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To cite this article: Mauro C. Westphalen, Viviana Motato-Vásquez, Michal Tomšovský & Adriana M. Gugliotta (2021): Additions to the knowledge of hydroid Steccherinaceae: *Cabalodontia*, *Etheirodon*, *Metuloidea*, and *Steccherinum*, *Mycologia*, DOI: [10.1080/00275514.2021.1894536](https://doi.org/10.1080/00275514.2021.1894536)

To link to this article: <https://doi.org/10.1080/00275514.2021.1894536>



Published online: 09 Jun 2021.



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Additions to the knowledge of hydroid Steccherinaceae: *Cabalodontia*, *Etheiroduon*, *Metuloidea*, and *Steccherinum*

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ABSTRACT

The family Steccherinaceae includes genera with smooth, hydroid, and poroid hymenophores, monomitic to dimitic hyphal systems, and generative hyphae with clamps or simple septa. *Steccherinum* is the largest genus in the family, with a worldwide distribution, and is characterized mainly by a dimitic hyphal system and presence of thick-walled encrusted cystidia. Species traditionally included in *Steccherinum*, however, have been transferred to other genera based on results of molecular phylogenetic analyses. Even though knowledge of Steccherinaceae has increased in the past few years, very little is known about the hydroid species of the family, especially from the Neotropics. In this study, we present morphological and phylogenetic analyses on hydroid specimens of Steccherinaceae collected in the Neotropics. Molecular data of nuc internal transcribed spacer region ITS1-5.8S-ITS rDNA (ITS) and portions of nuc 28S rDNA (28S), translation elongation factor 1- α (*tef1*), and the largest subunit of RNA polymerase II (*rpb1*) were obtained from Brazilian collections. Types and original collections were studied for morphological comparison. Samples we studied grouped in four different genera of Steccherinaceae: *Cabalodontia*, *Etheiroduon*, *Metuloidea*, and *Steccherinum*. Three new neotropical species, *Cabalodontia delicata*, *Etheiroduon purpureum*, and *Steccherinum larssonii*, are described. In addition, the new combinations *Cabalodontia albofibrillosa* and *Metuloidea reniformis* are proposed. The four genera presented in this study are compared and discussed in detail.

ARTICLE HISTORY

Received 9 September 2020
Accepted 21 February 2021

KEYWORDS

Mycodiversity; Neotropics; phylogeny; Polyporales; residual polyporoid clade; taxonomy; 5 new taxa

INTRODUCTION

The family Steccherinaceae Parmasto in its original concept included genera with a smooth, hydroid, or poroid hymenophore and microscopically characterized by the dimitic hyphal structure, generative hyphae with clamp connections, and variable presence of cystidia (Parmasto 1968; Maas Geesteranus 1971). With the addition of molecular data, some authors used broad treatments of the Steccherinaceae and consequently some genera were transferred to the Meruliaceae Rea (Larsson 2007; Zmitrovich 2018). Miettinen et al. (2012) used a multigene phylogenetic analysis that redefined the Steccherinaceae beyond the characteristics traditionally known for the family and included genera with a monomitic hyphal system and generative hyphae with simple septa. Later, Justo et al. (2017) provided an overview of families of Polyporales and recovered Steccherinaceae as monophyletic group nesting in the residual polyporoid clade.

Steccherinum Gray, typified by *S. ochraceum* (Pers.) Gray, is the largest genus in the Steccherinaceae, with

approximately 75 species currently accepted worldwide. It is morphologically characterized by the presence of thick-walled skeletocystidia, a dimitic hyphal system, and clamped generative hyphae. Originally, *Steccherinum* included only hydroid species, but recent phylogenetic studies showed that the hymenophore is variable in the genus, and its current circumscription also includes poroid species previously classified in *Junghuhnia* (Miettinen et al. 2012; Miettinen and Ryvarden 2016; Westphalen et al. 2018). Throughout the years, species with deviating microscopic features have also been placed in *Steccherinum*, such as *S. murashkinskyi* (Burt) Maas Geest. (with an almost trimitic hyphal system) and *S. queletii* (Bourdot & Galzin) Hallenb. & Hjortstam (with a monomitic hyphal system and cystidia fusoid at the apex). However, phylogenetic studies showed that these species do not belong to *Steccherinum* s. str., and they have been transferred to other genera, *Metuloidea* G. Cunn. and *Cabalodontia* Piątek, respectively (Miettinen et al. 2012). In the Neotropics, knowledge about *Steccherinum* and

the family Steccherinaceae is still sparse, having only one phylogenetic study focused on poroid species of the genus *Steccherinum* (Westphalen et al. 2018) and a few other hydroid species described based on morphological characteristics (Maas Geesteranus 1978; Hjortstam and Bononi 1986; Hjortstam 1999; Hjortstam and Ryvar den 2008). In this study, we aimed to provide new information on neotropical species of *Steccherinum* s. lat. through morphological examination of specimens, as well as phylogenetic analyses, including newly obtained sequences of Brazilian specimens. Discussions on the genera *Cabalodontia*, *Etheiroduon*, *Metuloidea*, and *Steccherinum* are presented, and three new species and two new combinations are proposed.

