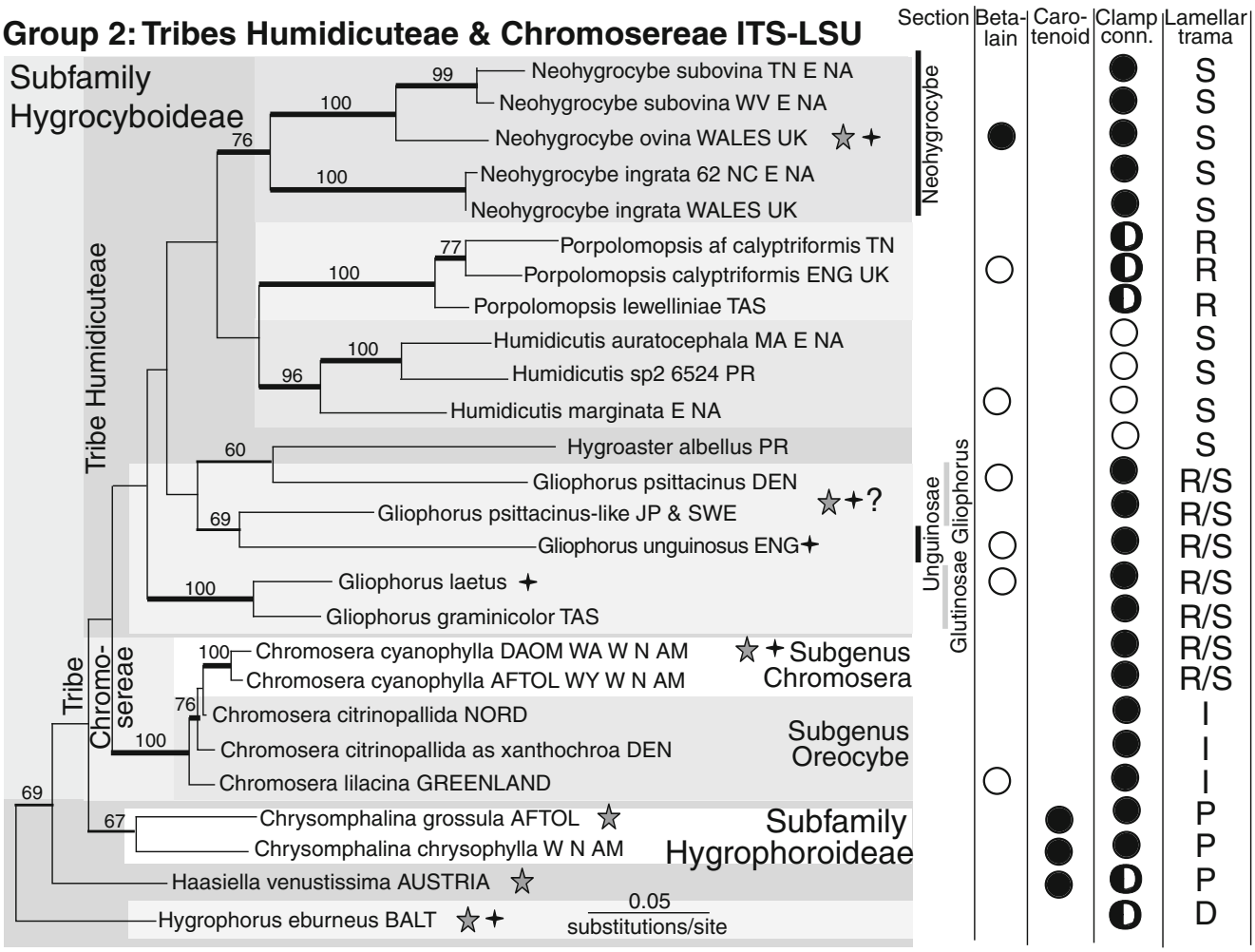


Fig. 15 Tribes *Humidicuteae* and *Chromosereae* (Group 2) ITS-LSU analysis rooted with *Hygrophorus eburneus*. Genes analyzed were ITS (ITS1, 5.8S & ITS2), LSU (LROR-LR5). Presence of betalain (DOPA based) and carotenoid pigments and presence of clamp connections are denoted by filled circles, empty circles denote their absence and half-filled circles appear for species with clamp connections at the base of the basidia but absent from the context (*Porpolomopsis* spp.), and *Haasiella venustissima* that has a clampless form with 2-spored basidia. Lamellar trama types are: D for divergent, I for interwoven, P for pachypodial, R for regular (parallel) and S for subregular. ML bootstrap values ≥50 % appear above the branches. Heavily bolded branches have ≥70 % and lightly bolded branches have 50–69 % ML bootstrap support

confined or not to a central strand; basidia arising from hyphae that diverge from the vertical generative hyphae, developing a pachypodial hymenial palisade consisting of chains of short segments with the same orientation as the basidia, thickening over time via proliferation of candelabra-like branches that give rise to new basidia or new subhymenial cells, thus burying older hymenial layers; spores thin- or thick-walled, often slightly pigmented, metachromatic or not, inamyloid; clamp connections usually absent (except in some *Haasiella*); yellow (and possibly green) pigments carotenoid, yellow colors may be absent because the carotenoid synthesis pathway is incomplete or may be obscured by encrusting pigments; growing on wood, woody debris, sclerophyllous dicotyledonous and bamboo litter, rarely on soil.

Phylogenetic support Two species of *Chrysomphalina* (*C. chrysophylla* and *C. grossula*) were included in all our analyses. *Haasiella venustissima* sequences were added late and thus included in only one of our two ITS-LSU analyses (Fig. 15) in which *Haasiella* falls between *Hygrophorus* and *Chrysomphalina* without significant branch support, and our ITS analysis (Online Resource 9) in which *Haasiella* is the basal member of a grade that includes *Chrysomphalina* and the terminal *Hygrophorus* clade. Although *Chrysomphalineae* is paraphyletic with the *Hygrophorus* clade in our analyses, an ITS analysis by Vizzini and Ercole (2012) [2011], shows support (0.91 B.P. for a *Chrysomphalineae* clade that is sister to *Hygrophorus*. As DNA was not successfully sequenced from *Aeruginospora*, it could not be included in molecular analyses and so is discussed after the other genera in this tribe.

Genera included Type genus: *Chrysomphalina*. *Haasiella* is included based on phylogenetic and morphological data, while *Aeruginospora* is included based on morphology.

Comments Romagnesi (1995), who first published this group as tribe "*Paracantharelleae*" (invalid because it was not formed from the type genus name, Art. 18.1) replaced it (1996) as tribe *Chrysomphalineae* in the Cantharellaceae. Romagnesi (1995) discounted the absence of stichobasidia in tribe *Chrysomphalineae* since stichic basidial nuclear division varies in the Cantharellaceae (see Pine et al. 1999), and both Romagnesi (1995) and Redhead et al. (2002) emphasized the carotenoid pigments shared by these groups. Prior to sequencing and phylogenetic analyses of *Haasiella*, Redhead et al. (2002) postulated a close relationship between *Haasiella* and *Chrysomphalina* based on pigments and micromorphology, although Kost (1986) concluded that these two genera were not closely allied based on micromorphology. Clémençon 1982) placed *Chrysomphalina grossula* with *Aeruginospora* in *Camarophyllus* subg. *Aeruginospora* owing to shared lamallar trama structure (Figs. 17 and 18). Romagnesi (1995) included *Haasiella* and *Phyllotopsis* E.-J. Gilbert & Donk ex Singer along with the type genus, *Chrysomphalina,* in this tribe. We emend Tribe *Chrysomphalineae* here to exclude *Phyllotopsis*, which lacks a hymenial palisade, and include *Aeruginospora*, which has pigmented spores and a pachypodial hymenial palisade and shares with *Haasiella* thick-walled spores with a metachromatic endosporium.

Chrysomphalina Clémençon, Z. Mykol. 48(2): 202 (1982).

Type species *Chrysomphalina chrysophylla* (Fr. : Fr.) Clémençon, Z. Mykol. 48(2): 203 (1982)

≡ *Agaricus chrysophyllus* Fr. : Fr., Syst. mycol. (Lundae) 1: 167 (1821).

Basidiomes gymnocarpous; lamellae decurrent; trama monomitic; lamellar trama bidirectional; subhymenium lacking, basidia arising directly from hyphae that diverge from vertically oriented generative hyphae; hymenium thickening and forming a pachypodial hymenial palisade over time via proliferation of candelabra-like branches that give rise to new basidia or subhymenial cells, thus burying older hymenia; spores thin-walled, lightly pigmented ochraceous salmon or green, not metachromatic, inamyloid; basidia five or more times longer than the basidiospores, variable in length; clamp connections absent; carotenoid pigments present, β-forms predominating over γ-forms; pileipellis not gelatinized; lignicolous habit. Differs from *Aeruginospora* and *Haasiella* in thin-walled and non-metachromatic basidiospores and from *Haasiella* in a non-gelatinized pileipellis, and from tetrasporic forms of *Haasiella* in the absence of clamp connections.

Phylogenetic support The *Chrysomphalina* clade has total support (100 % MLBS, 1.0 B.P. in our 4-gene backbone, Supermatrix and ITS analyses (Figs. 1 and 2, Online Resource 3), and moderate support in our LSU and ITS-LSU analyses (70, 67 %, 59 %% MLBS, Figs. 15 and 16). The LSU analysis by Moncalvo et al. (2002) also shows moderate support for *Chrysomphalina* (66 % MPBS). Lutzoni (1997) shows strong MPBS support in his analyses of LSU (98 %), ITS1 (99 %), and a combined ITS-LSU (99 %) data set with equally weighted parsimony analysis (Redhead et al. 2002, relabeled as the Lutzoni 1997 combined ITS-LSU tree). Similarly strong support for *Chrysomphalina* is shown by Vizzini et al. (2012) using a combined ITS-LSU data set (1.0 B.P. 94 % MLBS), and Matheny et al. (2006) using a 5-gene Supermatrix analysis (1.0 B.P. 77 % MLBS).

Species included Type species: *Chrysomphalina chrysophylla*. Additionally supported by molecular data is *C. grossula* (Pers.) Norvell, Redhead & Ammirati var. *grossula*. We also include the morphologically supported *C. aurantiaca* (Peck) Redhead, *C. chrysophylla* var. *hoffmanii* (Peck) Norvell, Redhead & Ammirati, *C. chrysophylla* var. *salmonispora* (H.E. Bigelow) Norvell, Redhead & Ammirati, and *C. grossula* var. *belleri* (Bon) P.A. Moreau & Courtec.

Comments The pachypodial hymenial construction (Fig. 17) is found in all species of *Chrysomphalina*, though the hymenial palisade is shallow in some species (Norvell et al. 1994). The yellowish and pinkish orange pigments in *Chrysomphalina* and *Haasiella* are carotenoids (Arpin 1966; Arpin and Fiasson 1971; Gill and Steglich 1987; Fig. 15), but they are predominantly β-forms in *Chrysomphalina* and mostly γ-forms in *Haasiella* (Fiasson and Bouchez 1968). *Chrysomphalina grossula* is initially intensely greenish yellow but these colors are later obscured or replaced by a brownish residue (Norvell et al. 1994). The spore color of *C. grossula* (=*Omphalina bibula*, =*O. wynneae*) also differs from the typical ochraceous salmon tint in spore deposits of other *Chysomphalina* spp., and is pale green or greenish cream (Josserand 1955; Norvell et al. 1994, Quélet 1882; 1888). The green pigment might be carotenoid as these are known in ascomycetes (Goodwin 1952).

Haas (1962) considered *Agaricus chrysophyllus* Fr. and *A. venustissimus* congeneric based on shared spore pigmentation, but his attempt to establish *Chrysomphalina* to accommodate them was invalid. Kotlaba and Pouzar (1966) subsequently established *Haasiella*, typified by *A. splendidissima*, and recombined *A. venustissimus* Fr. in *Haasiella*. Raithelhuber (1973) recombined *A. chrysophyllus* in *Haasiella* – a placement later rejected by Clémençon (1982), who instead validated *Chrysomphalina* Clémençon (typified by *C. chrysophylla*). Clémençon (1982) included *C. strombodes* (Berk. & Mont.) Clémençon in *Chrysomphalina*. Norvell et al. (1994) later excluded *C. strombodes* from *Chrysomphalina* based on its lack of a

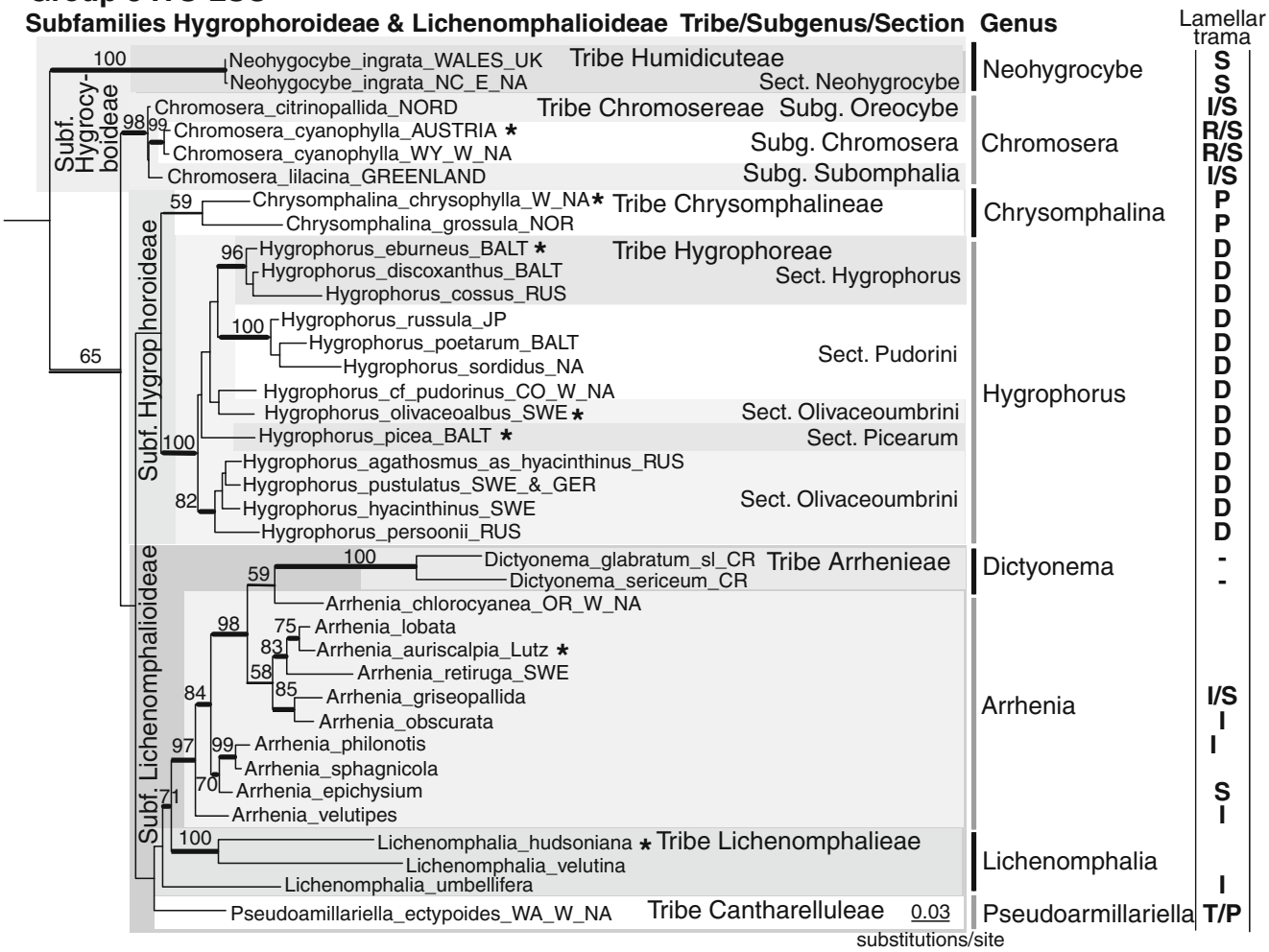


Fig. 16 Subfamilies *Hygrophoroideae* and *Lichenomphalioideae* (Group 3) ITS-LSU analysis rooted with *Neohygrocybe ingrata*. Genes analyzed were ITS (ITS1, 5.8S & ITS2), LSU (LROR-LR5). Presence of betalain (L-DOPA based) and carotenoid pigments and presence of clamp connections are denoted by filled circles, empty circles denote their absence. Lamellar trama types are: D – divergent; I – interwoven; P – pachypodial; R – regular/parallel; S – subregular; T – tri-directional. ML bootstrap values ≥50 % appear above the branches. Heavily bolded branches have ≥70 % and lightly bolded branches have 50–69 % ML bootstrap support

pachypodial hymenial structure in favor of Singer (1962) [1961] and Redhead's (1986) placement in *Gerronema*. Redhead (1986) noted that sarcodimitic tissue in *G. strombodes* differed from monomitic tissue of *Chrysomphalina*; Norvell et al. (1994) confirmed that the type of *Gerronema* also had sarcodimitic tissue. The molecular phylogeny by Moncalvo et al. (2002) placed *G. strombodes* in the hydropoid clade (Marasmiaceae) and *Chrysomphalina* in the Hygrophoraceae. Redhead (1986) transferred *Omphalia aurantiaca* to *Chrysomphalina,* based on the presence of a weak pachypodial hymenial palisade below the active hymenium. Norvell et al. (1994) transferred *Agaricus grossulus* Pers. from *Omphalina* to *Chrysomphalina,* recognizing *A. umbelliferus* var. *abiegnus* Berk. & Broome [= *Omphalina abiegna* (Berk. & Broome) Singer] and *Hygrophorus wynneae* Berk. & Broome as synonyms.

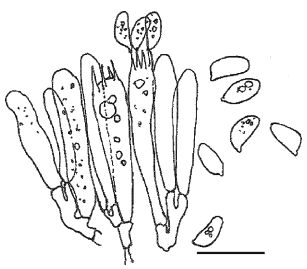


Fig. 17 Subf. *Hygrophoroideae*, tribe *Chrysomphalineae*, *Chrysomphalina chrysophylla* hymenial section (ID-3, T. Birbak, McCall, Idaho, 2008). Scale bar=20 μm

Haasiella Kotl. & Pouzar, Ceská Mykol. 20(3): 135 (1966).

Type species *Haasiella venustissima* (Fr.) Kotl. & Pouzar ex Chiaffi & Surault (1996)

≡ *Agaricus venustissimus* Fr., Öfvers Kongl. Svensk Vet.-Akad, Förh. 18: 21 (1861).

Basidiomes gymnocarpous; lamellae decurrent; trama monomitic; lamellar trama bidirectional; subhymenium lacking, basidia arising directly from hyphae that diverge from vertically oriented generative hyphae; hymenium thickening and forming a pachypodial hymenial palisade over time via proliferation of candelabra-like branches that give rise to new basidia or subhymenial cells, thus burying older hymenial layers; basidiospores pigmented pale yellowish salmon, thick-walled, endosporium (red) metachromatic; carotenoid pigments present, predominantly γ-forms; pileipellis gelatinized; clamp connections present if tetrasporic; mostly xylophagous habit. Differs from *Chrysomphalina* in presence of thick-walled spores with a metachromatic endosporium and a gelatinized pileipellis. Differs from *Aeruginospora* in yellowish salmon (not green) basidiospores, and abundant clamp connections if tetrasporic.

Phylogenetic support Haasiella, represented by a single *H. venustissima* collection, appears between *Chrysomphalina* and *Hygrophorus* in our ITS-LSU analysis, the topology of which agrees with classification based on micromorphology, pigment chemistry, and ecology. Our ITS (Online Resource 3) and one LSU analysis (not shown) place *Haasiella* as sister to *Hygrophorus* with low support (32 % and 55 % MLBS). In the ITS-LSU analysis by Vizzini et al. (2012), one *H. venustissima* and four *H. splendidissima* collections are shown as conspecific, with the *Haasiella* clade (100 % MLBS, 1.0 BPP support) appearing as sister to *Hygrophorus* (65 % MLBS and 1.0 BPP support). Their analysis (Vizzini et al. 2012) places *Chrysomphalina* basal to *Hygrophorus* and *Haasiella*, but without backbone support.

Species included Haasiella is monotypic, as *H. splendidissima* Kotl. & Pouzar is a tetrasporic, clamped, heterothallic form of the type species, *H. venustissima* (Vizzini et al. 2012).

Comments As noted by Vizzini et al. (2012) the type of *Haasiella*, *Agaricus* (*Clitocybe*) *venustissimus* Fr. (1861), has been classified in various genera beginning with *Clitocybe* (Karsten 1879), *Omphalia* (Quélet 1886), *Hygrophoropsis* (Haas 1958), *Chrysomphalina* (Haas 1962, nom. invalid), and *Omphalina* (Lange 1981; 1992; Ludwig 2001). Redhead (1986) distinguished *Haasiella* from *Chrysomphalina* based on the absence of a pachypodial trama, whereas Clémençon (1982), Clémençon et al. (2004) and Reijnders and Stalpers (1992) found a pachypodial hymenial palisade in both genera (Fig. 17). Though Kost (1986) and Norvell et al. (1994) reported *Haasiella* as terrestrial, most collections have been made on wood or woody debris (including the original described by Kotlaba and Pouzar 1966), as noted by Vizzini et al. (2012), which removes one purported contrast with *Chrysomphalina*. *Haasiella* differs from *Chrysomphalina*, however, in its thick-walled metachromatic spores and gelatinized pileipellis (Kost 1986; Norvell et al. 1994, Vizzini et al. 2012). *Haasiella* is morphologically most similar to *Aeruginospora*, and if found to be congeneric, *Aeruginospora* would have priority. *Haasiella* and *Aeruginospora* both have bidirectional trama, a thickening pachypodial hymenial palisade, and thick-walled spores with a metachromatic endosporium – a combination of characters not found elsewhere in the Hygrophoraceae (Figs. 18 and 29; Online Resource 10). *Haasiella* differs from *Aeruginospora* in having abundant clamp connections in tetrasporic forms, yellowish salmon rather than green tinted spores, and *Aeruginospora* was reported on soil under bamboo whereas *Haasiella* is mostly lignicolous. As with *Haasiella*, basing a habit on few collections may mislead. It is unknown if *Aeruginospora* has carotenoid pigments – a character found in both *Haasiella* and *Chrysomphalina*.

Aeruginospora Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 117: 1012 (1908),

Type species: *Aeruginospora singularis* Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 117: 1012 (1908).

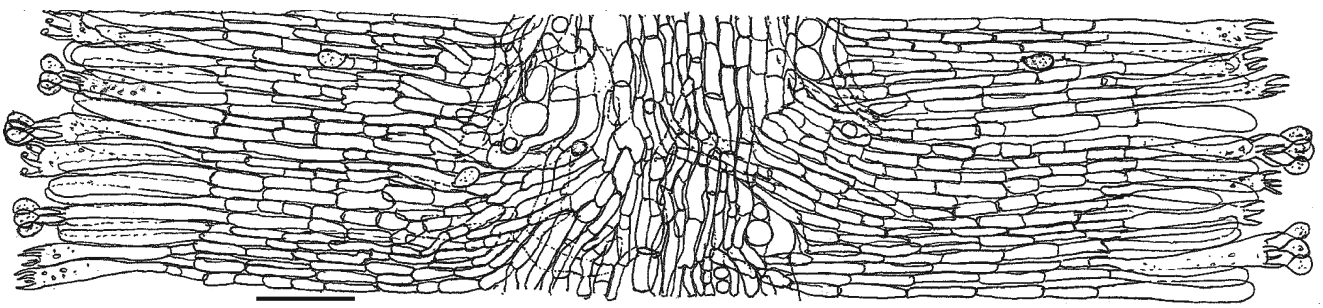


Fig. 18 Subf. *Hygrophoroideae*, tribe *Chrysomphalineae*, *Aeruginospora singularis* lamellar cross section (v. Overeem 601 A, BO-93, Bogor Botanical Garden, Indonesia, 1921). Scale bar=20 μm

Aeruginospora **emended here by Lodge & E. Horak** as hymenial pachypodial palisade present.

Basidiomes robust, cuphophylloid or cantharelloid; pileus cream colored with gray-brown or ochraceous tint in center, sometimes red-brown on margin or overall, weakly radially wrinkled or smooth. Lamellae decurrent, with 2–3 lengths of lamellulae inserted, occasionally forked, fleshy, waxy, hygrophanous, fragile, colored pale bluish-green from the basidiospores. Stipe cylindrical, flared at apex, sometimes bent; surface smooth, dry. Trama monomitic, hyphae thin-walled, some walls up to 0.8 μm thick, narrow, 2–7(−10) μm wide; lamellar trama bidirectional, often with a subregular central strand 15–30 μm wide, especially toward the pileus, some hyphae parallel to the lamellar edge woven through these in the lateral strands, but not abundant; subhymenium lacking, basidia arising directly from hyphae that diverge from vertically oriented generative hyphae; hymenium thickening to 30–60 μm and forming a pachypodial hymenial palisade over time via proliferation of candelabra-like branches that give rise to new basidia or subhymenial cells, thus burying older hymenial layers; basidia tetrasporic, 30–40(−45)×4.8–7.2 μm, sterigmata 6–8×1–2 μm, basal clamp connection absent, chiastic nuclear division; basidiospores pale blue-green in deposit, near sky blue microscopically when fresh, loosing color during storage, thin- and thick-walled (to 0.5 μm), smooth, short-ellipsoid, subglobose or rarely ovoid, 4.8–6×4–4.8(−5.2) μm, inamyloid, not cyanophilic, red metachromatic endosporium in cresyl blue. Clamp connections almost completely absent, one observed in pileipellis. Pileipellis structure uncertain or variable, of repent or erect slender hyphae, possibly gelatinized. On ground in dense stand of bamboo.

Species included Aeruginospora is monotypic, consisting of the type, *A. singularis* Höhn. Various authors have added species to *Aeruginospora*, but the following excluded species were correctly placed in *Camarophyllopsis*: *A. foetens* (W. Phillips) M.M. Moser, *A. hiemalis* Singer & Clémençon, *A. hymenocephala* (A.H. Sm. & Hesler) Singer, *A. microspora* (A.H. Sm. & Hesler) Singer, *A. paupertina* (A.H. Sm. & Hesler) Singer, and *A. schulzeri* (Bres.) M.M. Moser. *Aeruginospora furfuracea* Horak merits further study but may also belong in *Camarophyllopsis*.

Comments In addition to Horak's (1968) study of the 1908 type collection, Singer (1951, 1973, unpublished drawings) also annotated the type (Harvard University 00284744). While visiting Leiden, Singer copied Boedjin's annotation of a collection by Brink in 1931 as well as Boedjin's copy of Overeem's annotations of his 1921 collection, both from the type locality at the Bogor Botanical Garden in Indonesia, and he copied Maas Geesteranus' drawings of nuclear division in basidia of *A. singularis* in the type; there is no part of Overeem's (BO 601A, 601B) or Brink's (BO 12204) collections at Leiden. Although Horak photographed Overeem's paintings of his 1931 (601*A* and B) *A. singularis* collections (Online Resource 10) while at the herb. Bogoriensis, he was unable to examine them microscopically as the collection was being moved. Lodge examined parts of Overeem and Brink's collections that had been stored in alcohol, augmented the diagnosis from the type studies above with observations on the pileipellis structure, spore wall thickness, spore reactions (acyanophilic, red metachromatic endosporium in cresyl blue) and illustrated a lamellar cross section and hymenial palisade (Fig. 18).