MATERIALS AND METHODS

Morphological analyses.—Fresh specimens were collected in southern Brazil between 2014 and 2019. Specimens from BPI, E, HR, ICN, O, PACA, and SP herbaria (herbarium abbreviations per Thiers [continuously updated]) were studied for morphological revision and comparison. Sections of basidiomes were observed under a compound microscope. Cotton blue (Merck 1275) in lactic acid solution was used to observe cyanophilic reactions of spores and/or hyphae (abbreviated CB+ or CB−) and for measurement of microstructures. Since all Steccherinaceae are negative in Melzer reagent, this information is not shown on the descriptions, but the reactions were tested to confirm this. A minimum of 25 of each structure was measured when possible. Illustrations of microstructures were made with the aid of a drawing tube at 1000× magnification, with the exception of spores, which were drawn freehand based on the measurements. Illustrations were then imported and redrawn to vector graphics on Inkscape 0.91 (Free Software Foundation Inc., Boston, Massachusetts, USA). Abbreviations and codes used for measurements were the following: Lm × Wm = mean length and width, Q = range of length/width ratio, Qm = length/width mean, and n = x/y [x = number of measurements from a given number (y) of specimens]. Numbers in parentheses indicate extreme sizes found in less than 5% of the measurements taken.

DNA extraction and amplification.—Total DNA was extracted from cultures or small pieces of dried basidiomes using the protocol of lysis buffer consisting of 2% cetyltrimethylammonium bromide (CTAB), 1.4 M NaCl, 0.10 M Tris-HCl, 0.1% mercaptoethanol, 20 mM ethylenediaminetetraacetic acid (EDTA), incubated

at 65 C for at least 2 h. After one round of chloroform extraction, DNA was precipitated with isopropyl alcohol (Doyle 1987). Amplification of nuc internal transcribed spacer region ITS1-5.8S-ITS2 rDNA (ITS) and a region of nuc r28S DNA (28S) was performed using primers ITS1/ITS4 and LR0R/LR7 (Nikolcheva and Bärlocher 2004), respectively, following Tomšovský et al. (2010). Amplification of a region of translation elongation factor 1- α (*tef1*) used primers 983F/2218R or 983F/1567R (Matheny et al. 2007). The region between domains A–C of the largest subunit of RNA polymerase II (*rpb1*) was amplified using the primers *rpb1*-Af/*rpb1*-Cr (Matheny et al. 2002). For amplification of the *tef1* and *rpb1* regions, a touchdown polymerase chain reaction (PCR) with a gradually reduced annealing temperature (60–50 C) was performed. Amplicons were purified using polyethylene glycol (PEG) 3% solution (Paithankar and Prasad 1991) and sequenced in both directions at Macrogen (Seoul, Korea). The same primers used in the amplification were used for sequencing.

Phylogenetic analyses.—A data set was prepared using four molecular loci: ITS, 28S, *tef1*, and *rpb1*. Reference sequences were chosen based on studies by Miettinen et al. (2012), Justo et al. (2017), Westphalen et al. (2018, 2019) and by BLAST searches of the National Center for Biotechnology Information (NCBI) database. The sequences used in this study are summarized in TABLE 1. The data set was aligned using MAFFT 7 online (<http://mafft.cbrc.jp/alignment/server/>) under the auto mode for strategy. Low-homology regions of *tef1* and *rpb1* (introns), as well as of ITS1 and ITS2, were removed before phylogenetic analyses. Bayesian inference (BI) analyses were conducted in MrBayes 3.2.6 (Ronquist et al. 2012). Nucleotide substitution models were specified for each gene fragment based on the corrected Akaike information criterion (AICc) generated in jModeltest 2.1.4 (Darriba et al. 2012). The data set was subdivided into six data partitions: ITS, 5.8S, ITS2, 28S, *tef1*, and *rpb1*. BI analysis was implemented by running four Markov chain Monte Carlo (MCMC) independent runs for 10 million generations, sampling every 1000 generations. The first 25% of the sampled trees were discarded as a burn-in, and those remaining were used to reconstruct a 50% majority-rule consensus tree. Posterior probabilities support values above 0.9 were considered strongly supported. Maximum likelihood (ML) analyses were conducted in RAXML-HPC 8 (Stamatakis 2014) using a rapid