Horak drew a narrow, regular mediostratum bounded by subregular strata of narrow, wavy hyphae in the lateral zones (Harvard University 00284744), and reported in the type study (Horak 1968) a 100 μm wide hymenium with horizontally oriented short hyphae and basidia, with basidia long, 5–6 μm broad and lacking clamp connections. Singer (1951, 1973) did not mention a distinct mediostratum in the type but did note that the central hyphae became more axillary (vertical) toward the pileus context. Singer (unpublished) drew a subregular stratum (but said there was no distinct mediostratum) bounded by vertical hyphae interwoven with horizontal hyphae in the lateral strata near the pileus (but described it as irregular); a bi-directional trama near the lamellar edge (vertical hyphae and cross sections of horizontal hyphae running parallel to the lamellar edge); and a pachypodial palisade below the basidia, basidia 29–45×5–6.3 μm, lacking clamps. Lodge found in v. Overeem 601 and Brink 12204 a subregular mediostratum 26–30 μm wide bounded by lateral strata 85–100 μm wide comprised of vertical hyphae with some diverging toward the hymenium and giving rise to the pachypodial palisade, and a few cross sections of horizontal hyphae parallel to the lamellar edge. The pachypodial hymenial palisade is 30–60 μm wide, which together with the 30–45 μm long basidia comprise a hymenium up to 100 μm thick, comparable to the depth reported in Horak's (1968) type study. Studies of all collections reported spore dimensions in the same range (4.2–) 5–6.2(−8)×(4–)3.8–5(−5.6). The original diagnosis and Horak's (1968) and Singer's (1951, 1973) type studies did not mention thick-walled spores, though these are visible in Overeem's painting of part A (Online Resource 10). Lodge found that spores with slightly thickened (0.2–0.4 μm), lightly pigmented walls were dominant in the most mature collection (Overeem 601A), rare in the less mature Overeem 601B, and absent in the least developed collection (Brink, hymenial palisade 20–30 μm deep). Lodge also found a metachromatic spores on basidia and a few metachromatic in Overeem 601A that were embedded in the pachypodial hymenial palisade 30–40 μm below the active basidia. All descriptions of the type, Singer's (unpublished) notes, and annotations of Overeem's and Brink's collections agree that the context and pileipellis hyphae

are narrow, 2–6(−10) μm wide, and lack clamp connections, though Lodge found one pileipellis clamp in Overeem 601A.

It is uncertain whether the pileipellis of *Aeruginospora* is gelatinized (as in *Haasiella*) or dry (as in *Chrysomphalina*) as reported for the type by Höhnel in Höhnel and Litschauer (1908) and Horak (1968). Neither descriptions of the type nor descriptions or paintings of subsequent collections by Overeem (601a& b, 1921, BO-93) or Brink (1931, BO 12204, det. and desc. by Boedjin) suggest a gelatinized pileipellis. Among the collections stored in alcohol at Herb. Bogoriensis, however, Lodge found a distinctly gelatinized ixotrichodermium in the v.d. Brink (youngest) collection, and part A of Overeem's collection had a little adhering debris and a slight gelatinous coating on the pileipellis hyphae. The erect hyphae in the Brink collection may match those found by Horak (1968) in his type study. It is possible that since the basidiomes of this enigmatic species are long-lived that the gelatinized surface is eroded with time. It is unknown whether *Aeruginospora* contains carotenoid pigments or a partial pigment pathway as was found in most other members of Tribe *Chrysomphalineae*. Some carotenoid pigments are green as in the discomycete, *Caloscypha fulgens* (Pezizales, Ascomycota).

Singer transferred *A. singularis* first to *Armillariella*, (1951, p. 216) and then *Camarophyllus* sect. *Aeruginospora* (1973) with emphasis on elongated basidia, small spores, and absence of clamp connections led to descriptions and new combinations of eight additional species in *Aeruginospora*. Several authors later transferred the added *Aeruginospora* species to *Camarophyllopsis*, including four spp. placed in *Aeruginospora* by Singer (1962), three Moser spp. (1967) and one species described by Singer and Clémençon (1971). *Camarophyllopsis* has since been excluded from the Hygrophoraceae based on molecular phylogeny (Matheny et al. 2006).

Tribe *Hygrophoreae* P. Henn., in Engler & Prantl, Nat. Pflanzenfam. 1: 209 (1898),

Type genus: *Hygrophorus* Fr., Fl. Scan.: 339 (1836) [1835].

Tribe *Hygrophoreae* emended by Kühner in Bull. mens. Soc. linn. Lyon 48: 617 (1979).

Basidiomes medium to large, gymnocarpous or secondarily mixangiocarpous and then glutinous from a universal veil; white to pallid or colored grey, olive, brown, yellowish orange, or red; pileus broad, convex, obtuse or with a low umbo, sometimes with a depressed disc, margin often inrolled when young but flattening in age; lamellae thick, usually distant, broadly adnate, subdecurrent to deeply decurrent, waxy; stipe smooth or with a glutinous-fibrous annulus, sometimes floccose-fibrillose at the apex, usually tapering towards the base; trama inamyloid, lamellar trama divergent, generative hyphae diverging from a central strand giving rise directly to basidia; subhymenium lacking; basidiospores thin-walled, inamyloid, not metachromatic or cyanophilous, hyaline, white in mass; known pigments muscoflavin; antimicrobial compounds include hygrophorones and chrysotrione; host and odors are often diagnostic for species; habit ectomycorrhizal; most species fruit late in the season.

Phylogenetic support Support for a monophyletic tribe and gen. *Hygrophorus* is high in most of our analyses including the 4-gene backbone (100 % MLBS and 1.0 BPP), Supermatrix (96 % MLBS) and ITS-LSU (100 % MLBS). Similarly, Larsson (2010) shows 81 % MPBS support for the tribe and gen. *Hygrophorus* in a four-gene phylogenetic analysis. Although *Hygrophorus* is monophyletic in our LSU and ITS analyses, support is not significant. However, the LSU analysis by Moncalvo et al. (2002) shows 97 % MPBS support for a monophyletic *Hygrophorus* represented by two species, *H. sordidus* and *H. bakerensis*.

Genera included Hygrophorus.

Comments While tribe *Hygrophoreae* is often attributed to Kühner (1979) (e.g., in Arnolds 1990), it was previously published by P. Hennings in Engler and Prantl (1889) (see Young and Mills 2002).

Hygrophorus Fr., Fl. Scan.: 339 (1836) [1835].

Type species: *Hygrophorus eburneus* (Bull. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 321 (1836) [1836–1838]

≡ *Agaricus eburneus* Bull., Herb. Fr. 3: tab. 118 (1780) : Fr.

Characters are the same as in tribe *Hygrophoreae*.

Phylogenetic support Support is same as for tribe *Hygrophoreae*.

Subgenera included We recognize three subgenera: *Hygrophorus* emend., *Colorati* (Bataille) E. Larss., subg. nov. and *Camarophyllus* Fr., emend.

Comments Species of *Hygrophorus* ss have a characteristic divergent lamellar trama (Fig. 19) which sets them apart from all other Hygrophoraceae (Young 1997; Hesler and Smith 1963, as *Hygrophorus* subg. *Hygrophorus*). The genus *Hygrophorus* was formally described by Fries in 1836. Later, in Epicrisis Sytematis Mycologici, Fries (1838) organized species into unranked, infrageneric 'tribes'. Most of the species now classified as *Hygrophorus* s.s. (including the type species, *H. eburneus*) were from part of Fries' *Hygrophorus* tribe *Limacium* and the remainder are from part of Fries' *Clitocybe* tribe *Camarophyllus*. Fries designated these tribes as *Hygrophorus* subgenera in 1849, they were treated as subgenera by Karsten (1876), but treated as genera by Kummer (1871) and Karsten (1879). An overview of the major classifications from Fries (1821) to Bon (1990) is given

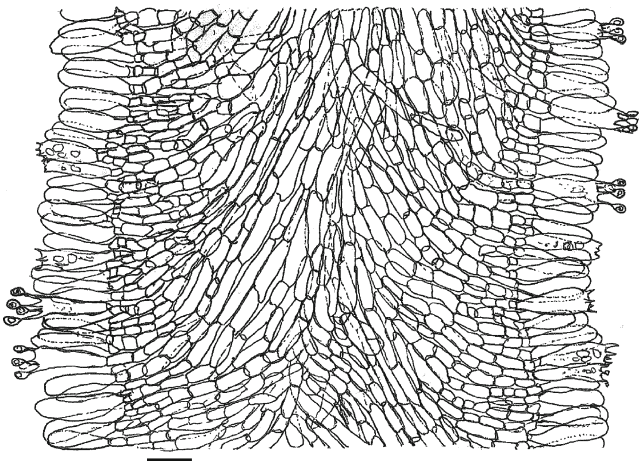


Fig. 19 Subf. *Hygrophoroideae*, tribe *Hygrophoreae*, *Hygrophorus hypothejus* var. *aureus* lamellar cross section (DR-2146, DJL02DR43, Dominican Republic). Scale bar=20 μm

by Candusso (1997). As the micro-morphological characters are similar in most *Hygrophorus* species the current classifications are still based on basidiocarp color, color changes, and the presence or absence of a universal glutinous veil and specific odors (Hesler and Smith 1963, Singer 1986, Arnolds 1990, Candusso 1997; Kovalenko 2012).

In Epicrisis Fries (1838) recognized twenty species in the tribe *Limacium*. Fries (1874) introduced five groupings below tribes based on pileus color; *Albi l. albolutescentes* for the white to yellow species; *Rubentes* for the red to reddish species, *Fulventes l. flavi* for the brown to tan or bright yellow species; *Olivaceoumbrini* for the olivaceous species; *Fuscocinerei l. lividi* for the gray to blackish species. Bataille (1910) similarly did not designate ranks below subgenus in *Hygrophorus*, and he used part of Fries' classification. Many of Fries' and Battaille's names have subsequently been combined by other authors at designated ranks. Important modifications by Bataille (1910) were use of type species and addition of morphological characters besides pileus color. Bataille also inserted unranked names between subgen. *Hygrophorus* and species groups, *Albi* (from Fries), later renamed sect. *Hygrophorus* by Singer as it contains the type species (Art. 22.1), and *Colorati*. We emend the subgenera by removing Bataille's *Colorati* from subg. *Hygrophorus* and making it a new subgenus; we have retained subg. *Camarophyllus* (Fr.) Fr. and emend it by removing species of *Cuphophyllus* and other unrelated taxa.

As both morphological characters and ecology in Fries' time were broadly described, later mycologists applied the names based on their own experiences. Thus regional traditions in naming species have developed and it is obvious that the same name is used for different species but also that different names are applied to the same fungus. For example, Fries selected *H. eburneus* as type species for *Hygrophorus* – the only white *Hygrophorus* species name sanctioned by Fries in Systema Mycologicum (Fries 1821). Fries described *H. eburneus* as a common species growing in deciduous forest. Most mycologists later interpreted *H. eburneus* as a species growing with *Fagus,* which is likely correct as *Fagus* forests were common in Femsjö and Lund near where Fries lived. In 1835 Fries moved to Uppsala where *Fagus* is absent and instead forests are dominated by *Betula, Picea,* and *Pinus*. This likely contributed to the change in species interpretation in later descriptions. In Sweden, the species growing with *Picea* that was long regarded as *H. eburneus* (Lundell and Nannfeldt 1939) is now known as *H. piceae* Kühner.

The number of *Hygrophorus* species recognized worldwide has grown to about 100 (Kirk et al. 2008) with contributions from Velenovsky (1920), Kühner (1949), Hesler and Smith (1963), Moser (1967), Arnolds (1979), Gröger (1980) and Orton (1984), and new species and varieties are continually discovered and described (eg. Jacobsson and Larsson 2007; Pérez-de-Gregorio et al. 2009). With the exception of the monograph by Hesler and Smith (1963), in which North American species are treated together with some of the European names, most monographs are regional. There is no recent monograph and classification that considers all described species.

In this study sequences of 19 species in *Hygrophorus* were generated including the types of the four sections of *Hygrophorus* accepted by Singer (1986); *Hygrophorus – H. eburneus; Pudorini – H. pudorinus; Discoidei – H. discoideus; Colorati – H. olivaceoalbus*. Our Supermatrix and ITS phylogenies show eight to nine clades, but their composition does not correspond well with the morphology based classifications of Hesler and Smith (1963), Singer (1986) or Arnolds (1990). A more detailed, five-gene analysis by Larsson (2010 and unpublished data) shows a 13-clade tree. The best concordance with our ITS and the five-gene phylogeny by E. Larsson (unpublished and 2010) is found with some infrageneric taxa delineated by Bataille (1910) and Candusso (1997), so we used or emended these to minimize changes.

Hygrophorus* subgen. *Hygrophorus [autonym] (1849).

Type species: *Hygrophorus eburneus* (Bull. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 321 (1836) [1836–1838]

≡ *Agaricus eburneus* Bull., Herb. Fr. 3: tab. 118 (1780) : Fr.

Hygrophorus subgen. *Hygrophorus* **emended here by E. Larss.** to remove Bataille's *Colorati.*

Pileus usually glutinous or subviscid when moist, white or pallid, sometimes tinted yellow, salmon-buff, fulvous, gray, bistre or reddish brown in center, sometimes darkening with age and upon drying; lamellae adnate to decurrent, subdistant to distant, white or pallid, sometimes darkening with age and upon drying; stipe usually glutinous or viscid, apex dry, floccose-fibrillose; sometimes with an aromatic odor.

Phylogenetic support The four-gene analysis presented by Larsson (2010; unpublished data) shows a monophyletic clade comprising sects. *Discoidei* and *Hygrophorus*, except sect. *Piceae* appears as an adjacent clade; support for this topology is lacking. Our LSU analysis shows a monophyletic subg. *Hygrophorus*, but it also lacks significant BS support, and *H. piceae* appears on a separate branch. Subg. *Hygrophorus* is polyphyletic in our Supermatrix and ITS analyses.

Sections included Hygrophorus sects. *Discoidei, Hygrophorus,* and *Picearum,* E. Larss. sect. nov.

Comments We emend subg. *Hygrophorus* by removing Bataille's *Colorati*. The composition of this group is not concordant with any group in Bataille (1910), partly concordant with subsect. *Hyrophorus* in Singer (1986), mostly concordant with subsect. *Hygrophorus* in Kovalenko (1989, 1999, 2012), Arnolds (1990) and Candusso (1997), and entirely concordant with Bon's (1990) subsect. "*Eburnei*" Bataille [invalid].

Hygrophorus* [subgen. *Hygrophorus*] sect. *Hygrophorus [autonym].

Type species: *Hygrophorus eburneus* (Bull. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 321 (1838).

Pileus glutinous to viscid, white or pallid, sometimes tinted yellow, salmon-buff, fulvous, reddish brown in center, sometimes darkening with age and upon drying; lamellae white or pallid, sometimes darkening with age and upon drying; stipe usually glutinous or viscid, apex dry, floccose-fibrillose; when fresh sometimes with a distinct aromatic odor. Ectomycorrhizal, predominantly associated with deciduous trees.

Phylogenetic support Strong support for a monophyletic sect. *Hygrophorus* is shown in our ITS-LSU (Fig. 16; 96 %) and in our ITS analysis (Online Resource 3; 97 % MLBS). Sect. *Hygrophorus* appears as a grade in our Supermatrix analysis (Fig. 2). In our LSU analysis, sect. *Discoidei* appears in sect. *Hygrophorus*, rendering the latter polyphyletic, but there is no support for the supporting branches. In the four-gene analysis presented by Larsson (2010; unpublished data), sect. *Hygrophorus* appears as a monophyletic group with 54 % MPBS support.

Subsections included Hygrophorus subsects. *Fulventes* subsect. nov. and *Hygrophorus*.

Comments Sect. *Hygrophorus* is delimited more narrowly here than traditionally. Most authors have included subsect. *Chrysodontes* (Singer 1986; Kovalenko 1989, 1999, 2012; Arnolds 1990; Candusso 1997) or Series *Chrysodontini* (Hesler and Smith 1963) and subsect. *Pallidi* ([invalid] Smith and Hesler 1939) = *Pallidini* [invalid] Singer Singer 1986; Arnolds 1990; Candusso 1997) which are now placed in subg. *Camarophyllus* and subg. *Colorati,* respectively.

Hygrophorus* [subgen. *Hygrophorus* sect. *Hygrophorus*] subsect. *Hygrophorus [autonym].

Type species *Hygrophorus eburneus* (Bull. : Fr.), Epicr. syst. mycol. (Upsaliae): 321 (1838).

Pileus glutinous, white or pallid, sometimes darkening with age and upon drying; lamellae white, often with salmon orange tinge, sometimes darkening with age and upon drying; stipe glutinous, concolorous with pileus, often with a salmon orange tinge at base, apex dry floccose-fibrillose; when fresh with a distinct aromatic odor (*Cossus* odor).

Phylogenetic support Our ITS analyses show subsect. *Hygrophorus* as a monophyletic group with either high or low support (Online Resources 3 and 8, 97 % and 49 % MLBS, respectively). Our LSU analysis shows a mostly monophyletic subsect. *Hygrophorus* except that *H. discoideus* of subsect. *Discoidei* is included; BS support is lacking. Our Supermatrix analysis shows subsect. *Hygrophorus* as a polyphyletic grade with *H. leucophaeus* of subsect. *Fulventes* embedded in it; backbone support is lacking. In the four-gene analysis presented by Larsson (2010; unpublished data), subsect. *Hygrophorus* is primarily a monophyletic clade with 58 % MPBS, but *H. hedrychii* appears in an adjacent unsupported branch.

Species included Type species: *Hygrophorus eburneus*. *Hygrophorus cossus* (Sow.) Fr., *H. discoxanthus* (Fr.) Rea and *H. hedrychii* (Velen.) K. Kult are included based on morphological and phylogenetic support.

Comments This subsection contains *H. eburneus,* which is the type species of the gen. *Hygrophorus*, so the name must exactly repeat the genus name (Art. 22.1). Bataille (1910) included a mixture of species from subsect. *Hygrophorus* and sect. *Olivaceoumbrini* in his [unranked] *Eburnei*. Bon's sect. *Hygrophorus* subsect. *Eburnei* Bataille [invalid] however, is concordant with the four-gene molecular phylogeny presented by Larsson (2010; unpublished data). The composition of subsect. *Hygrophorus* in Arnolds (1990) and Candusso (1997) is also concordant with the molecular phylogeny presented by Larsson (2010) if *H. gliocyclus* (sect. *Aurei*) is excluded. Singer (1989) included *H. flavodiscus* and *H. gliocyclus* (both in sect. *Aurei*) in subsect. *Hygrophorus,* rendering it polyphyletic. Subsect. *Hygrophorus* in Kovalenko (1989, 1999, 2012) is also polyphyletic. The controversy of name interpretation in subsect. *Hygrophorus* was disentangled by Larsson and Jacobsson (2004).

Hygrophorus* subsect. *Fulventes E. Larss., subsect. nov. MycoBank MB804961.

Type species *Hygrophorus arbustivus* Fr., Anteckn. Sver. Ätl. Svamp.: 46 (1836).

= *Hygrophorus*, 'Tribus' *Limacium* [unranked] Fulventes l. flavi. Fr., Hymen. Eur.: 408 (1874)

Neotype here designated: *Hygrophorus arbustivus* Fr., Anteckn. Sver. Ätl. Svamp.: 46 (1836). SWEDEN, Öland Island, Lilla Vikleby Nature Reserve, Coll. Björn Norden BN001118, 18 Nov. 2000, deposited GB, ITS sequence UDB000585.

[= *Hygrophorus* subsect. "*Fulvoincarnati*" A.H. Sm. & Hesler, Lloydia 2: 36 (1939), invalid, Art. 36.1].

Pileus glutinous to viscid, pallid, tinted yellow, salmon-buff, fulvous, reddish brown in center; lamellae subdecurrent, subdistant, white or pallid; stipe glutinous or viscid, pallid, apex dry floccose-fibrillose.

Phylogenetic support We included only *H. arbustivus* in our ITS analysis. In the four-gene analysis presented by Larsson (2010; unpublished data), subsect. *Fulventes* (*H. arbustivus*, *H. carpini*, *H. leucophaeo-ilicis*, *H. lindtneri*, *H. roseodiscoideus,* and *H. unicolor*) appears as a paraphyletic grade basal to subsect. *Hygrophorus* (54 % MPBS support for basal branch).

Species included Type species *H. arbustivus*. *Hygrophorus carpini* Gröger, *H. leucophaeo-ilicis* Bon & Chevassut, *H. lindtneri* M.M. Moser, *H. roseodiscoideus* Bon & Chevassut and *H. unicolor* Gröger are included based on morphological and phylogenetic data.

Comments Singer (1986) and Kovalenko (1989, 1999, 2012) placed the type of subsect. *Fulventes* together with species from sect. *Pudorini* in subsect. *Fulvoincarnati* A.H. Sm. & Hesler (1939)[invalid] making it polyphyletic. Bon (1990) and Candusso (1997) placed a similar mixture of species in sect. *Fulventes* (Fr.) Bon. [invalid] Series *Fulventes* (Hesler and Smith 1963, invalid because basionym was three words) and is consequently also polyphyletic.

Hygrophorus* [subgen. *Hygrophorus*] sect. *Discoidei (Bataille) Konrad & Maubl., Icon. Sel. Fung. 6: 428 (1937).

Type species: *Hygrophorus discoideus* (Pers. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 323 (1838) [1836–1838]

≡ *Agaricus discoideus* Pers., Syn. meth. fung. (Göttingen) 2: 365 (1801) : Fr.

Basionym: *Hygrophorus* [unranked] *Discoidei* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 162 (1910).

Pileus viscid when moist, pale yellowish brown, fulvous, sometimes with a gray tone, or disc reddish brown; lamellae, concolorous, sometimes with a violaceous gray tone; stipe viscid, pale or fulvous, sometimes with a gray tinge, apex floccose-fibrillose.

Phylogenetic support Sect. *Discoidei* is only represented by the type species in our Supermatrix and LSU analyses, and *H. subviscifer* in our ITS analysis. In the analysis presented by Larsson (2010; unpublished data), sect. *Discoidei* is a monophyletic clade with 100 % MPBS.

Species included Type species: *H. discoideus*. *Hygrophorus subviscifer* (P. Karst.) Harmaja is included based on morphology and phylogeny.

Comments Bataille (1910) included *H. arbustivus* (the type of subsect. *Fulventes*) and *H. mesotephrus* (sect. *Olivaceoumbrini*) along with the type in *Discoidei*. Series *Discoidei* (Hesler and Smith 1963) and sect. *Discoidei* (in Singer 1986; Kovalenko 1989, 1999, 2012; Arnolds 1990) are also polyphyletic. Bon (1990) only included *H. roseodiscoideus* (from the adjacent sect. *Fulventes*) in subsect. *Discoideini* Bataille [invalid]. Similarly, Candusso (1997) included *H. roseodiscoideus* and *H. lindtnerii* from the adjacent sect. *Fulventes*, (listing *H. carpini, H. leucophaeus* and *H. unicolor* as synonyms of the latter).

Hygrophorus* [subgen. *Hygrophorus*]** sect. ***Picearum E. Larss., sect. nov.

MycoBank MB804087.

Type species: *Hygrophorus piceae* Kühner, Bull. mens. Soc. linn. Lyon 18: 179 (1949).

Etymology: picea – Latin name for the host plant genus, *Picea* (spruce).

Pileus white, viscid when moist; lamellae decurrent, distant, white, sometimes with a weak yellowish or incarnate tint; stipe white, subviscid when moist, apex dry floccose-fibrillose; no specific odor; ectomycorrhizal with *Picea*.

Phylogenetic support Sect. *Piceae* is a moderately supported (78 % MPBS) monophyletic group in the analysis presented by Larsson (2010; unpublished data).

Species included Type species *H. piceae*. This is currently monotypic, but the analysis presented by Larsson (2010; unpublished data) suggests this is a complex of several taxa.

Comments Hygrophorus piceae was placed by most authors in Sect. *Hygrophorus* together with other white and pale species, by Hesler and Smith (1963) in subsect. *Camarophylli* and series *Clitocyboides*, by Candusso (1997) in subsect. *Pallidini* [invalid], and by Kovalenko (2012) in subsect. *Hygrophorus*. It was not treated by Singer (1986) or Arnolds (1990).

Hygrophorus*, subgen. *Colorati (Bataille) E. Larss., stat. nov.

MycoBank MB804109.

Type section: *Olivaceoumbrini* (Bataille) Konrad & Maubl., Icon. Sel. Fung. 6: 137 (1937).

Type species *Hygrophorus olivaceoalbus* (Fr. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 324 (1838) [1836–1838] designated by Singer, Lilloa 22: 148 (1951) [1949],

≡ *Agaricus olivaceoalbus* Fr., Observ. Mycol. (Havniae) 1: 5 (1815),

Basionym: *Hygrophorus* subgen. *Limacium* [unranked] *Colorati* Bataille, Mém. Soc. Émul. Doubs, sér. 8 4: 158 (1910) [1909].

Hygrophorus, subgen. *Colorati* **emended here by Larsson** to exclude sect. *Discoidei.*

Basidiomes glutinous from a universal veil or dry to subviscid, with or without a partial veil sometimes forming an annulus; pileus usually colored, at least in the center or white to lightly pigmented.

Phylogenetic support Our LSU analysis shows subg. *Colorati* as a paraphyletic grade with 72 % MLBS support for the branch separating it from sect. *Chrysodontes* (subg. *Camarophylli*). Our Supermatrix analysis also shows subg. *Colorati* as a grade, but with sect. *Chrysodontes* within it; there is no significant support for these branches. Our ITS-LSU analysis also shows a polyphyletic subg. *Colorati*. Our ITS analysis (Online Resource 9) shows subg. *Colorati* as a paraphyletic grade, but sect. *Aurei* is polyphyletic. In the analysis presented by Larsson (2010, unpublished), subg. *Colorati* is a monophyletic group lacking significant support, but the inner clade comprising subsects. *Olivaceoumbrini*, *Pudorini* and *Tephroleuci* has 71 % MPBS.

Sections included Sects *Aurei* (Bataille) E. Larss., stat. nov., *Olivaceoumbrini,* and *Pudorini*.

Comments Bataille (1910) created five unranked groups within *Colorati*, of which one name was from Fries (1874) (i.e., *Olivaceo-umbrini*), and the new names were *Aurei*, *Discoidei*, *Pudorini* and *Tephroleuci*. Singer (1949) assumed section rank for Bataille's *Colorati*, and designated a type species, but sect. *Colorati* (Bataille) Singer is illegitimate because Konrad and Maublanc (1937) had previously erected sect. *Olivaceoumbrini* with the same type species (*H. olivaceoalbus*). Singer restricted sect. *Colorati* to subsects *Olivaceoumbrini* and *Tephroleuci*, and Kovalenko (1989, 1999, 2012) subsequently used Singer's (1951) narrower delimitation of sect. *Colorati* (Kew Bull. 54: 699). While the branch joining subsects. *Olivaceoumbrini* and *Tephroleuci* has 64 % MPBS support in a four-gene analysis (Larsson 2010), this clade is embedded in a larger clade that is largely concordant with Bataille's (1910) *Colorati*; we therefore retained Bataille's broader classification for subg. *Colorati*, but emend it by removing sect. *Discoidei* as it is recovered on a separate branch (Online Resource 9 and Larsson 2010, unpublished data).

Hygrophorus* [subgen. *Colorati*] sect. *Olivaceoumbrini (Bataille) Konrad & Maubl., Icon. Sel. Fung. 6: 137 (1937).

Type species: *Hygrophorus olivaceoalbus* (Fr. :Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 324 (1838)

≡ *Agaricus olivaceoalbus* Fr., Observ. Mycol. (Havniae) 1: 5 (1815).

[≡ sect. *Olivaceoumbrini* (Bataille) Bon 1990, superfluous, nom. illeg.,

≡ sect. *Colorati* (Bataille) Singer (1951)[1949], superfluous, illeg., Art. 52.1].

Basionym: *Hygrophorus* [unranked] *Olivaceo-umbrini* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 163 (1910).

Pileus glutinous when moist, gray, olive, olive bister or fuliginous, sometimes fading or yellowing with age, usually darker in center; lamellae adnate to subdecurrent; stipe glutinous, with or without remnants of a partial veil sometimes forming an annulus.