Table 1. List of sequences used in this study.

| Species | Voucher | Locality | GenBank accession nos. | | | |
|---------------------------------------|-----------------|----------|------------------------|------------|---------------|-------------|
| | | | ITS | 28S | <i>tef1-a</i> | <i>rpb1</i> |
| <i>Antella americana</i> | HHB-4100-Sp | US | KP135316 | KP135196 | | KP134885 |
| <i>Antella chinensis</i> | Dai 9019 | CN | JX110844 | KC485542 | | |
| <i>Antrodiella faginea</i> | KHL 11977 | NO | JN710514 | JN710514 | JN710712 | |
| <i>Antrodiella semisupina</i> | Miettinen X242 | CA | JN710521 | JN710521 | | |
| <i>Antrodiella stipitata</i> | FD-136 | US | KP135314 | KP135197 | | KP134886 |
| <i>Butyrea luteoalba</i> | FP-105786 | US | KP135320 | KP135226 | | KP134887 |
| <i>Butyrea luteoalba</i> | KHL 13238b | EE | JN710558 | JN710558 | JN710719 | |
| <i>Butyrea japonica</i> | MN 1065 | JP | JN710556 | JN710556 | JN710718 | |
| <i>Cabalodonia albofibrillosa</i> | SWFC 006394 | CN | MK838859 | | | |
| <i>Cabalodonia albofibrillosa</i> | Sanyal 6903 | IN | KP401770 | | | |
| <i>Cabalodonia delicata*</i> | MCW 564/17 | BR | MT849295 | MT849295 | MT833934 | MT833947 |
| <i>Cabalodonia delicata*</i> | MCW 670/19 | BR | MT849296 | MT849296 | MT833935 | |
| <i>Cabalodonia delicata*</i> (T) | MCW 693/19 | BR | MT849297 | MT849297 | MT833936 | MT833948 |
| <i>Cabalodonia delicata*</i> | MV370 | BR | MT849298 | MT849298 | | |
| <i>Cabalodonia queletii</i> | CBS 233.56 | FR | MH857599 | MH869147 | | |
| <i>Cerrena unicolor</i> | KHL-GB | SE | JQ031127 | JQ031127 | JX109891 | |
| <i>Etheiroidon fimbriatum*</i> | HR97926 | CZ | MT849299 | | MT833937 | MT833954 |
| <i>Etheiroidon fimbriatum*</i> | HR98811 | CZ | MT849300 | | MT833938 | MT833955 |
| <i>Etheiroidon aff. fimbriatum</i> | HHB2878sp | US | KY948822 | KY948864 | | KY948950 |
| <i>Etheiroidon purpureum*</i> (T) | MCW 642/18 | BR | MT849301 | MT849301 | MT833939 | |
| <i>Frantisekia mentschulensis</i> | AH 1377 | AT | JN710544 | | | |
| <i>Frantisekia fissiliformis</i> | CBS 435.72 | US | MH860521 | MH872232 | | |
| <i>Junghuhnia crustacea</i> | Miettinen X1127 | ID | JN710554 | JN710554 | | |
| <i>Metuloidea cinammomea</i> | Ryvarden 43626 | VE | KU926963 | | | |
| <i>Metuloidea fragrans</i> | LE295277 | RU | KC858281 | | | |
| <i>Metuloidea murashkinsky</i> | Spirin 2367 | RU | JN710588 | JN710588 | | |
| <i>Metuloidea reniforme*</i> | MCW 523/17 | BR | MT849302 | MT849302 | | MT833949 |
| <i>Metuloidea reniforme*</i> | MCW 542/17 | BR | MT849303 | MT849303 | MT833940 | MT833950 |
| <i>Metuloidea rhinocephala</i> | Miettinen X460 | AU | JN710562 | JN710562 | | |
| <i>Mycorrhaphium adustum</i> | KHL 12255 | US | JN710573 | JN710573 | JN710727 | |
| <i>Mycorrhaphium hispidum</i> | MCW 429/13 | BR | MH475307 | MH475307 | MH475318 | |
| <i>Nigroporus vinosus</i> | BHS2008-100 | US | JX109857 | JX109857 | JX109914 | |
| <i>Steccherinum atumnale</i> | Spirin 2957 | RU | JN710549 | JN710549 | JN710716 | |
| <i>Steccherinum bourdotii*</i> | HR102002 | CZ | MT849310 | | MT833946 | MT833953 |
| <i>Steccherinum bourdotii*</i> | HR99893 | CZ | MT849311 | | MT833945 | MT833951 |
| <i>Steccherinum bourdotii*</i> | MT 10/19 | CZ | MT849312 | | MT833944 | MT833952 |
| <i>Steccherinum collabens</i> | KHL11848 | SE | JN710552 | JN710552 | JN710717 | |
| <i>Steccherinum formosanum</i> | TFRI 652 | — | EU232184 | EU232268 | | |
| <i>Steccherinum fimbriatellum</i> | Miettinen 2091 | RU | JN710555 | JN710555 | | |
| <i>Steccherinum lacerum</i> | Niemelä 8246 | FI | JN710557 | JN710557 | | |
| <i>Steccherinum laeticolor</i> | Fp102480sp | US | KY948823 | KY948868.1 | | KY948948 |
| <i>Steccherinum larssonii*</i> (T) | MCW 593/17 | BR | MT849306 | MT849306 | MT833941 | MT833956 |
| <i>Steccherinum larssonii*</i> | MCW 594/17 | BR | MT849307 | MT849307 | MT833942 | |
| <i>Steccherinum larssonii*</i> | MCW 621/17 | BR | MT849308 | MT849308 | MT833943 | |
| <i>Steccherinum meridionale</i> | MR 284 | — | KY174992 | KY174992 | KY175019 | |
| <i>Steccherinum neonitidum</i> | MCW 371/12 | BR | KY174990 | KY174990 | KY175017 | |
| <i>Steccherinum nitidum</i> | FP-105195-Sp | US | KP135323 | KP135227 | | KP134888 |
| <i>Steccherinum ochraceum</i> | KHL11902 | SE | JN710590 | JN710590 | JN710730 | |
| <i>Steccherinum oreophilum</i> | HHB13202sp | US | KY948824 | | | KY948949 |
| <i>Steccherinum oreophilum</i> | Niemelä 7691 | FI | JN710548 | JN710548 | | |
| <i>Steccherinum polycystidiferum</i> | MCW 419/12 | BR | KY174995 | KY174995 | KY175021 | |
| <i>Steccherinum pseudozilingianum</i> | Kulju 1004 | FI | JN710561 | JN710561 | JN710722 | |
| <i>Steccherinum robustius</i> | GB 1195 | SE | JN710591 | JN710591 | | |
| <i>Steccherinum tenue</i> | KHL 12316 | US | JN710598 | JN710598 | JN710733 | |
| <i>Steccherinum tenuispinum</i> (T) | LE231603 | RU | KM411452 | KM411469 | KM411484 | |
| <i>Steccherinum undigerum</i> | MCW 436/13 | BR | KY174988 | KY174988 | KY175020 | |
| <i>Steccherinum</i> sp. | FD-26 | US | KP135322 | KP135289 | | KP134889 |
| <i>Steccherinum</i> sp. 1 | Miettinen 13705 | ID | JN710592 | JN710592 | JN710731 | |
| <i>Steccherinum</i> sp. 3 | Miettinen 14391 | ID | JN710594 | JN710594 | JN710732 | |