Phylogenetic support The analysis presented by Larsson (2010, unpublished data) shows sect. *Olivaceoumbrini* as monophyletic with 65 % MPBS support comprising two strongly supported clades that are concordant with subsects *Olivaceoumbrini* and *Tephroleuci.* Our Supermatrix, LSU, ITS-LSU, and ITS analyses, however, show sect. *Olivaceoumbrini* as polyphyletic; all but the ITS-LSU analysis lack backbone support. Our ITS analysis (Online Resource 9) shows sect. *Olivaceoumbrini* as polyphyletic. Another ITS analysis (not shown) has low support for placing part of subsect. *Olivaceoumbrini* (i.e., *H. persoonii* = *H. limacinus* and *H. latitabundus*) as a sister clade to subsect. *Tephroleuci* (46 % MLBS).

Subsections included Olivaceoumbrini and *Tephroleuci*.

Comments Both Singer (1949) and Arnolds (1990) considered Bataille's (1910) *Olivaceoumbrini* and *Tephroleuci* as closely related, and placed them in the same section, (Singer in sect. *Colorati* Bataille, and Arnolds in sect. *Olivaceoumbrini* Bataille). However, Bataille's names were unranked, and Konrad and Maublanc (1937) were the first to combine Bataille's *Olivaceoumbrini* at section rank, making sect. *Colorati* (Bataille) Singer superfluous and thus illeg. Kovalenko (1989, 1999, 2012) and Arnolds (1990) followed Singer's classification, whereas Candusso recognized *Olivaceoumbrini* and *Tephroleuci* as separate sections. Bon (1990) recognized sect. *Olivaceoumbrini* Bataille but placed species belonging to the *Tephroleuci* clade in sect. *Ligati* Bataille [invalid]. Hesler and Smith (1963) recognized this group as a series in sect. *Hygrophorus*, but included species from other clades, rendering it polyphyletic.

Hygrophorus* [subgen. *Colorati* sect. *Olivaceoumbrini*] subsect. *Olivaceoumbrini (Bataille) Singer, Lilloa 22: 146, (1951) [1949].

Type species: *Hygrophorus olivaceoalbus* (Fr. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 324 (1838)

≡ *Agaricus olivaceoalbus* Fr. (1815), Observ. Mycol. (Havniae) 1: 5 (1815) : Fr.

Basionym: *Hygrophorus* [unranked] *Olivaceo-umbrini* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 163 (1910).

Pileus glutinous, bistre, grayish brown, fuliginous or olivaceous at least in center, sometimes fading or yellowing with age; lamellae subdecurrent, distant, white; stipe glutinous, white with grayish olive-brown fibrils from veil remnants, sometimes with a partial veil forming an annulus, apex white, dry, floccose.

Phylogenetic support Our ITS analysis (Online Resource 9) includes five taxa in subsect. *Olivaceoumbrini* (two clades of *H. olivaceoalbus* corresponding to western North America and Europe = *H. korhonenii* respectively, *H. persoonii*, *H. latitabundus* = *H. limacinus* and *H. mesotephrus*). In our Supermatrix, LSU and ITS analyses *H. olivaceoalbus* appears in a separate clade, but without backbone support. In the four-gene analysis presented by Larsson (2010, unpublished data), subsect. *Olivaceoumbrini* (represented by *H. bakerensis, H. korhonenii, H. latitabundus, H. mesotephrus, H. olivaceoalbus*, and *H. persoonii*) appears as a paraphyletic grade with 65 % MPBS support for the basal branch and 78 % MPBS support for the branch separating it from the monophyletic subsect. *Tephroleuci*.

Species included Type species: *Hygrophorus olivaceoalbus.* Species included based on morphology and phylogeny are *H. bakerensis* A.H. Sm. & Hesler, *H. korhonenii* Harmaja, *H. latitabundus* Britzelm., *H. mesotephrus* Berk., and *H. persoonii* Arnolds (=*H. limacinus* Fr.). Morphology indicates that *Hygrophorus occidentalis* A.H. Sm. & Hesler also belongs here (Hesler and Smith 1963; Kovalenko 1989, 1999).

Comments Subsect. *Olivaceoumbrini* is polyphyletic in our Supermatrix, LSU and ITS analyses, and a grade in the analysis presented by Larsson (2010). The composition of subsect. *Olivaceoumbrini* is mostly concordant with the morphologically based groups of Hesler and Smith (1963), Singer (1986), Kovalenko (1989, 1999) Arnolds (1990), Bon (1990) and Candusso (1997).

Hygrophorus* [subgen. *Colorati* sect. *Olivaceoumbrini*] subsect. *Tephroleuci (Bataille) Singer, Lilloa 22: 146 (1951) [1949].

Type species: *Hygrophorus tephroleucus* (Pers. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 325 (1838)

≡ *Agaricus tephroleucus* Pers. (1801) : Fr.

= *Hygrophorus pustulatus* (Pers.) Fr. (1838),

= *Agaricus pustulatus* Pers. (1801) : Fr.,

[Bataille's name is automatically typified by the type species epithet upon which the taxon name was based, thus type is NOT *Hygrophorus agathosmus* (Fr. : Fr.) Fr., as in Singer (1951, 1986) and Candusso (1997), Art. 22.6].

Basionym: *Hygrophorus* [unranked] *Tephroleuci* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 164 (1910).

Pileus viscid, white or gray, cinereous, bistre or grayish-brown; lamellae distant, subdecurrent, white; stipe usually dry or subviscid, white, basally with grayish tinges, sometimes with dark grayish brown fibrils or granules from veil remnants; often with a distinct odor.

Phylogenetic support Subsect. *Tephroleuci* is a monophyletic group with low MLBS support in our Supermatrix analysis (55 %), a clade lacking significant support in our ITS analysis (Online Resource 9) but is polyphyletic in our ITS-LSU analysis (Fig. 6). In a four-gene analysis presented by Larsson (2010, unpublished data), the subsect. *Tephroleuci* clade, comprising *H. agathosmus*, *H. pustulatus* and *H. hyacinthinus,* has 100 % MP BS support.

Species included Type species: *Hygrophorus pustulatus* = *H. tephroleucus*. *Hygrophorus agathosmus* (Fr.) Fr., *H. agathosmus* f. *albus* Candusso, *H. hyacinthinus* Quél. and *H. odoratus* A.H. Sm. & Hesler are included based on molecular phylogenies and morphology.

Comments Singer (1951) assumed Bataille's (1910) unranked name *Tephroleuci* was a designated subsection. Thus Singer (1951) inadvertently published the combination *Hygrophorus* subsect. *Tephroleuci* (Bataille) Singer. Bataille's groups were named for type species, so the type of *Tephroleuci* Bataille is *Hygrophorus tephroleucus* (Art. 22.6), not *H. agathosmus* as stated by Singer (1951, 1986) and Candusso (1997). Fries (1821) and Bataille recognized both *H. tephrolucus* and *H. pustulatus* (Pers.) Fr., though Konrad (1936) and Konrad and Maublanc (1937) apparently considered them conspecific and selected *H. pustulatus* over the competing name *H. tephroleucus; H. pustulatus* is the name in current use. The clade corresponding to subsect. *Tephroleuci* is concordant with Bataille's (1910) with exclusion of *H. fuscoalbus* Lasch., *H. lividoalbus* Fr., *H. lucandi* Gill., and *H. marzuolus* Fr. The composition of *Tephroleuci* in Singer (1986), Candusso (1997) and Kovalenko (1989, 1999) is only partly concordant with our phylogenies because they included species from subg. *Camarophyllus* (i.e., *H. camarophyllus, H. calophyllus*, and *H. atramentosus*). Bon (1990) included *H. agathosmus* and *H. odoratus*, which are all in the *Tephroleuci* clade, but he placed the type species, *H. pustulatus* (= *H. tephroleucus*), in sect. *Hygrophorus* subsect. *Fuscocinerei* (Fr.) Bon [illeg.], while including *H. mesotephrus*. from subsect. *Olivaceoumbrini*.

Hygrophorus* [subgen. *Colorati*] sect. *Pudorini (Bataille) Konrad & Maubl., Sel. Fung. 6: 427 (1937).

Type species *Hygrophorus pudorinus* (Fr.), Fr. Anteckn. Sver. Ätl. Svamp.: 46 (1836)

≡ *Agaricus pudorinus* Fr., *Syst. mycol.* (Lundae) 1: 33 (1821),

= *Hygrophorus persicolor* Ricek, Z. Pilzk. 40(1–2): 6 (1974).

Basionym: *Hygrophorus* [unranked] *Colorati* [unranked] *Pudorini* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 158 (1910).

Basidiomes usually dry, lacking a glutinous universal veil, sometimes with a cortinoid partial veil, usually white to pallid, with pinkish buff, pinkish tan, russet, pinkish orange or vinaceous tints or spots, or colored apricot, rose, red, purple or vinaceous purple, rarely completely white or cream colored; lamellae crowded to subdistant, adnate to subdecurrent; stipe dry, often with pruina, glandular dots or a cortinoid fugacious annulus.

Phylogenetic support Sect. *Pudorini* is an unsupported monophyletic group in our expanded *Hygrophorus* ITS (Online Resource 9) and Supermatrix analyses (21 % and 23 % MLBS, respectively). Sect. *Pudorini* is polyphyletic in our LSU analysis, but there is no significant backbone support. In the four-gene analysis presented by Larsson (2010; unpublished data), sect. *Pudorini* appears as a grade that is paraphyletic with regard to sect. *Olivaceoumbrini* (basal branch placing subsect. *Salmonicolores* as sister to subsects. *Pudorini* and *Olivaceoumbrini* with 71 % MPBS).

Subsections included Clitocyboides (Hesler & A.H. Sm.) E. Larss., stat. nov., *Pudorini*, and *Salmonicolores* E. Larss., subsect. nov.

Comments Bataille (1910) named an unranked group *Pudorini* and divided it into two parts, 1) *Exannulati* (lacking an annulus) with *H. miniaceus* Beck, *H. queletii* Bres., *H. pudorinus* Fr. var. *rubescens* Beck, *H. russula* var. *rubescens* Fr., and *H. capreolarius*, and 2) *Subannulati* (subannulate) with *H. purpurascens* (Alb. & Schwein.) Fr. and *H. persicinus* Beck. With one exception, the composition of Bataille's [unranked] *Pudorini* is consistent with sect. *Pudorini* in our analyses, though the subgroups *Exannulati* and *Subannulati* are not concordant with the main branches corresponding to subsections. Konrad and Maublanc (1937) combined Bataille's *Pudorini* at section rank in *Hygrophorus*. Singer (1986) recognized sect. *Pudorini* (Bataille) Konrad & Maubl., with subsects "*Erubescentes*" Hesler & A.H. Sm. and "*Fulvoincarnati*" Hesler & A.H. Sm. Neither subsect. "*Erubescentes*" nor "*Fulvoincarnati*" (Smith and Hesler 1939) are valid, however, because they lacked Latin diagnoses that were required beginning in 1935 (Art. 36.1). Singer's circumscription of subsect. "*Erubescentes*" (invalid) corresponds to a strongly supported (95 % MP BS) clade in the four-gene analysis presented by Larsson (2010; unpublished data) that combines subsects. *Pudorini* and *Clitocyboides*. Subsect. "*Fulvoincarnati*" [invalid] is largely concordant with the new subsect., *Salmonicolores*. Arnolds (1990) placed species belonging to the *Pudorini* clade in sect. *Hygrophorus*, with species of subsect. *Pudorini* in subsect. "*Erubescentes*" [invalid], and species of subsect. *Clitocyboides* in subsect. *Pudorini* owing to the misapplication of the name *H. pudorinus.* The type species of *H. pudorinus* Fr. matches *H. persicolor* Ricek, but the name has been misapplied to *H. abieticola*. The North American taxon called *H. 'pudorinus'* appears in a sister clade to *H. persicolor* in our ITS analysis (Online Resource 9), so it is close to the original concept of *H. pudorinus*. Both Arnolds (1990) and Candusso (1997) incorrectly assumed Bataille's (1910) unranked name *Pudorini* was published at subsection rank, but only Candusso (1997, p 112) provided sufficient information (a full and direct reference to Bataille) to inadvertently combine it in *Hygrophorus* as subsect. *Pudorini* (Bataille) Candusso. Candusso (1997) divided sect. *Pudorini* into subsects *Aurei*, "*Erubescentes*", and *Pudorini,* with subsect. "*Erubescentes*" [invalid] largely corresponding to subsects. *Pudorini* plus *Clitocyboides*. Bon (1990) attempted to resurrect a descriptive heading from Fries [unranked] *Rubentes* as a named section, but the name is invalid as Bon did not fully cite the basionym; further, the group is polyphyletic and thus not useful.

Hygrophorus* [subgen. *Colorati* sect. *Pudorini*] subsect. *Clitocyboides (Hesler & A.H. Sm.) E. Larss., stat. nov.

MycoBank MB804112.

Type species: *Hygrophorus sordidus* Peck, Torrey Bot. Club Bull. 25: 321 (1898)

[= subsect. "*Pallidi*" A.H. Sm. & Hesler, Llyodia 2:32 (1939) invalid, Art. 36.1].

Basionym: *Hygrophorus* [sect. *Hygrophorus* subsect. *Hygrophorus*] series *Clitocyboides* Hesler & A.H. Sm., North American Species of *Hygrophorus*: 309 (1963).

Basidiomes robust, dry to subviscid, lightly pigmented; pileus white to pallid cream, or colored incarnate to orange ochre or vinaceous purple; lamellae adnate to decurrent, mostly crowded, white sometimes turning incarnate or spotted vinaceous purple with age; stipe dry, white to pallid incarnate or with vinaceous purple spots.

Phylogenetic support Subsect. *Clitocyboides*, represented by *H. poetarum, H. russula* and *H. sordidus*, is strongly supported as monophyletic by our ITS-LSU analysis (100 % ML BS). Subsect. *Clitocyboides*, represented by *H. poetarum, H. russula,* and *H.* aff. *russula* is strongly supported in our

Supermatrix analysis and our ITS analysis by Ercole (Online Resource 3) (84 % and 100 % MLBS, respectively). Similarly, support for a monophyletic subsect. *Clitocyboides* (*H. nemoreus, H. penarius, H. penarioides, H. poetarum, H. russula,* and *H. sordidus*) is high in a four-gene analysis presented by Larsson (2010, unpublished data) (95 % MPBS). Our expanded ITS analysis of *Hygrophorus* (Online Resource 9) shows moderate support for a monophyletic subsect. *Clitocyboides* comprising *H. nemoreus, H. penarius, H. penarioides, H. poëtarum, H. russula, H.* aff. *russula,* and *H. sordidus* (55 % MLBS support), and *H. purpurascens* appears basal to the subsect. *Clitocyboides* clade (41 % MLBS) instead of being in the subsect. *Pudorini* clade.

Species included Type species: *H. sordidus. Hygrophorus nemoreus* (Pers.) Fr., *H. penarius* Fr., *H. penarioides* Jacobsson & E. Larss., *H. poetarum* R. Heim, *H. russula* (Schaeff.) Kauffman, and *H.* aff. *russula* are all included based on morphological and phylogenetic data.

Comments Smith and Hesler (1939) attempted to erect subsect. "*Pallidi*" with *H. sordidus* Peck, *H. subsordidus* Murr. and *H. subalpinus* A.H. Sm. in sect. *Clitocyboides* Hesler & A.H. Sm., but it was invalid (Art. 36.1). Singer first (1951) placed subsect. "*Pallidini*" [invalid] (*Clitocyboides*) in sect. *Candidi*, then changed the section name to *Hygrophorus* (1986). Singer (1986) tentatively included *H. penarius* (plus *H. karstenii*), but placed more highly pigmented *H. nemoreus* and *H. russula* together with *H. erubescens* and *H. purpurascens* in sect. *Pudorini* subsect. "*Erubescentes*" A.H. Sm. & Hesler [invalid]. Kovalenko (1989, 1999) distributed the species of subsect. "*Pallidini*" [invalid, = *Clitocyboides,* valid] among sect. *Hygrophorus* subsects. *Hygrophorus*, *Pudorini* and "*Fulvoincarnati* "A.H. Sm. & Hesler [invalid]. Arnolds (1990) only included *H. penarius* with the type species of subsect. "*Pallidini* "[invalid] (= *Clitocyboides*) and distributed the other species among subsects. "*Erubescentes*" [invalid] and *Pudorini*. Bon (1990) placed *H. penarius* in "sect. *Clitocyboides* Hesl. & Sm."[nonexistent — combination was never made at this rank], but assembled the other species into sect. "*Rubentes*" Fr. [invalid], subsect. *Exannulati* Bataille [possibly valid as subsect. *Exannulati* (Bataille) Bon], stirps *Russula* and *Erubescens*. Papetti (1997) provided a Latin diagnosis to validate Konrad and Maublanc's [unranked] *Nemorei* as sect. *Nemorei* Konrad & Maubl. ex Papetti with *H. nemoreus* as the type species and included *H. leporinus*, but other related species were placed elsewhere. Finally, Candusso (1997) placed species of the *Clitocyboides* clade in subsects. "*Pallidini*" [invalid] and "*Erubescentes*" [invalid], together with a mixture of species from other clades. Thus none of the previous classifications adequately reflect the composition of the well-supported subsect. *Clitocyboides* clade, and most of the infrageneric names they assigned were invalid.

Hygrophorus* [subgen. *Colorati* sect. *Pudorini*] subsect. *Pudorini (Bataille) Candusso, *Hygrophorus*. Fungi europ. (Alassio) 6: 212 (1997).

[= subsect. "*Erubescentes"* A.H. Sm. & Hesler, Llyodia 2: 4 (1939), invalid, Art. 36.1].

Type species: *Hygrophorus pudorinus* (Fr. : Fr.) Fr., Anteckn. Sver. Ätl. Svamp.: 46 (1836), (1836),

≡ *Agaricus pudorinus* Fr., *Syst. mycol.* (Lundae) 1: 33 (1821),

= *Hygrophorus persicolor* Ricek, Z. Pilzk. 40(1–2): 6 (1974).

Basionym: *Hygrophorus* [unranked] *Colorati* [unranked] *Pudorini* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 158 (1910).

Pileus viscid, white or white with vinaceous or pink tinges, often spotted vinaceous purple by age; lamellae adnate to subdecurrent, subdistant, white as young, then often turning vinaceous purple; stipe subviscid or dry, white as young and then often with vinaceous or pink tinges, sometimes becoming yellowish or spotted vinaceous purple by age, apex floccose-fibrillose, or with a partial veil giving rise to a fibrillose fugacious annulus.

Phylogenetic support We show an unsupported monophyletic subsect. *Pudorini* (*H. pudorinus* as *H. persicolor* and *H. erubescens*) in our ITS analysis, but *H. purpurascens* appears at the base of the adjacent clade (Online Resource 9). In the analysis presented by Larsson (2010; unpublished data), subsect. *Pudorini* (*H. erubescens, H. pudorinus* and *H. purpurascens*) appears as a paraphyletic group with 95 % support for the basal branch while subsect. *Clitocyboides* appears as a monophyletic clade.

Species included Type species: *Hygrophorus pudorinus* (= *H. persicolor* Ricek). *Hygrophorus erubescens* (Fr.) Fr. and *H. purpurascens* (Alb. & Schwein. : Fr.) Fr. are included based on morphological and phylogenetic data.

Comments The name *H. pudorinus* has been misapplied to a *Hygrophorus* species associated with *Abies*, now named *H. abieticola*. Examination of the type painting and comparisons with the protologue of *H. pudorinus* revealed that *H. persicolor* is a synonym. Candusso (1997) assumed Bataille's name, *Pudorini*, was published at subsection rank and inadvertently combined it at that rank in *Hygrophorus*.

Hygrophorus* [subgen. *Colorati* sect. *Pudorini*] subsect. *Salmonicolores E. Larss., subsect. nov.

MycoBank MB804113.

Type species *Hygrophorus abieticola* Krieglst. ex Gröger et Bresinsky, Regensb. Mykol. Schr.: 15: 211 (2008).

Etymology: salmon – salmon, colores – colored, for the salmon colored basidiomes.

Pileus subviscid, pale incarnate, salmon or ochraceous orange, universal and partial veil absent; lamellae distant, adnate to decurrent, white or with a pale salmon tinge; stipe dry or subviscid, white, yellowish or pale salmon orange, apex floccose-fibrillose; odor none or like turpentine.

Phylogenetic support The subsect. *Salmonicolores* clade (*H. abieticola* and *H. queletii*) is moderately supported (68 % MPBS) as a monophyletic clade in the analysis presented by Larsson (2010, unpublished data). These species were not included in our analyses.

Species included Type species: *Hygrophorus abieticola*. *Hygrophorus queletii* Bres. is included based on morphological and phylogenetic data. The ITS sequence from the western North America taxon diverges from European *H. abieticola* and likely needs a new name at species or variety rank.

Comments The name *H. pudorinus* has been misapplied to a *Hygrophorus* species associated with *Abies*. Krieglsteiner was the first to recognize the species associated with *Abies* as *H. abieticola*. The name was later validated by Gröger and Bresinsky (Bresinsky 2008) and it is the type of the new section, *Salmonicolores*. In Singer (1986), subsect. "*Fulvoincarnati* "Hesler & A.H. Sm. (1939, invalid, Art. 36.1) included *H. abieticola* (as *H. pudorinus*, but apparently a mixed species concept) and *H. queletii*, corresponding to subsect. *Salmonicolores*, except that the subsection also included the type species of sect. *Fulventes* (*H. arbustivus* Fr.). In addition to subsect. "*Fulvoincarniti* "being invalid, it would also be illegitimate if it had been validly published. The type species indicated for subsect. "*Fulvoincarnati*" was *H. pudorinus*, and not the taxon to which the name *H. pudorinus* was applied (i.e., *H. abieticola*), subsect. "*Fulvoincarnati* "thus would have been a superfluous (therefore, illegitimate) name for subsect. *Pudorini* rather than being a legitimate name for the new subsect. *Salmonicolores* if it had been validly published. Kovalenko (1989, 1999) followed Singer's classification, but included in subsect. "*Fulvoincarnati*" [invalid, illeg.] *H. secretanii* – a species that belongs in sect. *Aurei*.

Hygrophorus* [subgen. *Colorati*] sect. *Aurei (Bataille) E. Larss., stat. nov.

MycoBank MB804114.

Type species *Hygrophorus aureus* Arrh., in Fr., Monogr. Hymenomyc. Suec. (Upsaliae) 2: 127 (1863)

≡ *Hygrophorus hypothejus* (Fr. : Fr.) Fr. var. *aureus* (Arrh.) Imler, Bull. trimest. Soc. mycol. Fr. 50: 304 (1935) [1934]

= *Hygrophorus hypothejus* (Fr. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 324 (1838),

≡ *Agaricus hypothejus* Fr., Observ. Mycol. (Havniae) 2: 10 (1818).

Basionym *Hygrophorus* [unranked] *Aurei* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 161 (1910) [1909].

Pileus glutinous or subviscid when moist, color cream buff, yellow, olive, brown, gold or orange; stipe glutinous with a partial veil sometimes forming an annulus or dry. Ectomycorrhizal, predominantly associated with conifers.

Phylogenetic support Sect. *Aurei* appears as a monophyletic group in the analysis presented by Larsson (2010; unpublished data), including *H. hypothejus* (=*H. aureus*), *H. hypothejus* var. *aureus*, *H. gliocyclus*, *H. flavodiscus* and *H. speciosus* in subsect. *Aurei* and *H. karstenii* and *H. secretanii* in subsect. *Discolores*, but MPBS support for the branch is lacking. Sect. *Aurei* is polyphyletic in our ITS analysis (Online Resource 9).

Subsections included Subsect. *Aurei* and subsect. *Discolores*, E. Larss., subsect. nov.

Comments We added *H. karstenii* and *H. secretanii* to this distinctive group and raised the rank to section.

Hygrophorus* [subgen. *Colorati* sect. *Aurei*] subsect. *Aurei (Bataille) Candusso, *Hygrophorus*. Fungi europ. (Alassio) 6: 222 (1997).

Type species *Hygrophorus aureus* Arrh., in Fr., Monogr. Hymenomyc. Suec. (Upsaliae) 2: 127 (1863)

≡ *Hygrophorus hypothejus* (Fr. : Fr.) Fr. var. *aureus* (Arrh.) Imler, Bull. trimest. Soc. mycol. Fr. 50: 304 (1935) [1934],

= *Hygrophorus hypothejus* (Fr. : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 324 (1838),

≡ *Agaricus hypothejus* Fr., Observ. Mycol. (Havniae) 2: 10 (1818).

Basionym *Hygrophorus* [unranked] *Aurei* Bataille, Mém. Soc. émul. Doubs, sér. 8 4: 161 (1910) [1909].

Pileus glutinous, colored citrine, gold, yellow, orange, olive or brown; lamellae subdecurrent, pale, yellowish to orange; stipe glutinous with a partial veil sometimes forming an annulus, pale or stained yellowish, orange or brown.

Phylogenetic support Our LSU analysis shows high support (89 % MLBS) for the subsect. *Aurei* clade comprising *H. hypothejus* (as *H. speciosus* and *H. lucorum*) and *H. flavodiscus*. Support is high for a subsect *Aurei* clade comprising *H. flavodiscus* and *H. hypothejus* (as *H. lucorum*) in our Supermatrix analysis (100 % MLBS) and is also high (76 % MLBS) in our ITS analysis for the clade comprising *H. gliocyclus* and *H. hypothejus*. Larsson's (2010; unpublished

data) presentation shows 100 % MPBS support for subsect. *Aurei* including *H. hypothejus*, *H. hypothejus* var. *aureus*, *H. gliocyclus*, *H. flavodiscus* and *H. speciosus*.

Species included Type species: *Hygrophorus hypothejus*. Taxa included based on both molecular and morphological data are *H. hypothejus* var. *aureus* (≡ *H. aureus*), *H. gliocyclus* Fr., *H. flavodiscus* Frost, *H. lucorum* Kalchbr. and *H. speciosus* Peck. *H. whiteii* Hesler & A.H. Sm. is included based on morphology .

Comments The well supported clade representing subsect. *Aurei* is concordant with the morphology-based subsect. *Aurei* delineated by Bon (1990) and Candusso (1997), partly concordant with series *Aurei* in Hesler and Smith (1963), but not concordant with the classifications by Singer (1986), Kovalenko (1989, 1999, 2012) or Arnolds (1990).

Hygrophorus*, subsect. *Discolores E. Larss., subsect. nov. MycoBank MB804115.

Type species *Hygrophorus karstenii* Sacc. & Cub., Syll. Fung. (Abellini) 5: 401 (1887),

= *Hygrophorus bicolor* P. Karst. (1878), nom. illeg. homonym of *H. bicolor* Berk. & Broome (1871).

Etymology: dis – different, colores – color, for the contrasting color of the lamellae and pileus.

Pileus surface subviscid when moist, soon dry, dull, yellowish beige, sometimes with a red tint; lamellae decurrent, cream or egg yolk-yellow, more or less darkening upon drying; stipe dry, dull, pale yellowish beige or with age more ochre brown; odor none or like marzipan.

Phylogenetic support Hygrophorus secretanii and *H. monticola* A.H. Sm. & Hesler are included in our ITS analysis (Online Resource 9), while *H. karstenii* and *H. secretanii* are included in the 4-gene analysis presented by Larsson (2010, unpublished data). Although there is 100 % MLBS support for the subsect. *Discolores* clade in our ITS analysis, *H. monticola* is a synonym of *H. secretanii*. In the multigene phylogeny of Larsson (not shown), subsect. *Discolores* appears as a paraphyletic grade that is basal to subsect. *Aurei*. There is no significant support for the branches in this grade, except for the species (100 % MPBS).

Species included Type species: *Hygrophorus karstenii*. The inclusion of *H. secretanii* Henn. =*H. monticola* is supported by both morphological and molecular data.