*Sequences obtained in this study. (T) indicates type specimen. **ISO 3166 Alpha 2 Code.

bootstrap analysis and search for best-scoring ML tree with a GTRGAMMA+I model of evolution. The same partitions as described above were used. Bootstrap values >70% were considered significant or strongly supported. All analyses were conducted on the CIPRES Science Gateway portal (Miller et al. 2011).

RESULTS

The concatenated alignment resulted in 3708 positions, including 2595 conserved and 1113 variable sites. The best-fit models selected were TPM2uf+I+G for ITS1, JC+I for 5.8S, TPM3uf+I+G for ITS2,

GTR+I+G for 28S, TrN+I+G for *tef1*, and TPM2uf+I+G for *rpb1*.

Our phylogenetic and morphological analyses revealed three new hydroid species in the Steccherinaceae. The first of these was recovered as a sister taxon of the clade formed by *Cabalodontia queletii*, *Steccherinum albofibrilloseum* (Hjortstam & Ryvarden) Hallenb. & Hjortstam, and *Steccherinum oreophilum* Lindsey & Gilb. with high support (1.0, 88) (FIG. 1). The second species studied was

recovered within the genus *Etheirodon* Banker. The third species nested in *Steccherinum* s. str. as sister to *S. bourdotii* Saliba & A. David. In addition, sequences obtained of *Steccherinum reniforme* (Berk. & M.A. Curtis) Banker confirmed that it nests in the genus *Metuloidea* as sister taxon of the clade formed by *M. cinnamomea* (Iturr. & Ryvarden) Miettinen & Ryvarden and *M. murashkinskyi*. This phylogenetic result was also supported by morphological characteristics,

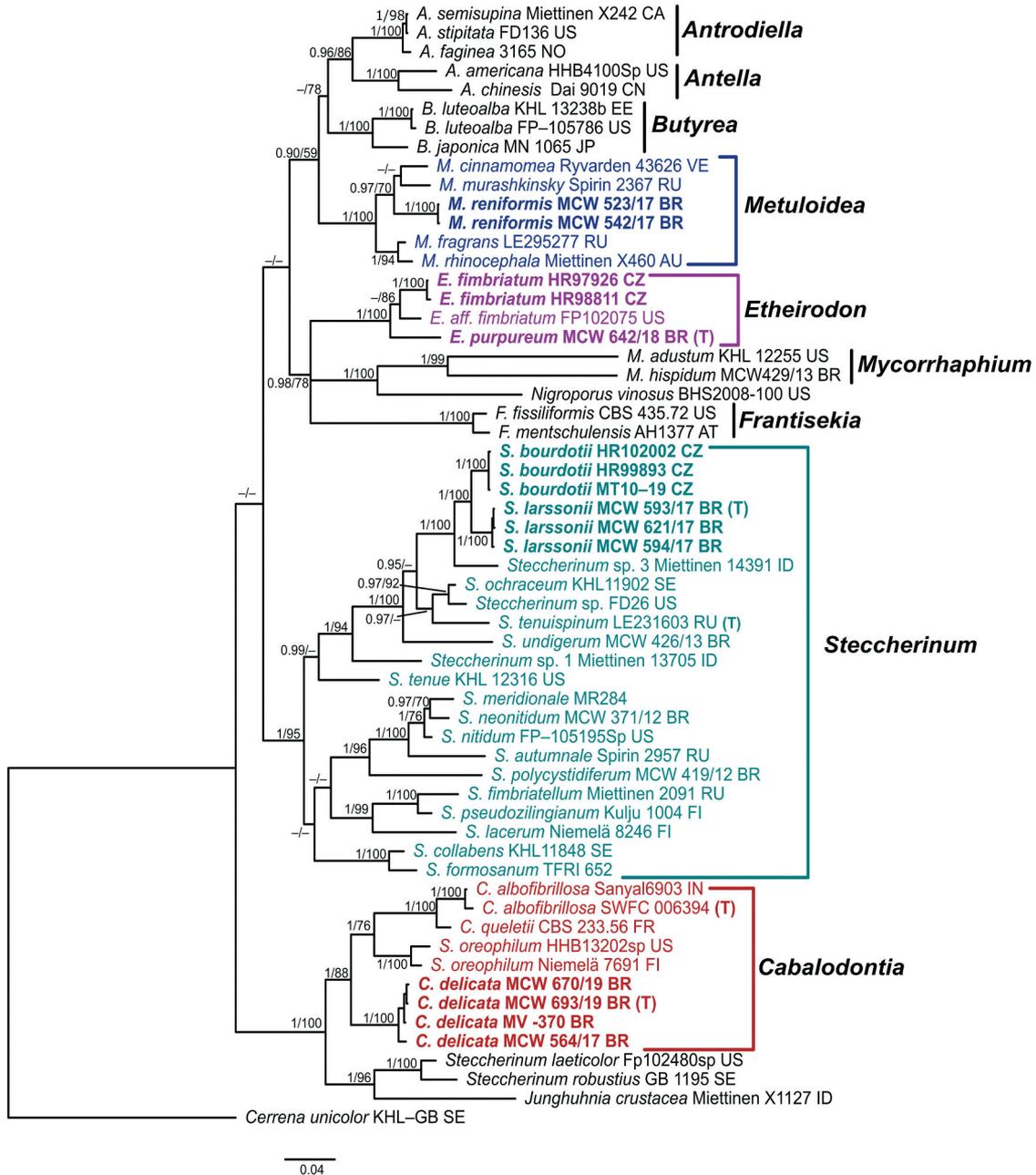


Figure 1. Phylogenetic relationships in the Steccherinaceae clade inferred from a combined data set of ITS, 28S, *tef1*, and *rpb1* sequences inferred by BI analyses. All sequences generated in this study are indicated in bold. Numbers at branches indicate Bayesian posterior probabilities/ML bootstrap frequency. (T) indicates type specimens. Codes after voucher specimens denote country of origin (ISO 3166, Alpha 2; ISO 3166-2:2013, Codes for the representation of names of countries and their subdivisions — Part 2: Country subdivision code). The bar indicates the number of expected substitutions per site.

which already indicated that *S. reniforme* belongs to this genus based on basidiome color and type of hyphae and cystidia.