Comments Hygrophorus karstenii and *H. secretanii* (syn. *H. monticola* Hesler & A. H. Sm.) are both northern boreal species associated with *Picea* and *Pinus*. The species were not treated by Arnolds (1990), but partly treated by Hesler and Smith (1963) and Singer (1986). The name *H. melizeus* Fr. is used for *H. karstenii* in both Candusso (1997) and Kovalenko (2012). The rather convoluted naming of these species will not be further discussed here.

Hygrophorus* subgen. *Camarophylli (as *Camarophyllus*) Fr., Summa veg. Scand., Section Post. (Stockholm) 2: 307 (1849).

Type species *Agaricus camarophyllus* Alb. & Schwein., Consp. Fung. Lusat.: 177 (1805) : Fr., [Art. 22.6]

≡ *Hygrophorus camarophyllus* (Alb. & Schwein. : Fr.) Dumée, Grandjean & L. Maire, Bull. Soc. mycol. Fr. 28: 292 (1912),

[= *Hygrophorus caprinus* (Scop.) Fr. (1838), superfluous to a sanctioned name, nom. illeg., Art. 13.1].

Hygrophorus subgen. *Camarophylli* **emended here by E. Larss.** to exclude *A. pratensis* and related species now placed in *Cuphophyllus*.

Pileus surface usually dry, gray, grayish blue, buff brown, reddish brown, bistre or fuliginous, or if glutinous then white with yellow floccose-fibrillose veil remnants on the margin; lamellae subdecurrent to decurrent; stipe surface dry, smooth or fibrillose, usually pale gray, grayish blue, buff brown, bistre or fuliginous, if white glutinous with yellow floccules from veil remnants especially near the apex; lamellar trama divergent giving rise directly to basidia, thus differing from the genus *Cuphophyllus*.

Phylogenetic support Our LSU analysis shows moderately high support (72 % MLBS) for *H. chrysodon* (subg. *Camarophylli*) as basal to the rest of the genus *Hygrophorus*. One ITS analysis (Online Resource 3) shows the same topology while another (Online Resource 9) shows *H. chrysodon* near the base, both without significant BS support. A four-gene analysis with more species presented by E. Larsson (2010 and unpublished data) also shows subg. *Camarophylli* as a basal group in *Hygrophorus*, where it appears as a paraphyletic grade (55 % MPBS for the branch separating it from subg. *Colorati*). *Hygrophorus chrysodon* and *H. camarophyllus* appear together in a basal clade in one of our ITS ML analyses (not shown), but *H. subviscifer* also appears in the clade, and BS support is lacking. Our Supermatrix analysis places *H. chrysodon* among sections of subg. *Colorati*, but without backbone support.

Sections included Type section *Camarophylli* P. Karst., sect. *Chrysodontes* (Singer) E. Larss., stat. nov. and a new section to accommodate *H. inocybiformis*, sect. *Rimosi* E. Larss., sect. nov., are included based on morphology and molecular phylogenies.

Comments Agaricus camarophyllus was included by Fries 1821 in his 'subtrib. *Camarophylli*' (invalid, Art. 33.9). In 1838, Fries presented this taxon in his'trib. *Camarophyllus*' (invalid, Art. 33.9) as *Agaricus caprinus* Scop., with *A.*

camarophyllus in synonymy. The first valid publication of subgen. *Camarophyllus* by Fries was in 1849. Fries' *Hygrophorus* subg. *Camarophylli* comprised the type species (*H. camarophyllus*), *H. nemoreus* (now placed in *Hygrophorus* subg. *Colorati*) and two species of *Cuphophyllus* (*C. pratensis* and *C. virgineus*), so we only retain Fries' type species. Fries (1874), Bataille (1910), Singer (1943, 1949), Hesler and Smith (1963), Arnolds (1990), Kovalenko (1989, 1999) and Candusso (1997) all treated sect. *Chrysodontes* (as subsect. *Chrysodontini*) within sect. *Hygrophorus*. Bon (1990) however, placed *H. chrysodon* in subg. *Hygrophorus* sect. *Ligati* (invalid). The yellow color and the glutinous pileus and stipe of sect. *Chrysodontes* differs from the dull colors and dry basidiomata in sect. *Camarophyllus,* but the placement is supported by Larsson's (2010) and our LSU analysis. Most authors did not classify *H. inocybiformis* (sect. *Rimosi*), but Fries (1874) placed it in subg. *Camarophyllus*, and Bon (1990), placed it in subg. *Neocamarophyllus* Bon [illeg.] sect. *Neocamarophyllus* Bon [illeg.] together with *H. camarophyllus*, *H. calophyllus*, and *H. marzuolus*. Although Bon's (1990) group is most concordant with our molecular phylogenies, his attempts to erect subgenus and sect. *Neocamarophyllus* were illegitimate because they lacked designated type species and Latin diagnoses. As noted by Bas (1990), the citation by Arnolds (1990) as tribe *Hygrophoreae* (Kühner) Bas & Arnolds was incorrect in two respects: 1. tribe *Hygrophoreae* was published earlier than Kühner by P. Hennings (1898), and 2. only names below genus are recombined (Art. 6.7), so authors of higher taxa remain the same when they are transferred to another family. Bas (1990) and Arnolds (1990) treated tribe *Hygrophoreae* in the fam. Tricholomataceae rather than Hygrophoraceae.

Hygrophorus* [subgen. *Camarophylli*] sect. *Camarophylli P. Karst. [as *Hygrophorus* sect. *Camarophyllus*], Bidr. Känn. Finl. Nat. Folk. 25: 197 (1876).

Type species *Agaricus camarophyllus* Alb. & Schwein. Consp. Fung. Lusat.: 177 (1805) : Fr. [Art. 22.6] [as *H. caprinus* (Scop.) Fr.],

≡ *Hygrophorus camarophyllus* (Alb. & Schwein. : Fr.) Dumée, Grandjean & L. Maire, Bull. Soc. mycol. Fr. 28: 292 (1912),

[= *Hygrophorus caprinus* (Scop.) Fr. (1838), superfluous to a sanctioned name, nom. illeg., Art. 13.1].

Basidiomes dry; pileus grayish blue, grayish brown, buff brown, reddish brown bistre or fuliginous; lamellae decurrent to deeply decurrent, white, sometimes with a grey or salmon-orange tinge; stipe grayish blue, grayish brown, buff brown, bistre or fuliginous; surface smooth or fibrillose. Lamellar trama divergent.

Phylogenetic support Species in this clade are not represented in our LSU, ITS-LSU or Supermatrix analyses. Our ITS analysis places *H. camarophyllus* on a separate branch near the base of *Hygrophorus*, but without backbone support. Sect. *Camarophylli* is also basal in the four-gene analysis presented by E. Larsson (2010, unpublished data), comprising *H. atramentosus, H. camarophyllus, H. calophyllus, H. capriolarius,* and *H. marzuolus*, but without backbone support.

Species included Type species: *Hygrophorus camarophyllus*. Additional phylogenetically supported species are *H. atramentosus* (Alb. & Schwein.) H. Haas & R. Haller Aar., *H. calophyllus* P. Karst., *H. capreolarius* Kalchbr. and *H. marzuolus* (Fr.) Bres.

Comments Fries (1821; 1838) used the name *Camarophylli* for an unrecognized infrageneric rank, "subtribu" (name invalid because "subtribu" were not included in the exception outlined in the Vienna Code, Art. 33.12), in "Tribu" *Clitocybe*, then validly published as *Hygrophorus* subg. *Camarophyllis* Fr. in 1849. Karsten (1876) validly published *Hygrophorus* sect. *Camarophylli* (as sect. *Camarophyllus*), and included a Latin diagnosis. Bon (1990) attempted to erect a section, *Neocamarophyllus,* which is superfluous and thus illegitimate, and he listed Fries' group as a synonym but erred in citing it (p. 90) as sect. *Camarophylli* (Fr.) Hesl. & A.H. Smith. Hesler and Smith (1963), however, classified *Camarophylli* at ranks of subsect. and series rather than section, and they only cited Fries as the basionym of series *Camarophylli* (Fr.) Hesler & A.H. Smith (p. 379) and not subsect *Camarophylli* A.H. Smith & Hesler (p. 309). Subsect. *Camarophylli* A.H. Smith & Hesler is invalid as Hesler and Smith (1963) cited Lloydia 2: 32 (1939), but only the description of sect. *Clitocyboides* (without authors or Latin diagnosis) appears on that page and there are no infrageneric taxa named '*Camarophylli*' anywhere in Smith and Hesler (1939). Nevertheless, Bon (1990) was the only author besides Fries (1849), Bataille (1910) and Hesler and Smith (1963) to recognize this group, in Bataille as *Hygrophorus* subg. *Camarophyllus*, [unranked] *Caprini*). Singer (1986) and Kovalenko (1989, 1999) classified *H. camarophyllus* and *H. marzuolus* in sect. *Hygrophorus* subsect. *Tephroleuci,* while Hesler and Smith (1963) included species from subsect. *Tephroleuci* with those of series *Camarophylli*. The composition of Bon's (1990) invalid sect.*Neocamarophyllus* (*H. atramentosus, H. camarophyllus, H. calophyllus, H. hyacinthinus* and *H. inocybiformis*) is closest to the composition of Sect. *Camarophylli* based on the four-gene analysis of Larsson (2010 and unpublished data).

Hygrophorus* [subgen. *Camarophylli*] sect. *Chrysodontes (Singer) E. Larss., stat. nov.

MycoBank MB804117.

Type species: *Hygrophorus chrysodon* (Batsch : Fr.) Fr., Epicr. syst. mycol. (Upsaliae): 320 (1838) [1836–1838]

≡ *Agaricus chrysodon* Batsch, Elench. Fung., cont. sec. (Halle): 79 (1789) : Fr.

Basionym: *Hygrophorus* sect. *Hygrophorus* subsect. *Chrysodontes* Singer (as *Chrysodontini*), Ann. Mycol. 3: 41 (1943).

Basidiomes glutinous when moist; pileus white with golden yellow floccose-fibrillose veil remnants on margin; lamellae decurrent, white, sometimes with yellow granules on the edges; stipe white with golden yellow floccose granules, especially at stipe apex, which may form an vague annulus.

Phylogenetic support There is high support (98 %–100 % MLBS) for sect. *Chrysodontes*in our Supermatrix, LSU and ITS analyses, as well as in a four-gene analysis presented by Larsson (2010, unpublished data). Our LSU analysis has strong support (72 % MLBS) for placing *Chrysodontes* as sister to the rest of the genus *Hygrophorus*. Sect. *Chrysodontes* is basal in the genus in the LSU, ITS and four-gene analyses, but not our Supermatrix analysis.

Species included Type species: *Hygrophorus chrysodon*. This was thought to be a monotypic group, but our ITS analysis suggests the taxon from western N. America is distinct, and the analysis presented by Larsson (2010, unpublished data) shows two distinct clades in N. Europe. *Hygrophorus chrysodon* var. *cistophilus* Pérez-De-Greg., Roqué & Macau is also divergent in its ITS sequence (E. Larsson, unpublished data). While specimens from the divergent *H. chrysodon* clades do not differ appreciably in morphology, they occur with different hosts or are geographically disjunct and may represent different varieties or species. *Hygrophorus chrysodon* var. *leucodon* Alb. & Schwein. is thought to be a color variant, but has not been sequenced.

Comments *Chrysodontes* was described as '*Chrysodontini*' by Singer (1943) as a subsection of sect. *Hygrophorus,* following the placement by Bataille (1910). All subsequent authors also placed *Chrysodontes*within sect. *Hygrophorus* (Kovalenko 1989, 1999; Arnolds 1990; Bon 1990; Candusso 1997) or as a series in subsect. *Hygrophorus* (Hesler and Smith 1963). Our LSU analysis shows strong support (72 % ML BS) for placing *Chrysodontes* as sister to the rest of the genus *Hygrophorus*, and the four-gene analysis presented by Larsson (2010, unpublished data) shows sect. *Chrysodontes* basal while sect. *Hygrophorus* is the most distal in the phylogeny, making the placement by Singer and others untenable. We have therefore raised this phylogenetically supported and morphologically distinctive group to section rank.

Hygrophorus* [subgen. *Camarophylli*] sect. *Rimosi E. Larss., sect. nov.

MycoBank MB804118.

Type species *Hygrophorus inocybiformis* A.H. Sm., Mycologia 36(3): 246 (1944).

Basidiomes dry; pileus appearing rimose from dark grayish brown fibrils on a pale ground, darker in the centre, fibrillose veil remnants on margin; lamellae white, distant, decurrent; stipe white with dark grayish brown fibrils from veil remnants, apex white; growing with *Abies* and *Picea*.

Etymology.—rimose = cracked, referring to the cracked appearance of the pileus surface.

Phylogenetic support Only the analysis presented by Larsson (2010) includes *H. inocybiformis*. In that analysis, *H. inocybiformis* is the most basal member of the subg. *Camarophyllus* grade; there is high support (81 % MPBS) for placing *H. inocybiformis* as sister to the rest of the genus *Hygrophorus*. Support for this monotypic clade is 100 % MPBS.

Species included Type species: *Hygrophorus inocybiformis*. The section is monotypic.

Comments Hesler and Smith (1963) placed *H. inocybiformis* in series *Camarophylli*, together with a mixture of species from subg. *Camarophylli* and *Colorati*. The dry basidiomes, dull colors, and cortinoid fibrillose veil fit well in subg. *Camarophylli*.

Subfamily *Lichenomphalioideae* Lücking & Redhead subf. nov.

MycoBank MB804120.

Type genus: *Lichenomphalia* Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 38 (2002).

Basidiomes omphalinoid, pleurotoid, stereoid-corticioid or lentoid-cyphelloid, rarely absent, usually fuscous, green or colorless, rarely orange or yellow; hymenium lamellate, cantharelloid, merulioid or smooth; basidia elongated or not; clamp connections present or absent; L-DOPA and (to date) carotenoid pigments absent; habit primarily bryophilous or phycophilous, often lichenized, rarely parasitic or saprobic.

Phylogenetic support Subf. *Lichenomphaloideae* appears as a moderately to well-supported monophyletic clade in our four-gene backbone analyses (81 % MLBS, 1.0 Bayesian PP), a monophyletic clade in our ITS-LSU analysis, a monophyletic clade with low support in our Supermatrix analysis (38 % ML BS), but as a paraphyletic grade lacking BS support in our LSU analysis. Previous LSU analyses show *Lichenomphaloideae* as a moderately supported monophyletic clade (Lutzoni 1997, 68 % and 53 % MP BS for unpruned and pruned data sets) or as three clades emerging from a backbone (Moncalvo et al. 2002). Using ITS together with LSU data improved support for a monophyletic *Lichenomphaloideae* in Lutzoni (1997; MPBS

83 % in equally weighted and 70 % in unequally weighted data sets) and Redhead et al. (2002; 79 % MP BS), but not in Lawrey et al. (2009). In the ITS-LSU analysis by Lawrey et al. (2009), *Lichenomphalia umbellifera* was separated from the other species in subf. *Lichenomphaloideae*, making it polyphyletic. Association with plant symbionts increased the rate of nucleotide substitutions after the adoption of a mutualistic lifestyle in four separate lineages of subf. *Lichenomphaloideae* (Lutzoni and Pagel 1997), and this affects topology in phylogenetic analyses (Lawrey et al. 2009). Subf. *Lichenomphaloideae* and *Hygrophoroideae* appear as sister clades in Redhead et al. (2002, represented by *Chrysomphalina*), a Supermatrix analysis presented by Lodge et al. (2006), the Supermatrix analysis presented here (68 % MLBS), and our four-gene backbone analyses (81 % MLBS; 1.0 BPP).

Tribes included Arrhenieae Lücking, tribe nov., *Cantharelluleae* Lodge & Redhead, tribe nov. and *Lichenomphalieae* Lücking & Redhead, tribe nov.

Comments The existence of a monophyletic clade within the Hygrophoraceae in which the species are primarily associated with bryophytes algae and cyanobacteria was shown by Lutzoni (1997), Redhead et al. (2002) and Lawrey et al. (2009), and this group is more strongly supported by our analyses. We also show the strongest support for subf. *Lichenomphalioideae* and *Hygrophoroideae* as sister clades – a relationship suggested by Redhead et al. (2002).

Tribe *Arrhenieae* Lücking, tribe nov.

MycoBank MB804121.

Type genus: *Arrhenia* Fr., Summa Veg. Scand., Section Post. (Stockholm): 312 (1849).

Basidiomes omphalinoid, pleurotoid, lentoid-cyphelloid or stereoid-corticioid, gray, gray-brown, green or white; hymenium lamellate, cantharelloid, merulioid or smooth; basidia elongated or not; clamp connections present or absent; DOPA and carotenoid pigments absent; habit primarily bryophilous, rarely phycophilous; parasitic and/or pathogenic on mosses and algae, lichenized, or saprotrophic; associated with scytonematoid bacteria if lichenized; thallus absent undifferentiated, squamose or foliose.

Phylogenetic support Tribe *Arrhenieae* appears as a strongly supported monophyletic clade in our four-gene backbone (97 % MLBS; 1.0 BPP), Supermatrix (99 % MLBS) and ITS-LSU (97 % MLBS) analyses, and moderately supported in our LSU analysis (67 % MLBS). Similarly, Lawrey et al. (2009) show strong support for a monophyletic *Arrhenieae* using a combined ITS-LSU data set (96 % MPBS and 100 % MLBS). Only our ITS analysis shows tribe *Arrhenieae* as a paraphyletic grade.

Genera included Arrhenia, Acantholichen, Cora, Corella, Cyphellostereum, Dictyonema and *Eonema.*

Comments The monophyly of the new tribe *Arrhenieae,* established by Lawrey et al. (2009), is confirmed here. It includes the non-lichenized genera *Arrhenia* s.l. (paraphyletic) and *Eonema* and the genera lichenized with cyanobacteria — *Acantholichen, Cora, Corella, Cyphellostereum*, and *Dictyonema* (Dal-Forno et al. 2013). In the analyses by Dal-Forno et al. (2013), *Corella* appears as a sister clade to *Acantholichen* with strong support in their combined ITS-LSU-RPB2 analysis (91 % MLBS; 0.98 BPP).

Acantholichen P.M. Jørg., Bryologist 101: 444 (1998).

Type species: *Acantholichen pannarioides* P.M. Jørg., Bryologist 101: 444 (1998).

Basidiomata absent; lichenized, thallus small, squamulose-sordiate, appearing on the margins of the foliose lichen; acanthohyphidia present; internal structure homomerous, composed of jigsaw cells; clamp connections absent.

Phylogenetic support Acantholichen is represented only by the type of this monotypic genus in our Supermatrix analysis (57 % MLBS), where it appears as sister to *Corella*. Similarly, the combined ITS-LSU- RPB2 analyses by Dal-Forno et al. (2013), show *Acantholichen* as sister to *Corella* (91 % MLBS, 1.0 B.P. with 88 % MLBS and 1.0 BPP support for the branch that subtends both).

Species included Type species: *Acantholichen pannarioides*. The genus is currently monotypic, but two undescribed species have been found in Brazil and the Galapagos Islands.

Comments Acantholichen was originally classified as an ascolichen because basidiomata are absent, and the spiny structures indicated placement in the Pannariaceae. Jørgensen (1998) reinterpreted the spiny structures as basidiomycete dendrohyphidia.

Cora Fr., Syst. orb. veg. (Lundae) 1: 300 (1825).

Type species: *Cora pavonia* (Sw.) Fr., Syst. orb. veg. (Lundae) 1: 300 (1825),

≡ *Thelephora pavonia* Sw., Fl. Ind. Occid. 3: 1930 (1806).

Basidiomes stereoid-corticioid; hymenium smooth; lichenized with cyanobacteria, thallus thelephoroid or foliose-lobate, gray and white; jigsaw shaped sheath cells present; clamp connections present.

Phylogenetic support Only a few representatives of *Cora* were included in our analyses – as *Dictyonema minus* isotype, *Cora glabrata* R06 & *C. glabrata* s.l. AFTOL. The ITS-LSU analysis of Lawrey et al. (2009) places *D. minus* in the same clade with *D. sericeum* (100 % MLBS) whereas our

Supermatrix analysis places *D. minus* as sister to *D. glabratum* s.l. AFTOL with strong support (80 % MLBS). The combined ITS-LSU-RPB2 analysis of Dal-Forno et al. (2013) shows *Cora* as sister to a clade formed by *Acantholichen* and *Corella*.

Species included Type *Cora pavonia* (Sw.) Fr., *C. byssoidea*, *C. glabrata* (Spreng.) Fr., *D. hirsutum* Moncada & Lücking and *D. minus* Lücking, E. Navarro & Sipman, as well as a large number of undescribed species are included (Dal-Forno et al. 2013).

Comments The generic name *Cora* was resurrected by Lawrey et al. (2009) and Yánez et al. (2012) based on correlations between phylogeny and thallus morphotypes in the *Dictyonema* s.l. clade. *Cora* is a monophyletic clade characterized by macrosquamulose to foliose thalli with a loose, palisadic upper cortex.

Dictyonema C. Agardh ex Kunth, Syn. pl. (Paris) 1: 1 (1822).

Type species: *Dictyonema excentricum* C. Agardh, in Kunth, Syn. pl. (Paris) 1: 1 (1822) = *Dictyonema thelephora* (Spreng.) Zahlbr., Cat. Lich. Univers. 7: 748 (1931) [current name],

= *Dictyonema sericeum* (Sw.) Berk., London J. Bot. 2: 639 (1843), ≡ *Dictyonema sericeum* f. *thelephora* (Spreng.) Parmasto, Nova Hedwigia 29: 111 (1978) [1977].

Basidiomata stereoid-corticioid or lentoid-cyphelloid; hymenium smooth; clamp connections absent; lichenized with cyanobacteria, thallus present, undifferentiated, jigsaw shaped hyphal sheath cells present.

Phylogenetic support Dictyonema, represented by *D. sericeum*, is strongly supported as a sister to *Cora* (as *D. glabratum* and *D. minus*) in our 4-gene backbone, ITS-LSU and LSU analyses (100 % MLBS). In our Supermatrix and ITS analyses, *Dictyonema* appears basal to the *Cora* clade (100 % MLBS). The *Dictyonema–Cora* clade appears on a long branch emerging from the *Arrhenia* grade in our 4-gene backbone analyses and our ITS-LSU analysis. The analyses by Dal-Forno et al. (2013) shows the most closely related groups that are basal to *Dictyonema* are *Eonema* and *Cyphellostereum* rather than the more distantly related *Arrhenia* included in our analyses. In the analysis by Lawrey et al., *Acantholichen* separates the *Cora* (*D. sericeum—D. minus*) and *Dictyonema* ss. (*D. aeruginosulum*, *D. phyllophilium* and *D. schenkianum*) clades, but without support for the branching order.

Species included Type *Dictyonema excentricum* [=*D. sericeum* (Sw.) Berk.). Additional species included based on molecular phylogenies of Lücking et al. (2009) and Dal-Forno et al. (2013) are *D. hernandezii* Lücking, Lawrey & Dal-Forno, *D. irpicinum* Mont., *D. minus* Lücking, *D. sericeum* f. *phyllophilum* Parmasto, *D. schenkianum* (Müll. Arg.) Zahlbr, and two new *Dictyonema* spp. aff. *D. sericeum.*

Comments While *Dictyonema* appears as a grade in most analyses, the combination of morphological and ecological characters set it apart, and topological tests cannot reject its potential monophyly. Resurrection of generic names *Cora* by Lawrey et al. (2009) and *Corella* by Dal-Forno et al. (2013) for the disjunct *Dictyonema* clades shown in Lawrey et al. (2009) resolves the problem of polyphyly in this group.

Cyphellostereum D.A. Reid, Beih. Nova Hedwigia, 18: 336 (1965).

Type species: *Cyphellostereum pusiolum* (Berk. & M.A. Curtis) D.A. Reid, Beih. Nova Hedwigia 18: 342 (1965),

≡ *Stereum pusiolum* Berk. & M.A. Curtis, J. Linn. Soc., Bot. 10 (no. 46): 330 (1869) [1868].

Basidiomata usually absent, cyphelloid when present; hymenium irregular; cystidia absent; clamp connections absent; lichenized with cyanobacteria; thallus appressed filamentose-crustose, undifferentiated, gray or white, hyphal sheath cells simple, not jigsaw puzzle shaped.

Phylogenetic support We included only one species of *Cyphellostereum* in our Supermatrix analysis (as *Dictyonema phyllogenum*), where it appears as sister to the *Dictyonema-Cora* clade with 100 % MLBS support, and distal to *Arrhenia*. Previous analyses by Lawrey et al. (2009) show *D. phyllogenum* together with the type of *Cyphellostereum, C. pusiolum*, in a strongly supported monophyletic clade (98 % MP and 100 % MLBS). Dal-Forno et al. (2013) show strong support for a monophyletic *Cyphellostereum* in their combined ITS-LSU-RPB2 analysis (73 % MLBS, 0.99 BPP). In Lawrey et al. (2009), *Cyphellostereum* is distal to *Eonema* and *Arrhenia* and basal to the *Dictyonema–Cora* clade. The topology shown in the combined ITS-LSU-RPB2 analyses of Dal-Forno et al. (2013) is similar, but *Cyphellostereum* appears as sister to *Dictyonema*, while *Eonema* is basal to both.

Species included Type *Cyphellostereum pusiolum*. *Dictyonema phyllogenum* (Müll. Arg.) Zahlbr. is included based on molecular phylogenies (Dal-Forno et al. 2013; Lawrey et al. 2009). Several undescribed species also belong in this clade. *Cyphellostereum laeve* (Fr. : Fr.) D.A. Reid is excluded based on phylogenetic analyses of Larsson (2007) that place it in the Hymenochaetales.

Comments Lawrey et al. (2009) were the first to show the type of *Cyphellostereum* is near the base of the clade named here as subf. *Lichenomphalioideae*, and they also confirmed

Oberwinkler's (1970) observations of an associated lichenized thallus. The genus is similar to *Dictyonema* s.s. in overall morphology but lacks the jigsaw-puzzle-shaped hyphal sheath cells.

Arrhenia Fr., Summa Veg. Scand., Section Post. (Stockholm): 312 (1849).

Type species: *Arrhenia auriscalpium* (Fr.) Fr., Summa Veg. Scand., Section Post. (Stockholm): 312 (1849),

≡ *Cantharellus auriscalpium* Fr., Elench. fung. (Greifswald) 1: 54 (1828)].

Basidiomes omphalinoid or pleurotoid, gray or grayish brown or bluish gray, rarely dark and scaly at center with beige or tan margin and then growing on sphagnum; hymenium paler, lamellate, cantharelloid, merulioid or smooth; basidia elongated or not; clamp connections present or absent; DOPA and carotenoid pigments absent; habit primarily bryophilous, rarely phycophilous; parasitic and/or pathogenic on mosses or algae, possibly saprobic on dung, not lichenized (thus lacking a thallus) as found in *Acantholichen*, *Dictyonema* or *Lichenomphalia*.

Phylogenetic support Arrhenia consistently appears as a paraphyletic grade in all analyses, and the same is true for tribe *Arrhenieae*.

Species included Type species: *Arrhenia auriscalpium*. Species included based on molecular phylogeny are *A. chlorocyanea* (Pat.) Redhead et al., Lutzoni, Moncalvo & Vilgalys, *A. epichysium* (Pers. : Fr.) Redhead et al., *A. griseopallida* (Desm.) Watling, *A. lobata* (Pers.) Kühner & Lamoure ex Redhead, *A. obscurata* (D.A. Reid) Redhead et al., *A. philonotis* (Lasch) Redhead et al., *A. sphagnicola* (Berk.) Redhead et al. and *A. velutipes* (P.D. Orton) Redhead et al. Species included in *Arrhenia* based on morphology in Redhead et al. (2002) are *A. acerosa* (Fr.) Kühner, *A. alnetora* (Singer) Redhead, *A. australis* (Clel.) Grgurinovic, *A. andina* (Corner) Redhead et al., *A. antarctica* (Singer) Redhead et al., *A. baeospora* (Singer) Redhead et al., *A. chilensis* (Mont.) Redhead et al., *A. elegans* (Pers.) Redhead et al., *A. fissa* (Leyss.) Redhead, *A. hohensis* (A.H. Sm.) Redhead et al., *A. lundellii* (Pilát) Redhead et al., *A. obatra* (J. Favre) Redhead et al., *A. obscurata* (D. A. Reid) Redhead et al., *A. omnivora* (Agerer) Redhead et al., *A. onisca* (Fr.:Fr.) Redhead et al., *A. parvivelutina* (Clémençon & Irlet) Redhead et al., *A. pauxilla* (Clémençon) Redhead et al., *A. peltigerina* (Peck) Redhead et al., *A. pubescentipes* (H.E. Bigelow) Redhead et al., *A. rainierensis* (H.E. Bigelow) Redhead et al., *A. retiruga* Redhead, *A. rickenii* (Hora) Watling, *A. rigidipes* (Lamoure) Redhead et al., *A. salina* (Høil.) Bon & Courtec., *A. spathulata* (Fr.) Redhead, *A. rustica* (Fr.) Redhead et al., *A. sphaerospora* (Lamoure) Redhead et al., *A. stercoraria* (Barrasa, Esteve-Rav. & Sánchez Nieto) Redhead et al., *A. subglobispora* (G. Moreno, Heykoop & E. Horak) Redhead et al., *A. subobscura* (Singer) Redhead et al., *A. subumbratilis* Redhead et al., *A. trigonospora* (Lamoure) Redhead et al., *A. umbratilis* (Fr.:Fr.) Redhead et al., *A. viridimammata* (Pilát) Redhead et al. and *A. volkertii* (Murrill) Redhead et al.

Comments Omphalinoid *Arrhenia* species were once classified in *Omphalina* (type species, *O. pyxidata*), a genus that is also bryophilous, but *Arrhenia* are gray-brown throughout while *Omphalina* have a reddish brown surface and colorless context (Redhead et al. 2002). *Arrhenia* was erected for species with drooping or pendant basidiomata with cantharelloid (wrinkled) hymenia (Corner 1966, Høiland 1976; Pilát and Nannfeldt 1954), but later expanded to include species with pleurotoid basidiomata, such as *Leptoglossum* and *Phaeotellus,* and omphalinoid basidiomata (Redhead et al. 2002). Because *Arrhenia* includes reduced species (e.g., *A. auriscalpium*, the type of *Arrhenia*, and *A. lobata*, the type of *Dictyolus* Quél.) as well as omphalinoid species, some are not readily distinguishable from other genera in the subfamily based on macromorphology. The ecology of *Arrhenia* often differs, however, in its association with mosses, or more rarely with microbial films, and it lacks a lichenized thallus.

Lawrey et al. (2009) note the paraphyly of *Arrhenia* in relation to *Dictyonema* and *Cora* using parsimony (MP) and likelihood (ML) methods whereas as a distance based method (ME) shows *Arrhenia* as monophyletic. Lawrey et al. (2009) suggested that the paraphyly of *Arrhenia* is likely real, and that the difference in topology using a distance method may be an artifact of having few synapomorphies in a rapidly evolving group.

Corella Vain., Acta Soc. Fauna Flora fenn. 7(2): 243 (1890).

Type species: *Corella brasiliensis* Vain., Acta Soc. Fauna Flora fenn. 7(2): 243 (1890),

≡ *Dictyonema pavonium* f. *brasiliense* (Vain.) Parmasto, Nova Hedwigia 29 (1–2): 106 (1978).

Basidiomes stereoid-corticioid; hymenium smooth; spores inamyloid; clamp connections absent; lichenized with cyanobacteria; thallus foliose, jigsaw shaped cells present.

Phylogenetic support Corella was not represented in our phylogenetic analyses. Analyses by Dal Foro et al. (2013) suggest the type species is part of a complex.

Species included Type species: *Corella brasiliensis* Vain. *Dictyonema melvinii* Chaves et al. (2004) is included.

Comments Corella brasiliensis was not accepted as a separate species or genus by Parmasto (1978) but is phylogenetically and morphologically distinct, differing from *Cora* in the presence of a paraplectenchymatous upper cortex and being more closely related to *Acantholichen* (Dal-Forno et al. 2013).

Eonema Redhead, Lücking & Lawrey, Mycol. Res. 113(10): 1169 (2009).

Type species: *Eonema pyriforme* (M.P. Christ.) Redhead, Lücking & Lawrey

≡ *Athelia pyriformis* (M.P. Christ.) Jülich, Willdenowia, Beih. 7: 110 (1972),

≡ *Xenasma pyrifome* M.P. Christ., Dansk bot. Ark. 19(2): 108 (1960).

Basidiomes corticioid-athelioid; hymenium smooth; spores hyaline, inamyloid; clamp connections absent; saprotrophic, thallus is absent.

Phylogenetic support As *Eonema* is monotypic, branch support is not relevant. However, support for *Eonema* as sister to *Cyphellostereum* is strong in MP and ML analyses of ITS-LSU in Lawrey et al. (2009, 96 % and 100 % MP and MLBS).

Species included Type species: *Eonema pyriforme*, is the only known species.

Comments The type, *E. pyriforme*, was previously classified among the corticioid fungi as a species of *Xenasma*, *Athelia* and *Athelidium*. In a review of corticioid fungi, Larsson (2007) suggested that a new genus be erected in the Hygrophoraceae to accommodate this species, hence the erection of *Eonema* by Redhead et al. in Lawrey et al. (2009).

Tribe *Lichenomphalieae* Lücking & Redhead tribe nov.

MycoBank MB804122.

Type genus: *Lichenomphalia* Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 36 (2002).

Basidiomata mostly omphalinoid, rarely arrhenioid and drooping; pileus usually convex-umbilicate, typically colored fuscous from melanized intraparietal or encrusting pigments and/or yellow from dissolved pigments; stipe present, cartilaginous or tough, surface usually pubescent; mostly uninucleate; clamp connections absent; lichenized stromata present, undifferentiated, squamulose or rarely foliose, totally enveloping *Coccomyxa* algal cells, in non-perforated sheaths of polygonal cells (not jigsaw shaped), forming either scattered spherules or irregular granules usually less than 1 mm diameter connected by filamentous hyphae.

Phylogenetic support Lichenomphalieae is strongly supported as a monophyletic clade in our 4-gene backbone Bayesian analysis (0.99 PP), moderately supported in our 4-gene ML analysis (69 % MLBS) but weakly supported in our Supermatrix and ITS analyses (< 50 % MLBS). Analyses by Lutzoni (1997) also show a monophyletic *Lichenomphalieae* clade with support varying from <50 % to 70 % MPBS. The inner *Lichenomphalieae* clade (excluding *L. umbellifera* = *L. ericetorum*) is strongly supported in all analyses (90 %–100 % ML or MPBS; 1.0 BPP). *Lichenomphalieae* appears polyphyletic in some analyses because of the divergent *L. umbellifera* (Lawrey et al. 2009, and our LSU and ITS-LSU analyses).

Genera included Lichenomphalia and tentatively *Semiomphalina,* based on morphology.

Comments Lutzoni (1997) showed that the lichenized omphalinoid fungi are a monophyletic clade, while Kranner and Lutzoni (1999) showed this group shares many characters including mononucleate basidiomes, a *Coccomyxa* algal host and lack of growth in axenic culture. *Semiomphalina* is a rare fungus with drooping, pale basidiomes that has not yet been sequenced, but it shares with *Lichenomphalia* stipe and thallus characters, and it is thought to be a sister genus based on morphology (Redhead et al. 2002).

Lichenomphalia Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 36 (2002).

Type species: *Lichenomphalia hudsoniana* (H.S. Jenn.) Redhead et al., Mycotaxon 83: 38 (2002),

≡ *Hygrophorus hudsonianus* H.S. Jenn., Mem. Carn. Mus., III 12: 2 (1936).

Basidiomes omphalinoid, lamellae decurrent; stipe cartilaginous or tough, usually pubescent; pigments of two types, intracellular pigments bright orangish yellow, intraparietal and encrusting pigments fuscous and melanized; pileus trama hyphae thin walled, large diameter generative hyphae together with smaller diameter connective hyphae; lamellar trama bidirectional or subregular; subhymenial cells elongated, forming a loose structure; hymenium slightly thickening; basidia of variable lengths; basidiospores hyaline, white in mass, inamyloid, not metachromatic in cresyl blue; cystidia absent; clamp connections absent; lichenized thallus squamulose, rarely foliose or undifferentiated, totally enveloping *Coccomyxa* algal cells, in non-perforated sheaths of polygon-shaped cells, not jigsaw shaped, forming either scattered sphaerules or irregular granules usually less than 1 mm diameter connected by filamentous hyphae, hyphal walls thickened; xeric habitats in arctic-alpine areas.

Phylogenetic support Support for a monophyletic clade comprising *Lichenomphalia* is presented above under tribe *Lichenomphalieae*.

Subgenera included Lichenomphalia and *Protolichenomphalia* Lücking, Redhead & Norvell, subg. nov.

Comments Lichenomphalia species are primarily found in arctic-alpine zones, though *L. umbellifera* extends into the boreal zone (Lutzoni 1997). Lutzoni (1997) found that *L. umbellifera* (as *L. ericetorum*) had the slowest molecular substitution rate within the lichenized omphalinoid group,

and is likely an extant species that most closely resembles the ancestral species that gave rise to this lichenized lineage. As noted above under phylogenetic support for Tribe *Lichenomphalieae*, *L. umbellifera* is also the most divergent species. We therefore recognize *L. umbellifera* as the type of a new subgenus, *Protolichenomphalia*.

The history of nomenclature in this group is complex, and as it was reviewed thoroughly in Redhead et al. (2002), only a short synopsis is presented here. Some of the names applied to this group were based on oldest named anamorphic, lichenized states, namely *Phytoconis* Bory (1797), *Botrydina* Bréb. (1839), and *Coriscium* Vain. (1890). Although the sexual states of ascolichens have long been named from types representing their lichenized state, an attempt to apply asexual names to the sexual state of basidiolichens (Clémençon 1997; Redhead and Kuyper 1988; Norvell et al. 1994 and many others listed in Redhead et al. 2002 and Gams 1995) was rejected and the asexual basidiolichen names were placed on a list of rejected names (Gams 1995; Greuter et al. 2000). *Lichenomphalia* was proposed by Redhead et al. (2002) to replace the rejected names. Although anamorph names were placed on equal footing with teleomorph names with regards to priority when the nomenclatural code was changed to eliminate dual nomenclature in January of 2013, a previously rejected name cannot be resurrected, leaving *Lichenomphalia* as the only available name for this genus.

Lichenomphalia* subgen. *Lichenomphalia [autonym], subg. nov.

Type species *Lichenomphalia hudsoniana* (H.S. Jenn.) Redhead et al., Mycotaxon 83: 38 (2002)

≡ *Hygrophorus hudsonianus* H.S. Jenn., Mem. Carn. Mus., III 12: 2 (1936).

Characters as in *Lichenomphalia*, basidiomes highly pigmented; lichenized with *Coccomyxa* algae; thallus usually squamulose, rarely foliose or undifferentiated, hyphal walls thickened; growing in xeric arctic-alpine habitats.

Phylogenetic support Subg. *Lichenomphalia* has strong support in our 4-gene backbone (99 % MLBS; 1.0 B.P. and Supermatrix (95 % MLBS) analyses, and moderate support in our LSU analyses (63 % MLBS). Analyses by Lutzoni (1997) also show strong support using LSU (95 % MPBS) combined ITS-LSU (92 %–93 % MPBS), and ITS1 and ITS2 (86 % and 82 % MPBS, respectively). ITS-LSU analyses by Redhead et al. (2002) and Lawrey et al. (2009) also show high support (83 %–98 % MPBS and 100 % ML BS) for a monophyletic subg. *Lichenomphalia*.

Species included Type *Lichenomphalia hudsoniana*. Additional species included based on phylogenies and morphology are *L. alpina* (Britzelm.) Redhead et al., *L. grisella* (P. Karst.) Redhead et al., and *L. velutina* (Quél.) Redhead et al. Species included based on morphology (Redhead et al. 2002) are *L. aurantiaca* (Redhead & Kuyper) Redhead et al., *L. chromacea* (Cleland) Redhead et al., and *L. lobata* (Redhead & Kuyper) Redhead et al.

Comments Subg. *Lichenomphalia* forms a well-supported, monophyletic clade that is concordant with the morphological and ecological characters that define the group. Species in subg. *Lichenomphalia* are found in high-light habitats that are more subject to drought than in subg. *Protolichenomphalia*, but they are presumably protected from ionizing radiation and desiccation by strong pigments and thick hyphal walls in the thalli (Redhead et al. 2002; Redhead and Kuyper 1987).

Lichenomphalia* subgen. *Protolichenomphalia Lücking, Redhead & Novell, subg. nov.

Mycobank MB 804123.

Type species: *Lichenomphalia umbellifera* (L.) Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 38 (2002)

≡ *Agaricus umbelliferus* L., Sp. pl. 2: 1175 (1753), sanctioned by Fr., Elench. fung. 1: 22 (1828).

Etymology—proto – first, lichenomphalia – *Lichenomphalia*.

Characters as in *Lichenomphalia*, basidiomes lightly pigmented; lichenized thallus undifferentiated, hyphal walls thin; growing in mesic habitats in arctic and boreal zones.

Phylogenetic support Phylogenetic support is irrelevant as this subgenus is monotypic.

Species included Type species: *Lichenomphalia umbellifera*.

Comments Redhead et al. (2002) noted that *L. umbellifera* has more ancestral features than other species now placed in subg. *Lichenomphalia*, i.e., the hyphae in the thallus are broader and not as thick-walled, so presumably more susceptible to desiccation (Redhead and Kuyper 1988). Furthermore, the type of subg. *Protolichenomphalia* has a broader geographical distribution, occupies wetter habitats, and its basidiomata are less protected by strong pigments than species in subg. *Lichenomphalia (*Redhead et al. 2002; Lawrey et al. 2009).

Semiomphalina Redhead, Can. J. Bot. 62(5): 886 (1984).

Type species: *Semiomphalina leptoglossoides* (Corner) Redhead, Can. J. Bot. 62(5): 886 (1984),

≡ *Pseudocraterellus leptoglossoides* Corner, Monogr. Cantharelloid Fungi: 161 (1966).

Basidiomes arrhenioid, drooping, pale; stipe and thallus similar to those of *Lichenomphalia umbellifera*.

Comments There are currently no published sequences of this lichenized, monotypic genus described from Papua New Guinea by Corner, but Redhead et al. (2002) suggested that it was related to *Lichenomphalia* based on morphology and

ecology. If *Semiomphalina leptoglossoides* and *Lichenomphalia hudsoniana* are later found to be congeneric, Article 14 in the Melbourne Code (2012) allows for selection of a widely used name, such as *Lichenomphalia,* over a more obscure one (*Semiomphalina*).

Tribe *Cantharelluleae* Lodge, Redhead, Norvell & Desjardin, tribe nov.

MycoBank MB804125.

Type genus: *Cantharellula* Singer, Revue Mycol., Paris 1: 281 (1936).

Basidiomata clitocyboid or omphalinoid; pileus convex, indented or infundibuliform, opaque; pileus and stipe surfaces yellowish or grayish brown; pileipellis hyphae with dissolved pigments, with or without encrusting pigments; lamellae decurrent, repeatedly forked, sometimes staining reddish brown; stipe central or eccentric; spores smooth, the length usually at least twice the diameter, hyaline, white in deposit, distinctly amyloid, acyanophilic; basidia with basal clamp connections, about 4 times the length of the basidiospores; cheilocystidia and pleurocystidia absent; lamellar trama partly gelatinized at the lamellar edge, tridirectional, with a subregular or regular central strand, lateral strands with frequent hyphae parallel to the lamellar edge woven through a few vertically oriented hyphae, and abundant generative hyphae oriented predominantly parallel to the basidia and giving rise to the subhymenial cells, but obliquely angled (divergent) at the lamellar edge; subhymenium subramose or pachypodial, of short- or long celled hyphal segments predominantly parallel and oriented in the same direction as the basidia, but a few highly curved and intertwined; forming a weak hymenial palisade via proliferation of basidia from subhymenial cells; habit bryophilous or lignicolous.

Phylogenetic support Support for a monophyletic clade corresponding to tribe *Cantharelluleae* is strong in our 4-gene backbone analyses (87 % MLBS; 1.0 B.P. and Supermatrix analysis (83 % MLBS), and moderate in our ITS-LSU (65 % ML, 60 % MP BS) and LSU analyses (64 % MLBS). Moncalvo et al. (2002; LSU), Lodge et al. (2006; four-gene Supermatrix) and Lawrey et al. (2009; ITS-LSU) show the same monophyletic clade, but only Lodge et al. (2006) shows significant support (>0.95 Bayesian PP).

Genera included *Cantharellula* and *Pseudoarmillariella.*

Comments The long, smooth, amyloid spores and tridirectional lamellar trama is a unique combination of characters that unite *Cantharellula* and *Pseudoarmillariella*. Singer (1986) described the hymenium of *Cantharellula* and *Pseudoarmillariella* as subirregular to almost intermixed, and the subhymenium as intermixed-subramose. Clémençon et al. (2004), however, listed *Cantharellula* among the genera with bilateral lamellar trama, defined as having vertically oriented hyphae woven through others that are parallel to the lamellar edge. Drawings by Lodge of *Cantharellula* and *Pseudoarmillariella* (Figs. 20 and 21) show typical bidirectional architecture, but they also show an abundance of hyphae that are perpendicular to both sets of hyphae in the bidirectional structure, making it tridirectional. The latter hyphae emerge from the mediostratum, are mostly parallel to the basidia and give rise to the subhymenial cells, in places forming a pachypodial structure in the subhymenium. The appearance of lamellar cross sections in tribe *Cantharelluleae* resembles the bilateral trama and pachypodial hymenium seen in *Aeruginospora* and *Chrysomphalina* Figs. 17 and 18), albeit with few signs of proliferation of basidia from candelabra-like branching of subhymenial cells and thus only forming a weak hymenial palisade such as found in subf. *Hygrophoroideae* tribe *Chrysomphalineae*. Our 4-gene backbone analyses, however, show strong support for placing *Cantharellula* in subf. *Lichenomphalioideae* rather than *Hygrophoroideae*. Nevertheless, subfamilies *Lichenomphalioideae* and *Hygrophoroideae*, are in adjacent clades, so the appearance of similar hymenial architecture in both clades suggests a possible homologous origin.

Tribe *Cantharelluleae* is the only group retained in the Hygrophoraceae with amyloid spores. *Neohygrophorus angelesianus* (A.H. Sm. & Hesler) Singer (= *Hygrophorus* subg. *Pseudohygrophorus* A.H. Sm. & Hesler) is shown as sister to Tribe *Clitocybeae* (Tricholomataceae) in a multigene Supermatrix analysis by Matheny et al. (2006), sister to the type of *Pseudoomphalina, P. kalchbrenneri,* (in the Tricholomataceae), in our 4-gene backbone analyses (100 % MLBS; 1.0 BPP), and sister to *Pseudoomphalina felloides* in previous Supermatrix (Lodge et al. 2006) and LSU analyses (Moncalvo et al. 2002; 70 % MPBS). Another species with amyloid spores, *Hygrophorus metapodius* (Fr.) Fr. [≡*Camarophyllus metapodius* (Fr.) Wünsche, ≡*Hygrocybe metapodia* (Fr.) M.M. Moser, ≡*Neohygrocybe metapodia*

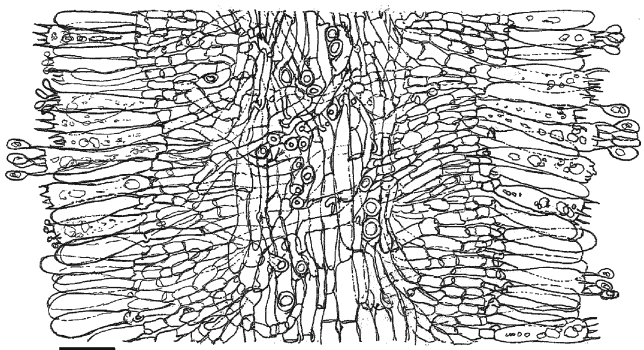


Fig. 20 Subf. *Lichenomphalioideae*, tribe *Cantharelluleae*, *Pseudoarmillariella ectypoides* lamellar cross section (DJL05, North Carolina, Great Smoky Mt. National Park, USA). Scale bar=20 μm

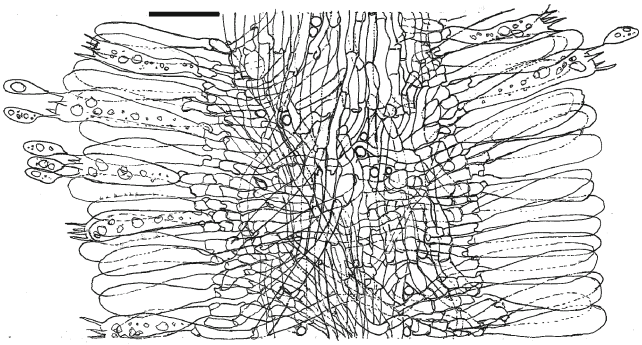


Fig. 21 Subf. *Lichenomphalioideae*, tribe *Cantharelluleae*, *Cantharellula umbonata* lamellar cross section (RDY-1366, R. Youst, California, USA). Scale bar=20 μm

(Fr.) Herink], was also transferred to the Tricholomataceae and recombined in gen. *Porpoloma* by Singer (1973).

Pseudoarmillariella ectypoides has been variously placed in *Clitocybe* (Saccardo 1887), *Clitocybula* (Raithelhuber 1980) and *Omphalina* (Bigelow 1982), while *Cantharellula* has been placed in *Cantharellus* (Persoon 1794), and *Hygrophoropsis* (Kühner and Romagnesi 1953). Singer (1942; 1948; 1986) recognized the close relationship between *Cantharellula umbonata* and *Pseudoarmillariella ectypoides,* but placed them together with other amyloid spored genera in the Tricholomataceae, tribe *Leucopaxilleae*. Singer transferred Peck's *Agaricus ectypoides* to *Cantharellula* in 1942, erected subg. *Pseudoarmillariella* Sing. in 1948 for *C. umbonata* and *C. ectypoides* (Peck) Singer, then raised subg. *Pseudoarmillariella* to genus rank for *P. ectypoides* in 1965. Moncalvo et al. (2002) were the first to show inclusion of tribe *Cantharelluleae* in the *Arrhenia–Lichenomphalia* clade (as cantharelloid clade 62) using an LSU analysis, but without significant branch support. Using a four-gene Supermatrix analysis, Lodge et al. (2006) were the first to show significant support for the *Cantharelluleae* clade, while Matheny et al. (2006) were the first to show significant Bayesian support (1.0 PP) for including *Pseudoarmillariella* in the *Hygrophoraceae* and subf. *Lichenomphalioideae*. Our 4-gene backbone analyses presented here strongly supports that placement.

Cantharellula Singer, Revue Mycol., Paris 1: 281 (1936).

Type species: *Cantharellula umbonata* (J.F. Gmel.) Singer, Revue Mycol., Paris 1: 281 (1936),

≡ *Merulius umbonatus* J.F. Gmel., Systema Naturae, Edn. 13, 2: 1430 (1792).

Basidiomata clitocyboid; pileus convex, indented or infundibuliform, opaque; pileus and stipe surfaces yellowish or grayish brown; lamellae decurrent, repeatedly forked, often staining reddish brown; stipe fleshy or fleshy-fibrous; spores smooth, hyaline, white in deposit, distinctly amyloid, acyanophilic, cylindric or ellipsoid-oblong; basidia mostly four times the length of the basidiospores; cheilocystidia and pleurocystidia absent; lamellar trama subgelatinized at the lamellar edge, with a subregular central strand 15–30 μm wide, lateral strands tridirectional, hyphae parallel to the lamellar edge woven through vertically oriented hyphae, and other hyphae that diverge more or less perpendicularly from the vertical hyphae, but obliquely angled (divergent) at the lamellar edge; subhymenial cells arising from similarly oriented hyphae that diverge from vertically oriented hyphae; subhymenium sometimes pachypodial, of short- or long-celled, mostly parallel hyphal segments oriented in the same direction as the basidia, but forming only a weak hymenial palisade via proliferation of basidia from candelabra-like branches of subhymenial cells; clamp connections present; habit bryophilous. Differs from *Chrysomphalina* in amyloid spore reaction and presence of clamp connections, and from *Chrysomphalina* and *Pseudoarmillariella* in the absence of encrusting pigments on the cuticular hyphae and presence of bright ochraceous pigments in the hymenium.

Phylogenetic support As only the type of *Cantharellula* was included in our analyses, branch support is irrelevant. Support for *Cantharellula* as sister to *Pseudoarmillariella* is strong in our 4-gene backbone (87 % MLBS; 1.0 B.P. and Supermatrix analyses (83 % MLBS), but moderate in our LSU and ITS-LSU analyses (60 %-65 % BS). Lodge et al. (2006) in a previous iteration of the 4-gene Supermatrix analysis show the same topology with high BPP support (>0.95) but lower MPBS support (50 % to 69 %). ITS-LSU analyses by Lawrey et al. (2009) show the *Cantharellula–Pseudoarmillariella* clade with *Hygrophorus* basal to it, but without branch support.

Species included Type *Cantharellula umbonata*. Singer (1986) included *C. infundibuliformis* Singer from Argentina based on morphology. *Cantharellula waiporiensis* (G. Stev.) E. Horak and *C. humicola* Corner are excluded.

Comments Singer (1936) erected gen. *Cantharellula* to accommodate *Merulius umbonatus* J.F. Gmel. We have excluded *C. humicola* as it appears in tribe *Leucopaxilleae* (Tricholomataceae) in our 4-gene backbone analysis (98 % MLBS), and it differs in having a regular hymenial trama and presence of cheilocystidia. Singer excluded *C. waiporiensis* based on presence of encrusting pigments on the pileipellis hyphae, and suggested it belonged in *Pseudoomphalina*. As noted above under tribe *Cantharelluleae*, the hymenophoral trama in *Cantharellula* is comprised of a subregular central strand and lateral strands with three sets of mutually perpendicular hyphae woven together, the subhymenial cells originate from hyphae that diverge at nearly a right angle from vertical generative hyphae and form an incipient hymenial palisade as indicated by some basidia originating at different depths and a pachypodial structure (Fig. 19).

Pseudoarmillariella (Singer) Singer, Mycologia 48: 725 (1956).

Type species: *Pseudoarmillariella ectypoides* (Peck) Singer [as '*ectyloides*'], Mycologia 48(5): 725 (1956),

≡ *Agaricus ectypoides* Peck, Ann. Rep. N.Y. St. Mus. 24: 61 (1872) [1871].

Basionym: *Cantharellula* subg. *Pseudoarmillariella* Singer, Mycologia 48(5): 725 (1956).

Pseudoarmillariella is **emended here by Lodge** to have a tri-directional lamellar trama with an incipient pachypodial hymenial palisade.

Basidiomata omphalinoid; pileus deeply infundibuliform, opaque; pileus and stipe surfaces yellowish or grayish brown, appressed-fibrillose; lamellae decurrent, repeatedly forked, deep ochraceous or yellowish clay color; stipe central or eccentric; spores smooth, hyaline, white in deposit, distinctly amyloid, acyanophilic, cheilocystidia and pleurocystidia absent; pileipellis hyphae nodulose-encrusted; lamellar trama subgelatinized at the lamellar edge, central strand subregular 15–30 μm wide, hyphae mostly thin-walled and 2–6 μm wide, and some larger diameter hyphae (3–7 μm) with thickened walls (1.0–1.2 μm) toward the pileus and adjacent pileus context; lamellar context lateral strands tridirectional, hyphae parallel to the lamellar edge woven through vertically oriented hyphae, and other hyphae that diverge more or less perpendicularly from the vertical hyphae, but obliquely angled (divergent) at the lamellar edge; subhymenial cells arising mostly from similarly oriented hyphae that diverge from vertically oriented hyphae; subhymenium sometimes pachypodial, of short- or long-celled, mostly parallel hyphal segments oriented in the same direction as the basidia, forming a weak hymenial palisade via proliferation of basidia from candelabra-like branches of subhymenial cells; clamp connections present; habit lignicolous. Differs from *Cantharellula* in presence of encrusting pigments on the cuticular hyphae and presence of bright ochraceous pigments in the hymenium. Differs from *Chrysomphalina* in amyloid reaction of the spores, presence of clamp connections and encrusting pigments on the cuticular hyphae.