Below, the new species *Cabalodontia delicata*, *Etheiroidon purpureum*, and *Steccherinum larssonii* are proposed, as well as the combinations of *Metuloidea reniformis* and *C. albofibrillosa*. Full descriptions of the new taxa and comments on the new combinations are presented. The main features of the genera *Cabalodontia*, *Etheiroidon*, *Metuloidea*, and *Steccherinum* are summarized in TABLE 2, and spore measurements obtained in this study are presented in TABLE 3. An identification key including all genera with hydroid, odontoid, or irpicoid species of the residual polyporoid clade is also provided.

TAXONOMY

Cabalodontia albofibrillosa (Hjortstam & Ryvarde) Westphalen, comb. nov.

Mycobank MB836502

Basionym: *Phlebia albofibrillosa* Hjortstam & Ryvarde, Mycotaxon 20:139. 1984.

≡ *Steccherinum albofibrillosum* (Hjortstam & Ryvarde) Hallenb. & Hjortstam, Mycotaxon 31:443. 1988.

Description and illustrations: Hjortstam and Ryvarde (1984) and Hallenberg and Hjortstam (1988).

Ecology and distribution: Causing a white rot in dead branches of angiosperms. Known from Nepal, China, and India.

Remarks: *Cabalodontia albofibrillosa* was originally described from Nepal in the genus *Phlebia* Fr. (Hjortstam & Ryvarde 1984) and characterized by the monomitic hyphal system with clamped hyphae, presence of encrusted cystidia, and subglobose basidiospores. Later, Hallenberg and Hjortstam (1988) transferred it to *Steccherinum* due to

the absence of agglutinated hyphae. In both treatments, the authors compared *P. albofibrillosa* with *Phlebia queletii* (≡ *Cabalodontia queletii*), from which it differed only by the shorter basidiospores. Sequences of *S. albofibrillosum*, from Asia, available on GenBank were used in our phylogenetic analyses and confirmed that it nests in a sister clade to *C. queletii*. Therefore, the morphological and molecular data support transferring this species to *Cabalodontia*. The three species included in *Cabalodontia* in this study are very similar morphologically, varying mostly in basidiospore size and shape. Whereas *C. albofibrillosa* has globose to subglobose basidiospores ($4-4.5(-5) \times 3.5-4 \mu\text{m}$) (Hjortstam and Ryvarde 1984), *C. delicata*, sp. nov. (described below), has narrower subglobose to oblong-ellipsoid basidiospores ($3.5-4.0(-4.5) \times 2.5-3.0(-3.5 \mu\text{m})$). *Cabalodontia queletii* has the longest basidiospores in the genus ($5-6 \mu\text{m}$), which are ellipsoid to short-cylindrical. In addition, the three species have different geographic distributions, with *C. queletii* occurring in Europe, *C. albofibrillosa* in Asia, and *C. delicata* (described below) in the Neotropics.

Cabalodontia delicata Westphalen & Motato-Vásq., sp. nov. FIGS. 2A, 3

Mycobank MB836503

Typification: BRAZIL. RIO GRANDE DO SUL: Caxias do Sul, Comunidade Nossa Senhora de Lourdes, 3a Légu, 28 Mar 2019, M.C. Westphalen 693/18 (**holotype** SP).

Etymology: *delicata* (Latin), delicate, referring to the fragile basidiomes.

Diagnosis: Characterized by annual, fragile, white basidiomes, broadly ellipsoid basidiospores, monomitic hyphal system, and cystidia with fusoid apices. Differs from *C. queletii* by the shorter basidiospores and from *C. albofibrillosa* by the narrower basidiospores. In addition, *C. delicata* has a neotropical distribution whereas the other species are from Europe and Asia, respectively.

Table 2. Main morphological characteristics of the genera *Cabalodontia*, *Etheiroidon*, *Metuloidea*, and *Steccherinum*.

| Element | <i>Cabalodontia</i> | <i>Etheiroidon</i> | <i>Metuloidea</i> | <i>Steccherinum</i> |
|------------------|--|--|---|--|
| Basidiomes | Resupinate. Entire margins. White to cream. Fragile and brittle | Resupinate. Strongly fimbriate and rhizomorphic margins. Pinkish, purplish or grayish. Papery and flexible | Pileate. Brownish, with a sweet smell when fresh. Entire margins. Corky to somewhat waxy | Resupinate to pileate. Entire to slightly fimbriate margins. Cream to ochraceous. Corky to slightly waxy |
| Hymenophore | Odontoid to hydroid | Warty, odontoid or more rarely hydroid | Poroid or hydroid | Poroid or hydroid |
| Hyphal structure | Monomitic. Clamped. Hyphae hyaline | Dimitic. Clamped. Skeletal hyphae yellowish to pale brown | Dimitic. Clamped. Strongly branched yellowish skeletal hyphae | Dimitic. Clamped or with simple septa. Skeletal hyphae hyaline |
| Cystidia | Thin-walled leptocystidia and incrustated thick-walled metuloids | Thin- to slightly thick-walled, incrustated and clavate | Variable. Thin- to thick-walled, usually with a visible lumen and a cap of crystals, fusoid-ventricose to clavate. Thin-walled septocystidia in <i>M. reniforme</i> | Thin-walled leptocystidia and clavate incrustated skeletocystidia |
| Basidiospores | Subglobose to ellipsoid | Ellipsoid to subcylindrical | Ellipsoid to cylindrical | Subglobose to cylindrical |