Phylogenetic support As we only included the type species, *P. ectypoides*, branch support is irrelevant. Support for placing *Pseudoarmillariella* as sister to *Cantharellula* is high, as described above under tribe *Cantharelluleae*.

Species included Type species: *Pseudoarmillariella ectypoides.* This genus may be monotypic, but *P. fistulosa* (Stevenson) Horak is tentatively included based on morphology.

Comments The description of the lamellar trama and hymenium of *Pseudoarmillariella* are emended here. *Pseudoarmillariella* shares with *Cantharellula* a unique combination of spores that are amyloid and elongated, and tridirectional lamellar trama (Fig. 20). The pachypodial structure and insipient hymenial palisade in *Pseudoarmillariella* (Fig. 20) more closely resembles the pachypodial structure of *Chrysomphalina chrysophylla* (Fig. 17) than the description given by Singer (1956, 1986), i.e., "subirregularly intermixed-subramose, its elements short, strongly interlaced-curved in all directions and therefore at times appearing cellular (much like the hymenium of *Cantharellula*)". *Pseudoarmillariella* and *Chrysomphalina* also share a thickened hymenium (Norvell et al. 1994). A microphotograph of the hymenium of *P. ectypoides* (DJL05NC106, from the Great Smoky Mountain National Park) shows spores and former basidia embedded in a hymenial palisade, candelabra-like branching of subhymenial cells and basidia that originate at different depths, as are found in *Chrysomphalina* and *Aeruginospora*. The 'thickened hymenium' noted by Norvell et al. (1994) in *Pseudoarmillariella* is reported as a "thickening hymenium" in Redhead et al. (2002), as found also found in *Chrysomphalina*. As reported in Norvell et al. (1994), Bigelow stated to Redhead in 1985 that he had transferred *P. ectypoides* to *Omphalina* in 1982 based on its similarities to *Chr. chrysophylla*, which he also placed in *Omphalina*, and our reinterpretation of the lamellar and hymenial architecture in *P. ectypoides* (Fig. 20) supports Bigelow's observations. *Pseudoarmillariella* is lignicolous, but it is unknown if it produces a white rot (Redhead et al. 2002), and it frequently occurs on mossy logs and branches.

The Cuphophylloid grade.

While most phylogenetic analyses show *Ampulloclitocybe*, *Cantharocybe* and *Cuphophyllus* at the base of the hygrophoroid clade (Binder et al. 2010; Matheny et al. 2006; Ovrebo et al. 2011), together they suggest an ambiguity as to whether they belong in the Hygrophoraceae s.s. In our four-gene backbone analyses, *Cuphophyllus* is only weakly supported as sister to the rest of the Hygrophoraceae; furthermore, support for a monophyletic family is significant if *Cuphophyllus* is excluded and not significant if it is included. In a six-gene analysis by Binder et al. (2010) and the LSU analysis by Ovrebo et al. (2011), two other genera in the cuphophylloid grade, *Ampulloclitocybe* and *Cantharocybe,* appear between *Cuphophyllus* and the rest of the Hygrophoraceae, but without support, while in the ITS analysis by Vizzini et al. (2012) [2011], genera belonging to the Tricholomataceae s.l. make the genus *Cuphophyllus* polyphyletic. The branching order along the backbone in this part of the Agaricales is unresolved and unstable so it is not clear if *Cuphophyllus*, *Cantharocybe* and *Ampulloclitocybe* should be included in the Hygrophoraceae s.s. or left with other genera in the basal Hygrophoroid clade. The ecological analysis of stable C and N isotope ratios by Seitzman et al. (2011) indicates that a large component of the Hygrophoraceae is

likely biotrophic, including *Cuphophyllus*, and *Cuphophyllus* sequences that have been recovered from rhizosphere and root samples. On the other hand, while Hygrophoraceae in general have not been sustained in axenic culture (Griffith et al. 2002), *Ampulloclitocybe clavipes* (Merlini et al. 2000), and putatively, *Cuphophyllus virgineus* (Farrell et al. 1977), have been cultured on agar media – a trait shared with saprotrophic species of the basal Hygrophoroid clade such as *Aphroditeola* (Redhead 2013), *Phyllotopsis nidulans* (Jayasinghe and Parkinson 2008), *Sarcomyxa serotina* (Kim et al. 2012), *Tricholomopsis rutilans* (Murphy and Mitchell 2001), *Xeromphalina* spp. (Johnson and Petersen 1997), *Typhula phacorrhiza* and *Macrotyphula* spp. (Dentinger and McLaughlin 2006). The pink cantharelloid genus, *Aphroditeola* Redhead & Manfr. Binder (IF550119) that was described in Redhead (2013) to accommodate *Cantharellus olidus* Quél. [= *Hygrophoropsis morganii* (Peck) H.E. Bigelow = *Cantharellus morganii* Peck] is strongly supported as basal to *Xeromphalina campanella* (100 % ML BS) in the basal hygrophoroid clade rather than in the cuphophylloid grade in our LSU analysis (not shown), and thus outside Hygrophoraceae s.s. While the stable isotope analyses of Seitzman et al. (2011) support retaining *Cuphophyllus* in Hygrophoraceae, the branching order in the phylogenies is too unstable and the support levels for the branching order along the backbone are too low to definitively include or exclude it from the Hygrophoraceae. The instability of the branching order among analyses in this basal region of the phylogenetic tree suggests that new/different genes or approaches will likely be needed to resolve these deep branches. We have tentatively retained *Cuphophyllus* in Hygrophoraceae s.s. because it has been traditionally placed there, its similar N and C isotope signatures imply similar trophic relations, and it is close to the base of family, but *Cuphophyllus* and the related genera, *Ampulloclitocybe* and *Cantharocybe,* may eventually be recognized in a separate family.

Cuphophyllus **(**Donk) Bon, Doc. Mycol. 14(56): 10 (1985)[1984].

Type species: *Cuphophyllus pratensis* (Fr.) Bon, Doc. Mycol. 14(56): 10 (1985)[1984]

≡ *Hygrocybe pratensis* (Fr.) Murrill, Mycologia 6(1): 2 (1914),

≡ *Agaricus pratensis* Fr., Observ. mycol. (Havniae) 2: 116 (1818), sanctioned by Fr., Syst. mycol. 1: 99 (1821).

Basionym: *Hygrocybe* subg. *Cuphophyllus* Donk (1962), Beih. Nova Nedwigia 5: 45 (1962)

[*Camarophyllus* P. Kumm., (1871) is an incorrect name for this group].

Cuphophyllus is **emended here by Lodge** to include species with subregular lamellar trama.

Basidiomes mostly clitocyboid, rarely omphalinoid or mycenoid; veils absent; pileus surface dry, lubricous or rarely viscid, smooth, pruinose or pubescent; pileus often white, cream, salmon, or orangish brown, sometimes brown, gray, grayish brown, or reddish brown, rarely yellow, orange, pinkish orange, lilac, pinkish lilac or reddish violet; lamellae mostly arcuate-decurrent, subdecurrent or decurrent, rarely sinuate, usually thick near the pileus, often forked or veined, usually brittle, often acquiring a chalky opaque appearance; stipe often stout, usually solid or hollow near apex, rarely hollow throughout, surface smooth or fibrous, moist or dry, not viscid; basidiospores frequently broadly ellipsoid, subglobose or globose, sometimes ellipsoid or oblong, hyaline, thin-walled, guttulate in KOH, white in mass, inamyloid, not metachromatic in cresyl blue; basidia long, typically 7−8 (rarely 5−6) times the length of the basidiospores, with basal clamp connection; cystidia absent; lamellar trama usually highly interwoven (rarely subregular), with or without a regular or subregular central strand; hyphae usually cylindrical, sometimes inflated, walls usually swollen to 0.5−1 μm thick and refractive in KOH mounts, pileipellis a cutis, ixocutis or trichoderm, hyphae predominantly or partly interwoven, usually with dissolved pigments, sometimes with intraparietal and encrusting pigments; clamp connections usually abundant, large, often medallion-form. Differing from *Hygrophorus* in absence of veils or glandular dots on the stipe apex, typically interwoven rather than divergent lamellar trama, presence of a subhymenium and non-ectomycorrhizal habit. Differing from *Cantharocybe* in absence of cheilo- and caulocystidia, ratio of basidia to basidiospore length exceeding 5 and usually having an interwoven (rarely subregular) rather than regular lamellar trama. Differing from *Ampulloclitocybe* in the ratio of basidia to basidiospore length exceeding 5, and pileipellis predominantly or partly interwoven rather than subparallel.

Phylogenetic support Cuphophyllus appears as a strongly supported monophyletic group in our 4-gene backbone analyses (80 % MLBS; 1.0 Bayesian PP) and Supermatrix analysis (86 % MLBS). Similarly, a strongly supported monophyletic *Cuphophyllus* is shown in the multigene Supermatrix analysis by Matheny et al. (2006; 96 % MPBS; 1.0 BPP). In their ITS-LSU analyses, Vizzini et al. (2012) show a strongly supported monophyletic *Cuphophyllus* separated from the hygrophoroid clade (71 % MLBS, 1.0 BPP), while we show a moderately supported (55 % MLBS) *Cuphophyllus* within the hygrophoroid grade (Fig. 22). *Cuphophyllus* appears as a paraphyletic grade lacking support in our LSU analysis whereas Ovrebo et al. (2011) show a monophyletic *Cuphophyllus* lacking support in their LSU analysis.

Support for *Cuphophyllus* as sister to the Hygrophoraceae is weak in our 4-gene backbone analysis (28 % MLBS; 0.87 B.P. and moderate in our Supermatrix analysis (65 % MLBS). Seitzman et al. (2011) show a strongly supported (82 % MPBS) *Cuphophyllus* as sister to the rest of the

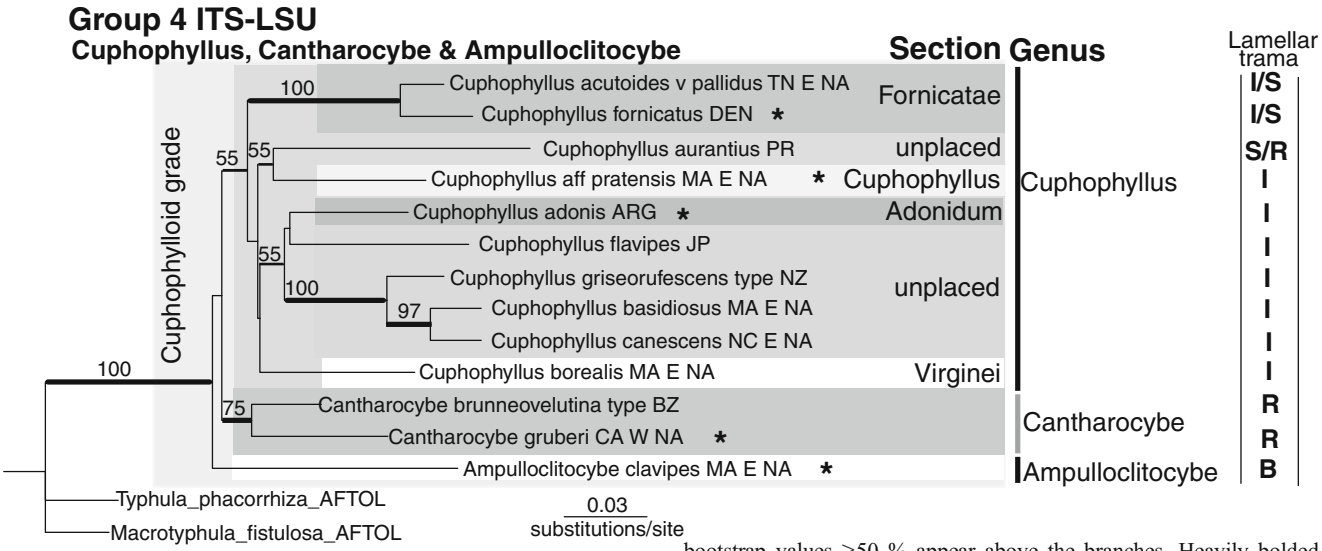


Fig. 22 Cuphophylloid grade (Group 4) ITS-LSU analysis rooted with *Macrotyphula fistulosa*. Genes included in the analysis were partial ITS (5.8S & ITS2), LSU (LROR-LR5). Lamellar trama types are: B – bidirectional; I – interwoven; R – regular/parallel; S – subregular. ML bootstrap values ≥50 % appear above the branches. Heavily bolded branches have ≥70 % and lightly bolded branches have 50–69 % ML bootstrap support

Hygrophoraceae using primarily ITS (5.8S) data. In contrast, the five-gene Supermatrix analysis by Matheny et al. (2006) places *Ampulloclitocybe* between *Cuphophyllus* and the rest of the Hygrophoraceae, while the six-gene RAxML analysis by Binder et al. (2010) places both *Ampulloclitocybe* and *Cantharocybe* between *Cuphophyllus* and the rest of the Hygrophoraceae. An LSU analysis by Moncalvo et al. (2002) shows the only true *Cuphophyllus* (*C. pratensis*) as an independent clade apart from the Hygrophoraceae. In their ITS-LSU analyses, Vizzini et al. (2012) show *Cuphophyllus* as basal to part of the Tricholomataceae and Hygrophoraceae, making the Hygrophoraceae a paraphyletic grade and the Tricholomataceae polyphyletic if *Cuphophyllus* is included in the Hygrophoraceae (64 % MLBS and 1.0 B.P. whereas Lawrey et al. (2009) show it among the genera of the basal hygrophoroid clade.

While the majority of species named in *Cuphophyllus* are ones with interwoven lamellar trama hyphae, the type species of its often applied synonym *Camarophyllus*, *Agaricus camarophyllus* Alb. & Schwein. :Fr., has divergent lamellar trama and is placed in gen. *Hygrophorus* s.s. Thus, the name, *Camarophyllus*, can only be applied to a group in *Hygrophorus* typified by *A. camarophyllus* Fries (1836). Singer (1986) argued that *A. pratensis* should be the type species for subgen. *Camarophyllus* as it was the one (of four noted) that most closely matched the protologue. Contrary to Singer's arguments, *A. camarophyllus* was automatically the type of the subgenus named after it under Art. 22.6. Thus, Singer was incorrect in selecting a new type, *A. pratensis,* as the type of subgen. *Camarophyllus*, which he raised to genus rank. Donk (1962) recognized the nomenclature problem and erected subgen. *Cuphophyllus* in *Hygrocybe* for the species with interwoven lamellar trama (Fig. 23), which Bon (1985) [1984] subsequently raised to genus rank. Thus, *Cuphophyllus* (Donk) Bon is the correct name for this genus. Further discussion can be found in Donk (1962), Courtecuisse and Fiard (2005), Melot (2005) and Young (2005).

Sections included Adonidum, *Cuphophyllus*, *Fornicati* comb. nov., and *Virginei.*

Comments As noted previously, *Cuphophyllus* is the correct name of this genus, and the name *Camarophyllus* that was

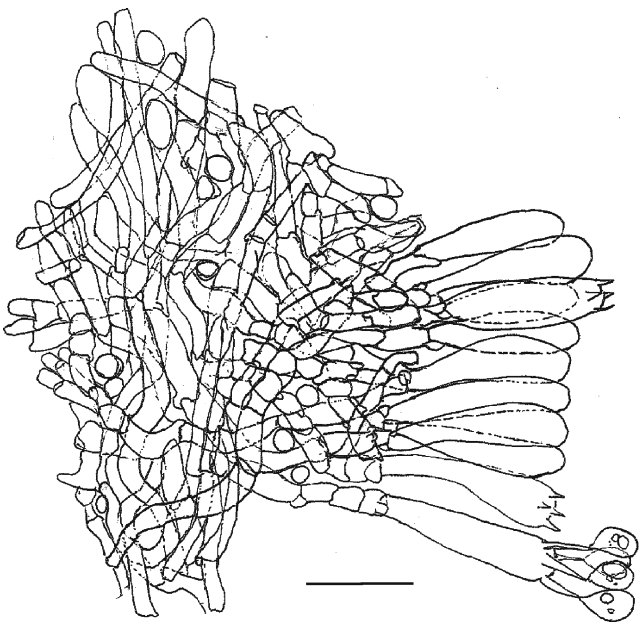


Fig. 23 *Cuphophyllus*, sect. *Fornicati*, *Cuphophyllus acutoides* var. *pallidus* lamellar cross section (DJL06TN124, Tennessee, Great Smoky Mt. Nat. Park, USA). Scale bar=20 μm

applied to this group by Singer (1986) and others can only be referred to a group in *Hygrophorus* s.s. typified by *H. camarophyllus*. Donk (1962) erected subgen. *Cuphophyllus* in gen. *Hygrocybe* to establish a valid name for the group, and Bon raised *Cuphophyllus* to generic rank in 1984. Though many persist in using combinations in *Hygrocybe* for species of *Cuphophyllus*, these genera appear at opposite ends of molecular phylogenies of Hygrophoraceae, which would render *Hygrocybe* polyphyletic. If *Cuphophyllus* and *Hygrocybe* were included in the same genus, it would necessitate applying the oldest name, *Hygrophorus*, to the entire family, including species with amyloid spores (*Cantharellula* and *Pseudoarmillariella*), lignicolous species (*Chrysomphalina*) and lichenized species (*Acantholichen*, *Cyphellostereum*, *Dictyonema* and *Lichenomphalia*) to keep it monophyletic.

Cuphophyllus has traditionally been placed in the Hygrophoraceae based on the highly elongated basidia and waxy hymenium. Relative length of basidia to basidiospores is variable in the Hygrophoraceae (Table 3), and some genera outside the Hygrophoraceae yield a waxy substance when crushed (e.g., *Camarophyllopsis* in the Clavariaceae, and *Neohygrophorus* in Tricholomataceae sl), so neither character is diagnostic for the family (Lodge et al. 2006). With the exception of sect. *Fornicati* in which there is a broad subregular mediostratum with more interwoven lateral strata (Fig. 24), and the *C. aurantius* complex in which the lamellar trama is subregular (Fig. 25), the trama hyphae in *Cuphophyllus* are typically highly interwoven (Fig. 23, at least in the lateral strands, if a subregular central strand is present), and in most species they are cylindrical with slightly thickened, refractive walls. The refractive, interwoven context hyphae probably accounts for the brittle texture and chalky appearance of the lamellae in many *Cuphophyllus* species.

We retain two sections, *Cuphophyllus* and *Virginei,* and recombine *Hygrocybe* sect. *Fornicati* (Bataille) Bon and *Camarophyllus* sect. *Adonidum* (as *Adonidi*) Singer as

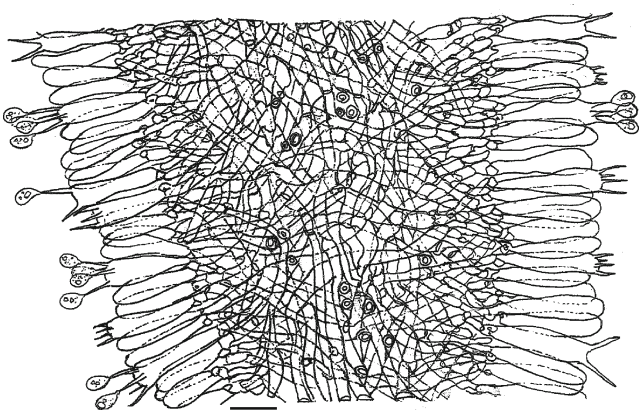


Fig. 24 *Cuphophyllus*, sect. *Cuphophyllus*, *Cuphophyllus* aff. *pratensis* lamellar cross section, (TN-177, DJL06TN51, Tennessee, Great Smoky Mt. Nat. Park, USA). Scale bar=20 μm

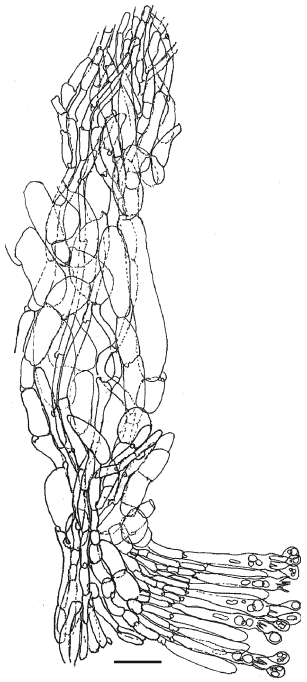


Fig. 25 *Cuphophyllus aurantius* lamellar cross section composite drawing comprised of an upper, middle and lamellar edge sections (PR-6601, Puerto Rico). Scale bar=20 μm

sections in *Cuphophyllus*, but we have refrained from making additional infrageneric changes for several reasons. The positions of several species are unstable, including *Camarophyllus adonis* Singer (type of *Camarophyllus* sect. *Adonidi* Singer), *C. basidiosus, C. canescens and C. flavipes* – a situation unlikely to be resolved without greater taxon sampling, especially from Australasia (e.g., *C. griseorufescens* from NZ in Fig. 22). In 2012, there were ca. 80 species with combinations in *Camarophyllus, Cuphophyllus* or *Hygrocybe*, and we have sequenced an additional ten unnamed species, so we conservatively estimate there are at least 100 species belonging in *Cuphophyllus* globally. Of the total, only 25 *Cuphophyllus* species are represented by an ITS or LSU sequence, and only seven have had four or more gene regions sequenced. It is clear from the support levels for *Cuphophyllus*, however, that multigene analyses are needed to resolve the structure and branching order of this group; new genes are also needed. There are no sequences of *C. cinereus* (Fr,) Bon or *C. hygrocyboides* (Kühner) Bon, the respective types of sect. *Cinerei* (Bataille) Bon (1989, p. 56) and *Hygrocyboideini* (Clémençon) Bon. Only ITS sequences are available for *C. subviolaceus*, the type of *Cuphophyllus* subsect. "*Viscidini* :(A.H. Sm. & Hesler) Bon and sect. "*Viscidi*" (Hesler & A.H. Sm.) Singer (1972*) (both invalid, Art. 36.1 – the basionym in Smith and Hesler 1942 lacked a Latin description; *Singer 1986 cited Singer 1972, but this reference was not found); preliminary analyses (Matheny, unpublished data) suggest *C. subviolaceus* is not conspecific with *C. lacmus*, despite being currently listed as a synonym of the latter. ITS

analyses by Dentinger et al. (unpublished) indicate that misapplied names resulted in polyphyletic phylogenies, and it will require considerable work to redetermine the vouchers, sequence types or authentic material and designate neotypes or epitypes to stabilize the nomenclature. The following new combinations are required so that sequences deposited in GenBank have the same (correct) generic name.

Cuphophyllus acutoides (A.H. Sm & Hesler) Lodge, Matheny & Sánchez-García, comb. nov.

MycoBank MB804126.

Basionym: *Hygrophorus acutoides* A.H. Sm. & Hesler, Sydowia 8: 325 (1954).

Type: USA: MICHIGAN, Mackinaw City, Sept. 16, 1950, H. Thiers and A.H. Smith 35847, MICH; paratype AHS 42960, MICH, ITS sequence GenBank HQ179684.

Cuphophyllus acutoides* var. *pallidus (A.H. Sm. & Hesler) Lodge, comb. nov.

MycoBank MB804127.

Basionym: *Hygrophorus acutoides* var. *pallidus* A.H. Sm. & Hesler, North American Species of *Hygrophorus*: 132 (1963).

Type: USA, MICHIGAN, Milford, A.H. Smith 15421, Sept. 17, 1940, MICH.

Comments Cuphophyllus acutoides var. *acutoides* and *C. acutoides* var. *pallidus* resemble the European *C. fornicatus*. The ITS sequences diverge more between the N. American and European collections (9.5 %) than between the two American taxa (5.2 %). As noted by Hesler and Smith (1963), *H. acutoides* var. *pallidus* differs from *H. acutoides* var. *acutoides* in having a pale pileus margin, basidiospores that are smaller (mostly 6–8×4–5 vs. 7–8×5–6 μm), and a thin gelatinous coating on the pileipellis instead of an ixocutis 18–30 μm thick. Although the morphological differences together with ITS sequence divergence between *H. acutoides* var. *acutoides* (AHS 42960, paratype from Michigan, GenBank HQ179684, and PBM3897 from North Carolina) and *H. acutoides* var. *pallidus* (DJL06TN124 from Tennessee, GenBank KF291096) warrant recognition of the latter at species rank, we are not changing its status at this time. The combination 'Cuphophyllus pallidus' is available, but using the variety name 'pallidus' for this taxon as the species epithet would cause confusion in the future with a species that may be recombined in *Cuphophyllus*, i.e., *Camarophyllus pallidus* (Peck) Murrill, and another that will be raised to species rank [*Cuphophyllus pratensis* var. *pallidus* (Cooke) Bon] by Dentinger et al. Furthermore, the basidiomes of *C. acutoides* var. *pallidus* are only pale relative to var. *acutoides*.

Cuphophyllus adonis (Singer) Lodge & M.E. Sm., comb. nov.

MycoBank MB804128.

Basionym: *Camarophyllus adonis* Singer 1952, Sydowia 6(1–4): 172,

TYPE: ARGENTINA, TIERRA DEL FUEGO, Nueva Argentina, Singer M351, LIL.

≡ [*Hygrocybe adonis* (Singer) Boertm., 2002].

Cuphophyllus aurantius (Murrill) Lodge, K.W. Hughes & Lickey, comb. nov.

MycoBank MB804129.

Basionym: *Hygrocybe aurantia* Murrill, 1911, [as '*Hydrocybe*'], Mycologia 3(4): 195.

TYPE: JAMAICA: ST. ANDREW PARISH; Morce's Gap, 5,000 ft. elev., Dec. 29–30, 1908, 2 Jan. 1909, W.A. and Edna L. Murrill 743, NY.

Cuphophyllus basidiosus (Peck) Lodge & Matheny, comb. nov.

MycoBank MB804130.

Basionym: *Clitocybe basidiosa* Peck, Bull. N,Y. St. Mus. Nat. Hist. 1(no. 2):5 (1887),

[≡ *Camarophyllus basidiosus* (Peck) Murrill, N. Am. Fl. (New York) 9(6): 389 (1916)].

Cuphophyllus bicolor (Dennis) Lodge & S.A. Cantrell, comb. nov.

Type: Sandlake. Rensselaer County, New York, August, NYS.

MycoBank MB804131.

Basionym: *Clitocybe bicolor* Dennis, Kew Bull 7(4): 490 (1952),

[≡ *Omphalia bicolor* Baker & Dale, illeg. (homonym), Fungi of Trinidad and Tobago, Comm. Mycol. Inst. Mycol. Pap. 33:91 (1951),

≡*Clitocybe ferrugineoalba* Singer, Sydowia 9: (1–6): 371 (1955), superfluous, nom. illeg.,

≡ *Camarophyllus ferrugineoalbus* (Singer) Singer, Beih. Sydowia 7: 3 (1973), illeg.,

= *Camarophyllus umbrinus* (Dennis) Singer ex Pegler, var. *clarofulvus* Lodge & Pegler].

Type: TRINIDAD: *Omphalia bicolor* Baker & Dale, Comm. Mycol. Inst. Mycol. Pap. 33: 91 (1951), coll. TRINIDAD, RED Baker and WT Dale, 1947, ICTA 1494, K.

Baker and Dale (1951) described *Omphalia bicolor* from Trinidad, but it is an illegitimate later homonym of *O. bicolor* (Murrill) Murrill (1946). Dennis (1952), cited *Omphalia bicolor* Baker & Dale as the basionym of a 'new combination', *Clitocybe bicolor*. Because an illegitimate name cannot serve as a basionym, *Clitocybe bicolor* is treated as a nom. nov. under ICN Art. 58.1, as *Clitocybe bicolor* Dennis (1952). Singer (1955) replaced the illegitimate Baker and Dale name with *Clitocybe ferrugineoalba* Singer, but this name is superfluous and hence illegitimate (ICN Art. 52) since the legitimate *Clitocybe bicolor* should have been adopted under the rules.

Cuphophyllus fornicatus (Fr.) Lodge, Padamsee & Vizzini, comb. nov.

MycoBank MB804132.

Basionym: *Hygrophorus fornicatus* Fr., Epicr. Syst. mycol. (Upsaliae): 327 (1838) [1836–1838], [≡ *Camarophyllus fornicatus* (Fr.) P. Karst., 1879, Bidr. Känn. Finl. Nat. Folk 32: 227],

≡ *Hygrocybe fornicata* (Fr.) Singer, Lilloa 22: 152,

≡ *Hygrophorus fornicatus* Fr., Epicr. Syst. mycol. (Upsaliae): 327 (1838) [1836–1838].

Lectotype here designated is an illustration cited by Fries, Epicr. Syst. mycol. (Upsaliae): 327 (1838) [1836–1838]: Battarra 1755, Fungorum Agri Arimensis Historia. Tab. XXI [21], fig. C.

Cuphophyllus griseorufescens (E. Horak) Lodge & Padamsee, comb. nov.

MycoBank MB804133.

Basionym: *Camarophyllus griseorufescens* E. Horak, N.Z. Jl Bot. 28(3): 277 (1990).

Type: NEW ZEALAND: AUCKLAND, Little Barrier Island, Mt. Hauturu, E. Horak ZT0919, Dec. 6, 1981, PDD 27230.

Cuphophyllus* sect. *Fornicati (Bataille) Vizzini & Lodge, comb. nov.

MycoBank MB804134.

Basionym: *Hygrophorus* Fr. [subg. *Camarophyllus* Fr.] [unranked] *Fornicati* Bataille, Mém. Soc. émul. Doubs. ser. 8 4: 170 (1909) [1910],

≡ *Hygrocybe*, subg. *Neohygrocybe* (Herink) Bon (1989), sect. *Fornicatae* (Bataille) Bon, Doc. Mycol 14 (75): 56 (1989),

≡ *Dermolomopsis* Vizzini, Micol. Veget. Medit. 26 (1): 100 (2011).

Type species: *Hygrophorus fornicatus* Fr., Epicr. syst. mycol. (Upsaliae): 327 (1838)

≡ *Cuphophyllus fornicatus* (Fr.) Lodge, Padamsee & Vizzini, comb. nov.

Basidiomes tricholomatoid, broadly conical or paraboloid, usually umbonate; surface dry or slightly greasy, smooth, often radially fibrillose-silky near margin, sometimes minutely squamulose at center, gray, grayish brown or pallid with brown tint; lamellae narrowly or broadly attached, often sinuate, not decurrent, broad, white or pale gray, drying opaque; stipe surface dry, fibrillose or fibrillose-silky, often squamulose; stipe context stuffed; pileus margin, lamellar edge and stipe base sometimes bruising rusty red; basidiospores hyaline, smooth, thin-walled, broadly ellipsoid, or obovoid, rarely phaseoliform, mean Q 1.4–1.6, inamyloid, not metachromatic in cresyl blue, uninucleate; basidia 4.8–6 times the length of the basidiospores; lamellar trama subregular or with a subregular mediostratum and interwoven lateral strata, hyphae 20–150 μm long, walls refractive, 0.6–0.8 μm thick in KOH; pileipellis hyphae interwoven near center and more radially arranged near margin, lacking encrusting pigments, hyphae with a thick gelatinous coating but not an ixocutis; clamp connections abundant, large, medallion form. Lamellae not subdecurrent or decurrent as in other sections of *Cuphophyllus*.

Phylogenetic support We show strong support for placing sects. *Fornicati* and *Cuphophyllus* together in a group that is sister to sect. *Virginei* (80 % MLBS; 1.0 BPP in the 4-gene backbone analysis, and 86 % MLBS in the Supermatrix analysis, Figs. 1 and 2). In our 4-gene backbone analysis, sect. *Fornicati* is one of four clades in a polytomy that has strong basal branch support (73 % MLBS, 100 % BPP). In contrast, the ITS analysis by Vizzini and Ercole (2012) [2011] shows *Cuphophyllus* as polyphyletic, with sects. *Cuphophyllus* and *Fornicati* as separate clades in a polytomy, while our ITS-LSU analysis (Fig. 22) shows sect. *Fornicati* as part of a moderately supported (55 % MLBS) monophyletic *Cuphophyllus*; none of these analyses, however, have significant backbone support. Our Supermatrix (Fig. 2) analysis includes an unknown species from New Zealand (PDD 81871) at the base of the clade.

Species included Type species: *Cuphophyllus fornicatus*. *Cuphophyllus acutoides* and *C. acutoides* var. *pallidus*,(DJL06TN124) are included based on morphological and molecular data. Un-named species identified via molecular phylogenies include a second UK/European clade (KM KM118132, EU784306; Vizzini and Ercole 2012 that may correspond to *Hygrocybe fornicatus* var. *lepidopus* (Rea) Boertm. & Barden (Dentinger et al., unpublished), a third UK clade that corresponds to *Hygrocybe clivalis* (Fr.) P.D. Orton, a collection from Russia identified as *Neohygrocybe ingrata* (AK-9), and an un-named species from New Zealand (PDD 81871).

Comments While taxa in the *C. fornicatus* complex generally resemble other groups in *Cuphophyllus*, they differ in having lamellae that are usually narrowly attached and often sinuate rather than subdecurrent or decurrent. *Cuphophyllus fornicatus* resembles species of *Neohygrocybe* in having brownish gray pigments, reddish brown staining reactions, and often narrowly attached lamellae, leading Bon (1990) and Kovalenko (1989) to place it in that group (Bon in *Hygrocybe* subg. *Neohygrocybe* sect. *Fornicati* and Kovalenko in *Neohygrocybe* sect. *Neohygrocybe*). The interwoven lateral strata in the lamellar context of sect. *Fornicati* (Fig. 24), however, is consistent with placement in *Cuphophyllus*; the subregular central mediostratum in the lamellar context has likely been interpreted by some as the context in toto and the interwoven lateral strata as part of the subhymenium, leading some to place this group in *Hygrocybe* or *Neohygrocybe*. Kühner (1977a, b, 1980), however, considered *H. fornicata* a true *Camarophyllus* (now *Cuphophyllus*) based on the irregular mediostratum, mononucleate spores and stipitipellis structure. Papetti (1985) also noted the

similarity of the aerifrerous hyphae on the stipe with *Camarophyllus* but retained *H. fornicata* in *Hygrocybe*. The type of sect. *Fornicati*, *H. fornicatus*, was described by Fries in 1838, and later placed by Fries (1849: 308) in *Hygrophorus* subg. *Camarophyllus* together with what are now the types of *Cuphophyllus* sect. *Cuphophyllus* (*C. pratensis*) and sect. *Virginei* (*C. virgineus*). Karsten (1879) classified *H. fornicatus* in the same group as Fries, but raised the rank of *Camarophyllus* from subgenus to genus. Bataille (1910) retained Fries' placement of *H. fornicatus* in *Hygrophorus* subg. *Camarophyllus,* but assigned it to a new unranked subgroup, *Fornicati*. Later authors placed *H. fornicatus* among species of *Hygrocybe*: in sect. *Hygrocybe*, subsect. *Puniceae* (Hesler and Smith 1963), *Hygrocybe* sect. *Tristes* (Bataille) Singer, *Hygrocybe* sect. *Fornicatae* (Bataille) Arnolds (illeg., failure to cite the basionym or place of publication), *Hygrocybe* subg. *Neohygrocybe* sect. *Fornicatae* (Bataille) Bon, or *N.* sect. *Neohygrocybe* (Herink 1959, Kovalenko 1989). Vizzini and Ercole (2012) [2011] placed *H. fornicatus* in a separate genus, *Dermolomopsis*, based on its divergent morphology and an ITS analysis that shows it on a separate branch in a polytomy in Hygrophoraceae.

Cuphophyllus acutoides from the eastern USA is related to the European *C. fornicatus*. *Hygrocybe clivalis* (Fr.) P.D. Orton & Watling was originally described as a variety of *Hygrophorus fornicatus* Fr., and is currently considered as such by most authors (Arnolds 1985b, Bon 1989, Boertmann 2010). A collection from the UK identified by E. Arnolds as *H. fornicata* var. *clivalis,* however, appears with a second UK collection in a distinct, highly supported clade in Dentinger et al.'s ITS analysis (100 % MLBS), supporting recognition at of *H. clivalis* at species rank. *Hygrocybe fornicatus* var. *lepidopus* (Rea) Boertm. & Barden is also currently recognized by most authors as a variety, but a collection from the UK identified as *H. lepidopus* (Rea) P.D. Orton & Watling appears in a separate, highly supported (100 % MLBS) clade in the ITS analysis by Dentinger et al. (unpublished), and if confirmed, this taxon should also be recognized at species rank.

Cuphophyllus*, sect. *Adonidum (Singer) Lodge & M.E. Sm., comb. nov.

MycoBank MB804136.

≡ *Cuphophyllus adonis* (Singer) Lodge & M.E. Sm., comb. nov.

Basionym: *Camarophyllus* sect. *Adonidum* (as *Adonidi*) Singer, Sydowia Beih. 7: 2 (1973).

Type species: *Camarophyllus adonis* Singer, Sydowia 6(1–4): 172 (1952)

Characters as in *Cuphophyllus*; basidiomes clitocyboid; pileus surface dry; pileus and lamellae pigmented violet, lilac or mauve; stipe white, cream or yellow; basidiospore Q mostly 1.1–1.5; ratio of basidia to basidiospore length 6.5–8; pileipellis a cutis, not an ixocutis.

Phylogenetic support Only the type species has been sequenced, so phylogenetic support is irrelevant. There is no significant support for placing *C. adonis* as sister to sect. *Cuphophyllus* in our Supermatrix, or as sister to the unplaced *C. basidiosus—C. canescens—C. griseorufescens* clade in our ITS-LSU analysis (Figs. 2 and 22, respectively).

Species included Type *Cuphophyllus adonis*. *Hygrocybe cheelii* A.M. Young and *H. reesiae* A.M. Young from Australia are placed in sect. *Adonidum* based on morphology and pigments.

Comments Sect. *Adonidum* most closely resembles sect. *Cuphophyllus* except for having violet and lilac rather than salmon and reddish brown pigments. These two sections share robust basidiomes with a dry pileus surface; lamellae that are thick and appear opaque from the refractive, interwoven context hyphae, subglobose to broadly ellipsoid spores, and long basidia relative to the length of the spores. Sects. *Adonidum* and *Cuphophyllus* may eventually be assigned to the same subgenus, possibly together with *C. aurantius,* and possibly also *C. basidiosus, C. griseorufescens* and *C. canescens*, but branch supports in our Supermatrix and ITS-LSU analyses are weak and the topology varies among analyses.

Cuphophyllus* sect. *Cuphophyllus [autonym]

Type species: *Cuphophyllus pratensis* (Fr.) Bon, Doc. Mycol. 14(56): 10 (1985) [1984]

≡ *Hygrocybe pratensis* (Fr.) Murrill, Mycologia 6(1): 2 (1914),

≡ *Agaricus pratensis* Fr., Observ. mycol. (Havniae) 2: 116 (1818), sanctioned by Fr., Syst. mycol. 1: 99 (1821).

Characters as in *Cuphophyllus*; basidiomes clitocyboid, pileus usually pigmented brown, orange, salmon, or buff, rarely cream; surface not or scarcely viscid; lamellae usually appearing opaque (chalky); pileipellis usually a cutis, not an ixocutis; basidiospores usually globose, subglobose or broadly ellipsoid, mean spore Q mostly 1.2–1.4, rarely up to 1.8.

Phylogenetic support In our Supermatrix analysis (Fig. 2), sect. *Cuphophyllus* is a strongly supported (99 % MLBS) monophyletic group. Sect. *Cuphophyllus* is also highly supported in our LSU analysis (Fig. 3), but only species in the *C. pratensis* complex are included. The ITS analysis by Dentinger et al. (unpublished) shows a strongly supported *C. pratensis* clade (100 % MLBS) comprising a terminal clade (100 % MLBS) and a subtending grade with very deep divergences, while *C. pratensis* var. *pallida* appears as a separate clade nearby (100 % MLBS).

Species included Type species: *Cuphophyllus pratensis*. Molecular phylogenies indicate *C. pratensis* is a species complex. *Cuphophyllus bicolor* is included based on strong

support in our Supermatrix analysis, morphology and pigments. Species included based on morphology alone are *Camarophyllus panamensis* Lodge & Ovrebo, *Cuphophyllus neopratensis* Courtec. & Fiard, *Camarophyllus subpratensis* (Beeli) Heinem., *Camarophyllus subrufescens* (Peck) Murrill, *Cuphophyllus umbrinus* (Dennis) Courtec., *Hygrocybe austropratensis* A.M. Young, and *Hygrocybe watagensis* A.M. Young. *Cuphophyllus pratensis* var. *pallidus* (Cooke) Bon. is strongly supported in an ITS analysis by Dentinger et al. (unpublished data).

Comments Sect. *Cuphophyllus* is strongly supported, but greater taxon sampling is needed as sequences are limited to the *C. pratensis* species complex. Support for inclusion of *C. bicolor* in sect. *Cuphophyllus* is strong in our Supermatrix analysis (99 % MLBS) and weak in our ITS-LSU analysis (55 % MLBS). *Cuphophyllus bicolor, Cam. panamensis* and *Cuph. umbrinus* differ from other species in sect. *Cuphophyllus* in having a central strand of nearly parallel hyphae bounded by lateral strata with interwoven hyphae in the lamellar context.

Cuphophyllus* sect. *Virginei (Bataille) Kovalenko, in Nezdoiminogo, Opredelitel' Gribov SSSR (Leningrad): 37 (1989)

Type species: *Cuphophyllus virgineus* (Wulfen : Fr.) Kovalenko (1989)

≡ *Hygrocybe virginea* P.D. Orton & Watling, Notes R. bot. Gdn Edinb. 29(1): 132 (1969),

≡ *Agaricus virgineus* Wulfen, in Jacquin, Miscell. austriac. 2: 104 (1781), sanctioned by Fr., Syst. mycol. 1: 100 (1821).

Characters as in *Cuphophyllus*; basidiomes clitocyboid, pileus white or cream, sometimes with buff, pinkish buff or pale brown tints, not strongly pigmented orange, brown or gray; surface lubricous, viscid, or subviscid; lamellae often translucent; pileipellis an ixocutis; at least some basidiospores more elongated than in sect. *Cuphophyllus*, ellipsoid, ovoid or oblong, rarely strangulated, mean spore Q mostly (1.3–) 1.5–1.9.

Phylogenetic support Sect. *Virginei* (represented by *C. borealis*) is strongly supported as sister to the clade with most of the remaining species of *Cuphophyllus* in our four-gene backbone analysis (80 % MLBS; 1.0 BPP), and our Supermatrix analysis with *C. lacmus* (86 % MLBS). Support for sect. *Virginei* (represented by *C. borealis* and *C. virgineus*) is strong in our Supermatrix analysis (96 % MLBS); the darkly pigmented *C. lacmus* appears in a sister clade (82 % MLBS).

Species included Type species: *Cuphophyllus virgineus*. Species included based on molecular phylogenies and morphology include *C. borealis* (Peck) Bon ex Courtec. (1985) and *C. russocoriaceus* (Berk. & Jos. K. Mill.) Bon. *Cuphophyllus ceraceopallidus* (Clémençon) Bon is also thought to belong in sect. *Virginei* based on morphology.

Comments Sect. *Virginei* is restricted here to pale species, as in Kovalenko (1989, 1999). Deeply pigmented brown and gray-brown species with a viscid pileus [*C. colemannianus* (Bloxam) Bon and *C. lacmus* (Schumach.) Bon] appear in a sister clade to the pale species in an ITS analysis by Dentinger et al. (unpublished), and *C. lacmus* appears basal to sect. *Virginei* s.s. Kovalenko in our LSU and Supermatrix analyses. In our LSU analysis, the darkly pigmented species (*C. colemannianus, C. lacmus, C. subviolaceus* and possibly *C. flavipes*), are concordant with Kovalenko's (1989) delineation of *Cuphophyllus* sect. "*Viscidi*" (A.H. Sm. & Hesler) Bon (nom. invalid as Smith and Hesler's 1942 basionym lacked a Latin diagnosis, Art. 36.1). Bon (1990) treated this group as subsect. "*Viscidini*" (A.H. Sm. & Hesler) Bon, which is similarly invalid. Papetti (1996) named a subsect. "*Colemanniani*" Papetti in *Camarophyllus*, which is also invalid (Art. 36.1). In the ITS analysis by Dentinger et al. (unpublished data), *C. radiatus* (Arnolds) Bon] appears with *C. flavipes* and not near *C. lacmus* and *C. colemannianus*. The darkly pigmented species with a viscid pileus (*C. colemannianus* (A. Bloxam) P.D. Orton & Watling, *C. lacmus, C. subviolaceus,* and *C. flavipes*) are left unplaced here, pending further revisions to *Cuphophyllus*.

Additional unplaced *Cuphophyllus* species. *Cuphophyllus aurantius, C. basidiosus*, *C. canescens, C. cinerella, C. flavipes* and *C. griseorufescens.*

Comments Cuphophyllus flavipes is unstable in its position between analyses (sequences of four gene regions from a single collection from Japan). Similarly, the positions of *C. basidiosus* and *C. canescens* are unstable, so we have therefore left this group of species unplaced. *Cuphophyllus griseorufescens* from New Zealand is strongly supported as being basal in the *C. basidiosus* – *C. canescens* clade in our ITS-LSU analysis (Fig. 22).

Cuphophyllus aurantius and related species differ from other species of *Cuphophyllus* in having mycenoid basidiomes, bright pinkish orange pigments, and a subregular rather than interwoven lamellar trama (Fig. 25). In addition, *C. aurantius* differs from most species of *Cuphophyllus* in the absence of thickened hyphal walls and presence of highly inflated subglobose elements in the lamellar trama. Analysis of the lamellar trama by Lodge (Fig. 25) shows it is subregular near the pileus while below it has a regular mediostratum and lateral strata comprised of subregular elongated elements mixed with many inflated subglobose elements and somewhat divergent hyphae especially near the lamellar edge; the basidia arise from elongated subhymenial cells resembling a hymenial

palisade. It is therefore not surprising that *C. aurantius* has previously been classified in *Hygrocybe*. Analyses based on single genes and sequences from different collections and laboratories were consistent, negating the possibility of error. While *C. aurantius* always appears in the larger clade together with *C. pratensis*, it appears in a poorly supported internal clade with *C. pratensis* in our four-gene backbone analysis, paired with *Cantharocybe* in a clade that is sister to sect. *Cuphophyllus* in our LSU analysis, but basal to *C. canescens* in our Supermatrix analysis, all without support. One of our three ITS-LSU analyses weakly pairs *C. aurantius* with *C.* aff.. *pratensis* (55 % MLBS; Fig. 22), another as basal to *C. flavipes, C. canescens* (not shown) and *C.* aff. *pratensis* while the third pairs *C. aurantius* and *C. fornicatus* together (not shown), the latter two placements without significant support. While greater taxon and gene sampling are needed to resolve this group, there is strong phylogenetic support that *C. aurantius* belongs to the *Cuphophyllus* clade, whether the four gene regions are analyzed separately or together. ITS sequences of *C. aurantius* from the Smoky Mountains in SE USA are divergent from Greater Antillean sequences (the type is from Jamaica), and there are morphological differences between these and collections from Europe and Japan, indicating this is a species complex.

Cuphophyllus cinereus (Kühner) Bon is the type of sect. *Cinerei* (Bataille) Bon, but it has not been sequenced. *Cuphophyllus* sect. *Cinerei* might correspond to the unplaced, strongly supported *C. basidiosus–C. canescens–C. griseorufescens* clade in our ITS-LSU analysis (Fig. 22) based on shared morphology, but this hypothesis should be tested using molecular phylogeny. Bon (1989) cited p. 47 for the basionym of Bataille (1910), but the description of *Cinerei* appears on p. 173, a correctable error that does not invalidate publication (Art. 33.5). Boertmann (2010) interprets *C. cinereus* as a synonym of *C. lacmus* (Schum.) Bon.

Ampulloclitocybe Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 36 (2002).

Type species: *Ampulloclitocybe clavipes* (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys, Mycotaxon 83: 36 (2002)

≡ *Clitocybe clavipes* (Pers.) P. Kumm., *Führ. Pilzk.* (Zwickau): 124 (1871),

[≡ *Clavicybe clavipes* (Pers.) Harmaja, *Karstenia* 42(2): 42 (2002), nom. illeg., Art. 52.1]

≡ *Agaricus clavipes* Pers., *Syn. meth. fung.* (Göttingen) 2: 353 (1801)].

Basidiomes clitocyboid, gymnocarpous (veils absent), medium-sized, not lichenized; pileus at first convex with an inrolled margin, becoming indented or infundibuliform with age, often with a low umbo in center; surface not hygrophanous (but context hygrophanous), smooth or with appressed fibers in center, brown, tan, grayish or olivaceous brown. Lamellae decurrent, close or subclose, white or cream. Stipe sub-bulbous, cylindrical or tapered to base, context spongy, often becoming hollow, surface silky-fibrillose or fibrillose and often minutely hairy. Basidiospores broadly fusiform, ellipsoid or subglobose, hyaline, strongly guttulate, not cyanophilous, inamyloid, appearing smooth with light microscopy, minutely roughened-rugose when viewed with SEM; basidia 4-sterigmate; cystidia absent; lamellar trama hyphae cylindric, mostly thin-walled, some walls up to 0.5 μm thick, bidirectional (Fig. 26); subhymenium interwoven; pileipellis a cutis of subparallel hyphae, pigments intracellular; medallion clamp connections present. Type species produces aldehyde dehydrogenase and tyrosine kinase inhibitors. Gregarious or caespitose, growing saprotrophically in forest litter, often under conifers. Differs from *Clitocybe* s.s. (typified by *C. nebularis*) in having acyanophilous spores; differs from *Cuphophyllus* in having basidia less than 5 times the length of the basidiospores and subparallel rather than interwoven pileipellis hyphae; differs from *Infundibulicybe* (Tricholomataceae) in having basidiospores that are uniguttulate and ellipsoid, broadly fusoid or subglobose rather than lacrymoid with few small guttules, and walls roughened rather than smooth under SEM; differs from *Lichenomphalia* in being saprotrophic rather than biotrophic with bryophytes and having roughened rather than smooth spores under SEM (Figs. 27, 28 and 29).

Phylogenetic support Only our Supermatrix analysis includes more than one species of *Ampulloclitocybe* (*A. clavipes* and *A. avellaneoalba* (Murrill) Harmaja), which shows100 % MLBS support for the *Ampulloclitocybe* clade, and 65 % support for it being sister to *Cantharocybe*. Our 4-gene backbone analysis also shows *Ampulloclitocybe* as sister to *Cantharocybe*, but with low support (35 % MLBS). Binder et al. (2010) show the same pairing of *Ampulloclitocybe* and *Cantharocybe*, also without significant support in their six-gene analysis. Our

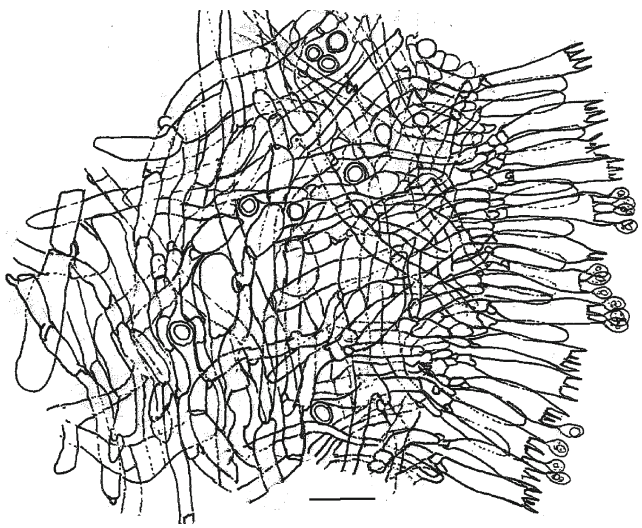


Fig. 26 *Ampulloclitocybe clavipes* lamellar cross section (DJL06TN40, Tennessee, Great Smoky Mt. Nat. Park, USA). Scale bar=20 μm

ITS-LSU analysis places *Ampulloclitocybe* as basal to both *Cantharocybe* and *Cuphophyllus*, but with low support Fig. (41 % MLBS; Fig. 22). In contrast, our LSU analysis places *Cantharocybe* near *Cuphophyllus* but *Ampulloclitocybe* as sister to *Omphalina* s.s., but without significant support. Moncalvo et al. (2002) show MPBS support for placing *Ampulloclitocybe* as basal in the *Omphalina* clade in their LSU analysis.

Species included Type *Ampulloclitocybe clavipes* (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys, and *A. avellaneoalba*. Harmaja (2003) also placed *Clitocybe squamulosoides* P.D. Orton in *Ampulloclitocybe*, but this needs to be verified by molecular analyses.

Comments As discussed in Redhead et al. (2002), Bigelow's lectotypification of gen. *Clitocybe* with *Clitocybe clavipes* is rejected because of earlier typifications (Greuter et al. 2000, Art. 9.17). Harmaja (2002) also described a new genus, "*Clavicybe*" Harmaja, illeg., based on the same type as *Ampulloclitocybe* (*Agaricus clavipes*), but publication of *Ampulloclitocybe* preceded by 2 months the publication of "*Clavicybe*", rendering the latter illegitimate. Scanning electron micrographs of spores of the type, *A. clavipes*, by Pegler and Young (1971) showed they were minutely ornamented. *Ampulloclitocybe clavipes* is known to produce a coprine-like (antabuse-like) aldehyde dehydrogenase inhibitor (Cochran and Cochran 1978; Yamaura et al. 1986) as well as a tyrosine kinase inhibitor named clavilactone (Cassinelli et al. 2000).

Cantharocybe H.E. Bigelow & A.H. Sm., Mycologia 65(2): 486 (1973), emend. Ovrebo, Lodge & Aime, Mycologia 103(5): 1103 (2011).