Table 3. Basidiospore measurements of specimens studied in μm .

| Species/Specimen (voucher) | Length | Lm | Width | Wm | Q | Qm | n |
|-------------------------------|---------------------|-----|---------------------|-----|-------------------------|------|-----|
| <i>Cabalodontia delicata</i> | 3.5–4.0(–4.5) | 3.8 | 2.5–3.0(–3.5) | 3.0 | (1.16–)1.20–1.31(–1.35) | 1.25 | 210 |
| F918861 | 3.5–3.8(–3.9) | 3.7 | 2.5–3.0(–3.3) | 2.8 | (1.18–)1.20–1.42 | 1.32 | 20 |
| KHL1132 | (3.6–)3.7–4.3(–4.4) | 4.0 | 2.9–3.5(3.6) | 3.2 | (1.18–)1.19–1.30(–1.31) | 1.25 | 20 |
| LR15438 | (3.6–)3.7–4.4(–4.6) | 4.0 | 3.0–3.6(–3.8) | 3.2 | (1.16–)1.17–1.28(–1.30) | 1.22 | 20 |
| MV370 | 3.5–4.3(–4.5) | 3.9 | 2.9–3.5(–3.8) | 3.2 | 1.12–1.32 | 1.21 | 25 |
| MV703 | 3.5–4.1(–4.2) | 3.8 | 2.9–3.4(–3.5) | 3.2 | (1.12–)1.14–1.28(–1.30) | 1.21 | 20 |
| MV860 | 3.4–3.9 | 3.6 | 2.7–3.0(–3.2) | 2.8 | (1.19–)1.20–1.35(–1.37) | 1.27 | 15 |
| MWC564 | 3.2–4.0(–4.4) | 3.7 | 2.5–3.1(–3.2) | 2.8 | (1.19–)1.21–1.40(–1.42) | 1.29 | 30 |
| MWC670/19 | (3.3–)3.4–4.4(–4.7) | 3.9 | (2.6–)2.7–3.5(–3.6) | 3.0 | (1.18–)1.19–1.33(–1.34) | 1.25 | 30 |
| MWC693/19 | (3.4–)3.5–4.2(–4.4) | 3.8 | (2.7–)2.8–3.3(–3.4) | 3.0 | (1.15–)1.19–1.33(–1.34) | 1.26 | 30 |
| <i>Etheiaron purpureum</i> | 4.0–4.5 | 4.1 | 2.0–2.5 | 2.2 | (1.70–)1.80–2.01(–2.10) | 1.90 | 100 |
| ICN169117 | 3.8–4.2 | 4.0 | (1.9)2.0–2.3(–2.4) | 2.2 | (1.73–)1.75–1.91(–2.05) | 1.83 | 25 |
| LR42280 | (3.8–)3.9–4.4(–4.6) | 4.1 | 2.0–2.3(–2.5) | 2.2 | (1.77–)1.79–1.99(–2.00) | 1.90 | 25 |
| MWC642/18 | 3.8–4.4(–4.5) | 4.1 | 1.9–2.4(–2.8) | 2.1 | (1.55–)1.77–2.13(–2.26) | 1.91 | 30 |
| PACA7143 | (3.8–)3.9–4.4(–4.5) | 4.1 | 2.0–2.4 | 2.2 | (1.75–)1.81–2.00 | 1.87 | 20 |
| <i>E. fimbriatum</i> | 3.5–4.0 | 3.8 | 2.0–2.5 | 2.4 | (1.43–)1.45–1.64(–1.72) | 1.55 | 50 |
| LR12402 | (3.4–)3.5–4.1(–4.2) | 3.8 | 2.2–2.7 | 2.5 | (1.40–)1.42–1.64(–1.77) | 1.54 | 25 |
| E00604800 | (3.4–)3.5–4.0(–4.1) | 3.8 | (2.2–)2.3–2.6 | 2.4 | (1.46–)1.48–1.65(–1.67) | 1.56 | 25 |
| <i>Metuloidea reniforme</i> | 3.5–4.0(4.5) | 3.7 | 1.5–2(–2.5) | 1.9 | (1.75–)1.79–2.19(–2.27) | 1.96 | 70 |
| MWC523/17 | (3.3–)3.4–4.0(–4.2) | 3.7 | (1.7–)1.8–2.0(–2.1) | 1.9 | 1.75–2.06(–2.11) | 1.91 | 20 |
| MWC544/17 | 3.5–4.1(–4.3) | 3.8 | 1.5–2.2(–2.3) | 1.8 | (1.80–)1.86–2.40(–2.53) | 2.08 | 25 |
| MWC550/17 | (3.2–)3.0–4.1(–4.2) | 3.7 | (1.7–)1.8–2.1(–2.3) | 1.9 | 1.75–2.10(–2.17) | 1.90 | 25 |