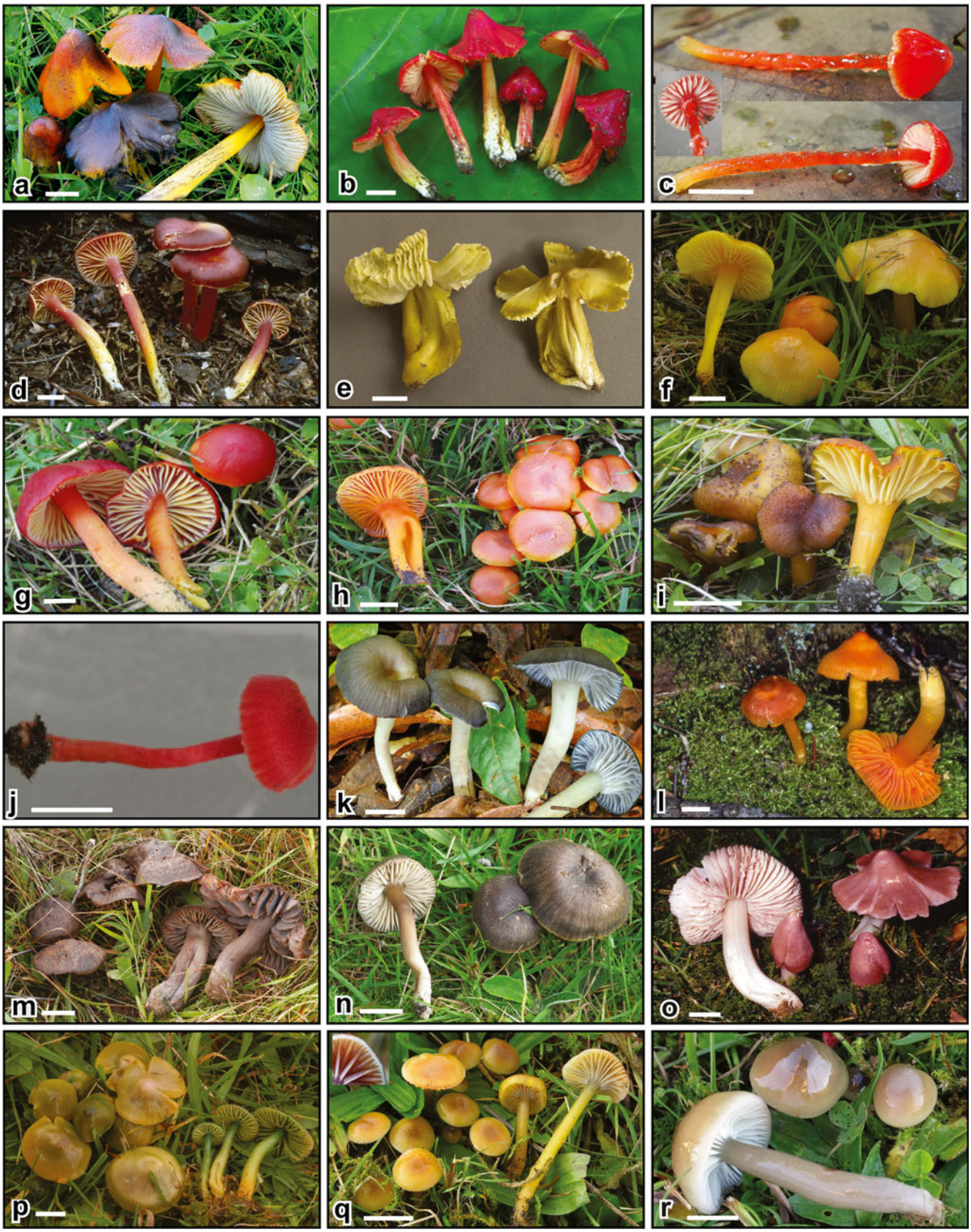
Type species: *Cantharocybe gruberi* (A.H. Sm.) H.E. Bigelow, Mycologia 65: 486 (1973)

≡ *Clitocybe gruberi* A.H. Sm., Mycologia 36(3): 245 (1944).

Basidiomes large, clitocyboid, pileus convex-hemispheric to broadly convex with inrolled margin; surface dry, smooth or finely velutinous or finely tomentose, sometimes areolate, margin not striate, yellow, dark brown or brownish gray. Lamellae broad, long decurrent or adnate with decurrent tooth, often anastomosing or forming a reticulum at the stipe apex. Stipe 30–95 mm long, 8–25 mm thick, slightly clavate, often tapered, surface dull, moist, glabrous or pruinose, concolorous with the pileus or brownish gray over lower half. Spores elliptical or narrowly elliptical to oblong, often slightly tapered to hilar appendage end, smooth, thin-walled, hyaline, inamyloid, acyanophilous. Basidia clavate, four-sterigmate, 4–4.4 times the length of the basidiospores. Cheilocystidia of two types: (i) lecythiform but sometimes with a mucronate apex, basal portion clavate to ventricose and narrowing toward the base, upper portion extending into an elongated neck with or without a rounded capitulum; (ii) body clavate with 1–4 sterigmoid or apical (or rarely lateral) appendages, extending at oblique angles and frequently swollen or capitate at the apex. Hyphae of lamellar trama parallel, becoming subregular toward the margin, with walls swelling slightly to 0.5–0.8 μm thick. Subhymenium ca. 15—20 μm deep, pseudoparenchymatous. Pileus surface either a cutis of appressed, slightly interwoven hyphae or a trichodermium with hyphal end segments or end cells vertical, angled or sometimes interwoven. Pileus trama of interwoven, radially disposed hyphae. Stipe surface often with appressed slightly interwoven hyphae near the base, and scattered caulocystidia like those of the lamellar edge, rarely secretory, sometimes mixed with fertile basidia on the upper part. Clamp connections present but not on all hyphal septa or at the base of every basidium. Differing from *Cuphophyllus* in having regular rather than typically interwoven lamellar trama, basidia to basidiospore length less than 5 and presence of cheilo- and caulocystidia; differing from *Ampulloclitocybe* in presence of cheilo- and caulocystidia and regular rather than bidirectional lamellar trama; differing from *Xeromphalina* in having inamyloid spores and a clitocyboid rather than marasmioid or collybioid form.

Phylogenetic support Support for a monophyletic *Cantharocybe* is strong in all of our analyses (99 % MLBS in the 4-gene backbone and Supermatrix analyses; 1.0 BPP in the backbone analysis; 97 % MLBS in LSU analysis; 75 % MLBS in the ITS-LSU). Similarly, Ovrebo et al. (2011) show 98 % MP and 100 % MLBS support for the monophyletic clade comprising *C. gruberi* and *C. brunneovelutina* in their analysis of the LSU region, while Esteves-Raventós et al. (2011) show 1.0 Bayesian support for *C. brunneovelutina* as sister to *C. gruberi* in their LSU analysis. In our 4-gene backbone analyses, support for placing *Cantharocybe* as sister to *Ampulloclitocybe* is high in the Bayesian (0.98 PP) but low in the ML analysis (35 % BS), and there is no significant support for the *Cantharocybe—Ampulloclitocybe* clade as basal to *Cuphophyllus*. In a six-gene analysis by Binder et al. (2010), MLBS support for the *Cantharocybe — Ampulloclitocybe* clade is also below 50 %, as is the branch supporting *Cuphophyllus* (as *Camarophyllus*) and *Cantharocybe*, though there is 1.0 BPP support for the latter branch. Similarly, our ITS-LSU analysis and an analysis of the LSU region by Ovrebo et al. (2011) place *Cantharocybe* as sister to *Cuphophyllus* with less than 50 % MLBS support. Ovrebo et al. (2011) show no significant support for *Xeromphalina* or *Ampulloclitocybe* as basal to the *Cantharocybe– Cuphophyllus* clade.

Species included Type species: *Cantharocybe gruberi*. *C. gruberi* var. *luteosaturatus* (Malençon) Esteve-Rav., Reyes & Alvarado and *C. brunneovelutina* Lodge, Ovrebo & Aime are included based on morphological and phylogenetic data.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◀ **Fig. 27** Color photographs of examples of subfamily *Hygrocyboideae*. **a**–**k**. Tribe *Hygrocybeae*. **a**–**j**. *Hygrocybe*. **a**–**f**. Subg. *Hygrocybe*. **a**–**b**. Sect. *Hygrocybe*. **a**. Subsect. *Hygrocybe*, *H. conica* (Jens H. Petersen/Mycokey, Denmark). **b**. Subsect. *Macrosporae*, *H. acutoconica* (D. Jean Lodge, Tennessee, USA). **c**. Sect. *Velosae*, *H.* aff. *hypohaemacta* (Claudio Angelini, Dominican Republic; inset showing pseudoveil by D.J. Lodge, Puerto Rico). **d**. Sect. *Pseudofirmae*, *H. appalachianensis* (Steve Trudell, Great Smoky Mt. National Park, USA). **e**. Sect. *Microsporae*, *H. citrinovirens* (Geoffrey Kibbey, Wales, UK). **f**. Sect. *Chlorophanae*, *H. chlorophana* (Jan Vesterholt, Denmark). **g**–**j**. *Hygrocybe* subg. *Pseudohygrocybe*. **g**–**i**. Sect. *Coccineae*. **g**. Subsect. *Coccineae*, *H. coccinea* (Jens H. Petersen/Mycokey, Denmark). **h**. Subsect. *Siccae*, *H. reidii* (David Boertmann, Denmark). **i**. Subsect. *Squamulosae*, *H. turunda* (Jens H. Petersen/Mycokey, Denmark). **j**. Sect. *Firmae*, *H. firma* (J.A. Cooper, New Zealand). **k**. *Hygroaster nodulisporus* (Jean-Luis Cheype, Guyana). **i**–**r**. Tribe *Humidicuteae*. **i**. *Humidicutis marginata* (Raymond McNeil, Quebéc, Canada). **m**–**n**. *Neohygrocybe*. **m**. Sect. *Neohygrocybe*, *N. ovina* (Jan Vesterholt, Denmark). **n**. Sect. *Tristes*, *N. nitrata* (David Boertmann, Denmark). **o**. *Porpolomopsis*, *P. calyptriformis* (Antonio Brigo, Italy). **p**–**r**. *Gliophorus*. **p**. Sect. *Gliophorus*, *G. psittacinus* (Jan Vesterholt, Denmark). **q**. Sect. *Glutinosae*, *G. laetus* (Jan Vesterholt, Denmark). **r**. Sect. *Unguinosae*, *G. unguinosus* (Jens H. Petersen/Mycokey). Scale bar =1 cm

Comments The regular to subregular lamellar context (Ovrebo et al. 2011, Fig. 7), forking and anastamosing lamellae, and presence of ornamented cheilocystidia set *Cantharocybe* apart from other genera in the cuphophylloid grade. As noted by Ovrebo et al. (2011), the type species of *Cantharocybe* has previously been placed variously in *Clitocybe* (Smith 1944), *Laccaria* (Singer 1951), and unplaced within the family Paxillaceae (Singer 1986), while Esteves-Raventós et al. (2011) show that a European variety of the type species had been placed in *Pleurotus*. The placement of *Cantharocybe* relative to other genera remains unresolved and sampling of other gene regions and additional taxa, especially from the Australasian region, will be needed to resolve the branching order of clades with strong bootstrap support for these very deep branches.

Excluded genera

Several genera have been excluded from the Hygrophoraceae based on either morphological or molecular phylogenetic data. *Camarophyllopsis* Herink (1959; syn. *Hygrotrama* Singer 1959) had been included in Hygrophoraceae at various ranks, but was excluded from the family by phylogenetic analyses (Matheny et al. 2006). Kühner (1980) noted that *Camarophyllopsis* had a hymeniform pileipellis and that the basidia were relatively short for Hygrophoraceae, but other taxa confirmed by molecular phylogenies to belong in Hygrophoraceae also have short basidia (Lodge et al. 2006). The placement of *Camarophyllopsis* in Matheny et al. (2006) varies depending on whether Maximum Parsimony or Bayesian analysis methods are used. Matheny et al. (2006) show *Camarophyllopsis* in the *Plicaturopsis* clade at the base of the Agaricales, whereas the six-gene analysis by Binder et al. (2010) places it in the Clavariaceae, also at the base of the Agaricales.

Singer described the monotypic genus *Neohygrophorus* to accommodate *Hygrophorus angelesianus* A.H. Sm. & Hesler (1963). Though *Neohygrophorus* has long basidia as in typical of Hygrophoraceae, it also has amyloid spores and the context turns red in weak potassium hydroxide (Hesler and Smith 1963). While amyloid spores are now known to occur in the Hygrophoraceae in *Pseudoarmillariella* (Lodge et al. 2006 and Matheny et al. 2006) and *Cantharellula* (Lawrey et al. 2009), the red reaction to alkali in *Pseudohygrophorus* is a distinctive character (Redhead et al. 2000). In 2000, Redhead et al. expanded *Pseudohygrophorus* to include two additional species with red staining reactions in alkali and amyloid spores. The analysis by Binder et al. (2010) shows *Neohygrophorus* in the tricholomatoid clade, but without support. Matheny et al. (2006) and Lawrey et al. (2009) included *Pterula* in their analyses, but the Pterulaceae falls outside the hygrophoroid clade in a six-gene analysis (Binder et al. 2010), and near *Radulomyces* among the corticioid fungi in Dentinger et al. (2009).

Previously, species of *Lichenomphalia* were often treated in *Omphalina* Quél. Analyses by both Lawrey et al. (2009) and our data, however, indicate that the *Omphalina* s.s. clade is basal to the Hygrophoraceae s.l. while *Lichenomphalia* falls within the family. Thus, we do not include infrageneric classification of *Omphalina* s.s. here but *Omphalina* has been treated elsewhere (Lamoure 1974; 1975, Lange 1981, Lutzoni 1997; Redhead et al. 2002).

The genus *Porpoloma* has been reassigned to the tricholomatoid clade. Herink (1959) made an attempt to erect a provisional section, "*Metapodiae*", nom. invalid, in *Neohygrocybe* for a fuscous, red-staining species with smooth, amyloid spores, *Porpoloma metapodium*. Singer (1952) erected gen. *Porpoloma* for three Argentinian species of *Nothofagus* forest, then combined the European *Hygrophorus metapodius* (Fr.) Fr. in *Porpoloma* in 1973. *Porpoloma metapodium* was treated as *Hygrophorus* by Hesler and Smith (1963, as *H.*sect. *Amylohygrocybe*), and as *Hygrocybe* by Moser (1967). Singer (1986) later placed *Porpoloma* in the Tricholomataceae, tribe *Leucopaxilleae* – a placement supported by molecular phylogenetic analysis of LSU sequences (Moncalvo et al. 2002).

General Discussion and Conclusions

For this partial revision of the Hygrophoraceae, we used a combination of previous and new molecular phylogenetic analyses together with morphological, chemical and

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◀ **Fig. 28** Color photographs of examples of subfamilies *Hygrocyboideae* (**a**–**d**) and *Hygrophoroideae* (**e**–**r**). Subf. *Hygrocyboideae,* tribe *Chromosereae*. **a**–**d**. *Chromosera*. **a**. Subg. *Chromosera*, *C. cyanophylla* (Thomas Læssøe, Russia). **b**. Subg. *Oreocybe*, *C. citrinopallida*, Jens *H.* Petersen/Mycokey, Fareo Islands). **c**. Subg. *Subomphalia*, *C. viola* (Giorgio Baiano, Italy). **d**. *Gloioxanthomyces vitellinus* (Jens H. Petersen/Mycokey, Denmark). **e**–**r**. Subf. *Hygrophoroideae,* genus *Hygrophorus*. **e**–**h**. Subg. *Hygrophorus*. **e**–**h**. Sect. *Hygrophorus*. **e**. Subsect. *Hygrophorus*, *H. eburneus* (Jens H. Petersen/Mycokey, Denmark). **f**. Subsect. *Fulventes*, *H. arbustivus* var. *quercetorum* (Fabrizio Boccardo, Italy). **g**. Sect. *Discoidei*, *H. discoideus* (Gaêtan Lefebvre, Quebéc, Canada). **h**. Sect. *Picearum*, *H. piceae* (Renée LeBeuf, Quebéc, Canada). **i**–**o**. Subg. *Colorati*. **i**–**j**. Sect. *Olivaceoumbrini*. **i**. subsect. *Olivaceoumbrini*, *H. olivaceoalbus* (Jens H. Petersen/Mycokey). **j**. Subsect. *Tephroleuci*, *H. pustulatus* (Jens H. Petersen/Mycokey, Denmark). **k**–**m**. Sect. *Pudorini*. **k**. Subsect. *Pudorini*, *H. pudorinus* (Ellen Larsson, Sweden). **l**. Subsect. *Clitocyboides*, *H. russula* (Renée LeBeuf, Quebéc, Canada). **m**. Subsect. *Salmonicolores*, *H. abieticola* (Luigi Perrone, Italy). **n**–**o**. Sect. *Aurei*. **n**. Subsect. *Aurei*, *H. hypothejus* var. *aureus* (Luigi Perrone, Italy). **o**. Subsect. *Discolores*, *H. karstenii* (Jan Vesterholt, Finland). **p**–**r**. Subg. *Camarophyllus*. **p**. Sect. *Camarophyllus*, *H. camarophyllus* (Jan Vesterholt, Sweden). **q**. Sect. *Chrysodontes*, *H. chrysodon* (Luigi Perrone, Italy).**r**. Sect. *Rimosi*, *H. inocybiformis* (Raymond McNeil, Quebéc, Canada). Scale bar=1 cm

ecological traits to evaluate previously proposed Linnaean-based higher-level classifications of taxa (above species rank). The use of cladistic approaches (Donoghue and Cantino 1988; De Queiroz and Guathier 1992; De Queiroz 1996a, b) versus classical Linnaean nomenclature (Brummitt 1996a, b; Orchard et al. 1996) has been hotly debated in biology, including mycology (Hibbett and Donoghue 1998). Two of the most vexing disparities between the Linnaean and cladistic approaches are recognition of paraphyletic groups in the Linnaean but not the cladistic system, and the temptation to proliferate Linnaean ranks based on cladistic analyses. Here, we only changed existing classifications if there was strong phylogenetic inference that groups were polyphyletic, we only named new groups that were strongly supported by phylogenetic and/or morphological data, we provide diagnoses – often emended – for all groups, but we did not alter named paraphyletic grades. This approach was largely successful in generating a coherent, integrated, holistic classification for the Hygrophoraceae that is based on nested Linnaean ranks and is phylogenetically supported.

The family Hygrophoraceae is among the early diverging lineages of the Agaricales (Matheny et al. 2006; Binder et al. 2010), and it comprises a relatively large number of genera (26) with many infrageneric taxa that have been proposed over the past two centuries. While the species appear to be primarily biotrophic, the genera vary in their morphology and ecology to the extent that there are few mycologists who have studied all of the genera in Hygrophoraceae. This challenge was addressed by using teams of experts to review different aspects and revise taxonomic groups, resulting in many coauthors (see attribution in Suppl. Table 3).

Our sampling design of using two representatives per clade for the 4-gene backbone analysis was successful in providing strong backbone support throughout most of Hygrophoraceae. The Supermatrix analysis was useful for incorporating more species into the analyses though it sometimes showed lower bootstrap support for branches and a few species and clades are oddly placed relative to other analyses despite our efforts to maintain a balanced data set. LSU and ITS analyses, alone and in combination, were especially helpful in resolving the composition of sections and subsections as more species are represented by sequences of one or both gene regions. Sampling short, overlapping segments of the family based on the branching orders in the backbone and Supermatrix analyses and using new alignments to limit data loss were part of that strategy. Incorporating a basal and distal member of each clade was informative and shows that most of the characters that are used to define groups do not correspond to the branching points for the corresponding clades and are thus not synapomorphic (TABLE IV).

The dearth of synapomorphic characters has been previously documented in the AFTOL publications on the Agaricales and Russulales (Matheny et al. 2006; Miller et al. 2006), so their absence in this study is not surprising. Some characters that are likely adaptive, such as hymenial proliferation of basidia in pachypodial structures and production of dimorphic basidiospores and basidia, appear in separate phylogenetic branches. Multiple independent origins were previously noted for other adaptive traits in the Basidiomycota, e.g.: fruit body morphology (Hibbett and Donoghue 2001; Hibbett and Binder 2002; Miller et al. 2006), ectomycorrhizal trophic habit (Bruns and Shefferson 2004), and brown rot of wood (Hibbett and Donoghue 2001). Many of the characters that are used in taxonomy of Hygrophoraceae are developmental morphological features, such as construction of the lamellar trama and subhymenium/hymenium, pileipellis and hypodermium, and presence of ornaments on the spores. With a few exceptions, such as production of regenerating hymenial surfaces in genera with a pachypodial hymenial palisade and production of dimorphic spores and basidia, most developmental characters are unlikely to be adaptive and thus may not be under strong selection pressure. If a trait is highly adaptive, it can lead to an adaptive radiation with the synapomorphic character defining the clade, but we rarely see this pattern with morphological characters in Hygrophoraceae. It may be coincidental that these developmental traits sometimes correspond to the branching points for subfamilies, tribes (e.g., divergent and pachypodial trama/hymenium in subf. *Hygrophoroideae*, tribes *Hygrophoreae* and *Chrysomphalineae*), genera (e.g., lamellar trama divergent in *Hygrophorus*; regular with long hyphae in *Porpolomopsis* vs. subregular with short elements in *Humidicutis* – its sister genus) and subgenera (mostly short basidia and long lamellar trama hyphal elements in subg. *Hygrocybe* vs. long basidia and short lamellar trama elements

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◀**Fig. 29** Color photographs of examples of subfamily *Lichenomphalioideae* and the Cuphophylloid grade. **a**–**b**. Subfamily *Hygrophoroideae*, tribe *Chrysomphalineae*. **a**. *Chrysomphalina chrysophylla* (Luigi Perrone, Italy). **b**. *Haasiella venustissima* (macrophoto by Thomas Læssøe in Russia; microphoto of metachromatic spores by Ledo Setti, Italy). **c**–**l**. Subfamily *Lichenomphalioideae*. **c**–**e**. Tribe *Lichenomphaleae*. **c**–**d**. *Lichenomphalia*. **c**. Subg. *Lichenomphalia*, *L. hudsoniana* (Steen A. Elborne, Norway). **d**. Subg. *Protolichenomphalia*, *L. umbellifera* (Joszef Geml, Alaska, USA). **e**. *Semiomphalina* aff. *leptoglossoides* (Robert Lücking, Costa Rica). **f**–**j**. Tribe *Arrhenieae*. **f**. *Arrhenia auriscalpium* (Jens H. Petersen/Mycokey, Denmark). **g**. *Acantholichen pannarioides* (Chaves 3910, Robert Lücking 9582a, Costa Rica). **h**. *Cora* aff. *glabrata* (Robert Lücking, Colombia). **i**. *Corella brasiliensis* (Robert Lücking, Colombia). **j**. *Dictyonema sericeum* (Robert Lücking 0411, Colombia). **k**–**l**. Tribe *Cantharelluleae*. **k**. *Cantharellula umbonata* (Drew Parker, California, USA). **l**. *Pseudoarmillariella ectypoides* (Renée LeBeuf, Quebéc, Canada). **m**–**r**. Cuphophylloid grade. **m**–**p**. *Cuphophyllus*. **m**. Section *Cuphophyllus*, *C. pratensis* (F. Boccardo, Italy). **n**. Section *Fornicati*, *C. fornicatus* (Jan Vesterholt, Denmark). **o**. Section *Adonidum*, C. *adonis* (Mathew Smith, Argentina). **p**. Section *Virginei*, C. *virgineus* (Jan Vesterholt, Denmark). **q**. *Cantharocybe brunneovelutina* (D. Jean Lodge, Belize). **r**. *Ampulloclitocybe clavipes* (Jens H. Petersen/Mycokey, Denmark). Scale bar=1 cm

in subg. *Pseudohygrocybe*). A case in point is a reversion in lamellar tramal hyphae to shorter lengths in part of sect. *Pseudofirmae* of subg. *Hygrocybe*. Characters that provide no selective advantage may become fixed in a lineage by being physically close to a gene under selection pressure on the same chromosome, and via random events such as founder effects and genetic drift following geographic or reproductive isolation. Diversification in lineages unrelated to adaptations have been called nonadaptive radiation and nonecological radiation (Rundell and Price 2009; Benton 2010; Venditti et al. 2010). Though most of the characters used in taxonomy of Hygrophoraceae are not diagnostic by themselves, as seen by the sweeps of character states in the synoptic key that is arranged by phylogenetic branching order (TABLE IV), combinations of traits are usually diagnostic.

In contrast to the likely nonadaptive characters noted above, some non-pigmented compounds are shown to be informative taxonomically and many are also bioactive, such as dehydrogenase and kinase inhibitors in *Ampulloclitocybe* (Farrell et al. 1977; Cochran and Cochran 1978; Yamaura et al. 1986; Cassinelli et al. 2000; Lübken et al. 2006) and are thus likely to be under selection pressure. Pigments are often antimicrobial; it is not known if the pigments in the Hygrophoraceae have these properties, but some of the bioactive compounds noted above may be pigment metabolic precursors. Given the presumed biotrophic habit of most Hygrophoraceae based on stable C and N isotope signatures, genes that are responsible for transfers of host N and especially C are more likely to be the basis of adaptive radiations and thus correspond to divergence points of clades than most of the developmental morphological features. The ectomycorrhizal habit of *Hygrophorus* s.s. is likely a synapomorphy (Seitzman et al. 2011), though the fungus may not be entirely beneficial to its host (Agerer 2012). The habit of parasitizing bryophytes and different types of algae (i.e., in bryophilous and lichen-forming species) is likely involved in several adaptive radiations within subfamily *Lichenomphalioideae*, though the most basal group, (*Arrhenia,* tribe *Arrheniae*) is apparently free-living (Lawrey et al. 2009). The trophic habits for many Hygrophoraceae remains unknown, but circumstantial evidence from environmental sequencing projects suggests the possibility that *Hygrocybe* s.l. and *Cuphophyllus* may obtain recent plant carbon as rhizosphere or endophytic symbionts.

Fungal systematists, parataxonomists and fungal conservationists use named subgenera, sections and subsections in *Hygrocybe* s.l. Many authors, but especially Donk (1962), Clémençon (1982), Redhead et al. (1995, 2002, 2011), Kovalenko (1988, 1989, 1999, 2012), Candusso (1997) and Lawrey et al. (2011) were instrumental in verifying and publishing correct generic and infrageneric names and combinations in the Hygrophoraceae, and we hope we have corrected most of the remaining errors. Some systematists and many conservationists and parataxonomists primarily use infrageneric names in *Hygrocybe* rather than the segregate genera recognized in this paper. With the exception of *Cuphophyllus*, the use of *Hygrocybe* s.l. is not incorrect as long as *Hygroaster* is assigned an infrageneric rank in *Hygrocybe*, so we provide a dual nomenclature of *Hygrocybe* s.l. for all user groups. *Cuphophyllus* appears at the base of the Hygrophoraceae near the backbone of the Agaricales whereas *Hygrocybe* is terminal, so placing these in the same genus would require using the oldest genus name, *Hygrophorus*, for the entire family.

Further work remains to be done in making new combinations, especially recombining species of *Camarophyllus*, *Hygrocybe* and *Hygrophorus* in *Cuphophyllus*. Many species previously believed to be amphi-Atlantic were found to not be conspecific as they belong to separate clades, and those that are not from the same region as the type locality will need new or resurrected names. Predominantly arctic-alpine taxa (e.g., *Lichenomphalia* spp.) likely are exceptions to this general trend, as they apparently are capable of frequent dispersals on a circumpolar scale (Geml et al. 2012). Sequencing more gene regions and new genes are needed to provide the basis for further higher level revisions, especially in *Hygrocybe* subg. *Pseudohygrocybe*, *Gliophorus* and *Neohygrocybe* in tribe *Humidicuteae*, and *Cuphophyllus*. Sequencing of more species is also needed in undersampled groups such as *Humidicutis*, *Gliophorus*, *Neohygrocybe* and *Cuphophyllus*, especially species from Australasia. The most basal species in several clades in our analyses are from the Australasian region, e.g., *Porpolomopsis lewelliniae*, *Gliophorus graminicolor* from Tasmania and a *G. psittacinus*-like collection from Japan, and two species from New Zealand, PDD81871

in *Cuphophyllus* sect. *Fornicatae* and *Cuphophyllus griseorufescens* in the unplaced *C. canescens – C. basidiosus clade*. The Australasian region may be the origin of the crown group for these lineages, or that region may have retained more ancestral species. Refining the synoptic key and diagnoses for tribes, genera, subgenera and sections requires inclusion of basal species within lineages because the character states that are used to delineate these groups often do not correspond to the branching point for the clades. Despite these gaps and shortcomings, we succeeded in establishing a higher-order structure for Hygrophoraceae that integrates morphological, ecological, chemotaxonomic and phylogenetic data, and where possible, determined which are the correct, legitimate, validly published names that can be applied to each group under the Linnaean system.

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