| <i>Steccherinum larsonii</i> | 3.5–4.0(–4.5) | 3.9 | 3–3.5(–4.0) | 3.2 | (1.13–)1.15–1.28(–1.30) | 1.21 | 220 |
| KHL11326 | (3.2–)3.3–3.9(–4.0) | 3.6 | 2.7–3.3 | 3.0 | 1.16–1.24(–1.26) | 1.20 | 15 |
| KHL11622 | (3.5–)3.6–4.4(–4.6) | 3.9 | 3.0–3.6(–3.9) | 3.2 | (1.10–)1.13–1.28 | 1.21 | 20 |
| KHL9806 | (3.6–)3.7–4.2(–4.3) | 3.9 | (3.0–)3.1–3.7(–3.9) | 3.4 | (1.10–)1.15–1.22(–1.23) | 1.16 | 15 |
| LR23000 | (3.6–)3.7–3.9 | 3.8 | 2.8–3.1(–3.3) | 3.0 | (1.15–)1.19–1.33(–1.36) | 1.27 | 15 |
| LR23024 | (3.6–)3.7–4.2 | 3.9 | (3.1–)3.2–3.6 | 3.4 | (1.10–)1.12–1.22(–1.24) | 1.16 | 15 |
| MV634 | (3.6–)3.7–4.3(–4.5) | 3.9 | 2.9–3.4(–3.50) | 3.1 | (1.17–)1.19–1.35(–1.38) | 1.28 | 35 |
| MWC593/17 | (3.5–)3.7–4.4(–4.5) | 4.0 | 3.0–3.6(–3.80) | 3.3 | (1.14–)1.17–1.27 | 1.21 | 25 |
| MWC594/17 | 3.6–4.3(–4.5) | 3.9 | (2.7–)2.0–3.5(–3.6) | 3.2 | 1.14–1.34(–1.40) | 1.23 | 25 |
| MWC621/17 | (3.5–)3.6–4.2(–4.3) | 3.9 | 3.1–3.6(–3.8) | 3.4 | (1.05–)1.10–1.22 | 1.15 | 30 |
| MWC676/19 | 3.5–4.4(–4.6) | 3.9 | (2.7–)2.8–3.4(–3.9) | 3.1 | (1.16–)1.18–1.34(–1.37) | 1.25 | 25 |
| <i>S. bourdotii</i> | 4.0–5 | 4.4 | (3.0–)3.5–4.0 | 3.6 | 1.12–1.27(–1.30) | 1.20 | 75 |
| HR99893 | (4.0–)4.1–4.8(–4.9) | 4.3 | (3.1–)3.4–4.0(–4.1) | 3.6 | 1.11–1.26(–1.29) | 1.21 | 25 |
| HR102002 | 4.0–4.7(–5.0) | 4.4 | 3.3–4.0(–4.4) | 3.6 | (1.11–)1.12–1.27 | 1.19 | 25 |
| MT 10/19 | (3.8–)4.0–5.0 | 4.5 | (3.2–)3.3–4.0(–4.1) | 3.7 | (1.13–)1.14–1.27(–1.29) | 1.21 | 25 |

Description: Basidiomes annual, resupinate, adnate, forming confluent patches on the substrate, soft and fragile; very thin, up to 0.5 mm thick; white to cream when fresh, unchanging or slightly darker when dried; sterile margins thin, entire to slightly mycelioid, up to 5 mm wide. Hymenophore formed by very small teeth up to 0.2 mm long, often somewhat collapsed upon drying, 5–8 per mm. Subiculum white, homogeneous, thin and cottony, up to 250 μm thick.

Hyphal structure monomitic. Generative hyphae clamped, thin- to thick-walled, often branching near the septa or at clamp connections, 2–5 μm wide, CB+. Cystidia of two types: (i) thin-walled leptocystidia in the hymenium, more commonly seen in the tips of the teeth, clavate, 3.5–6 μm wide; and (ii) thick-walled cystidia arising from sclerified generative hyphae in the subiculum and projecting toward the trama and the hymenium, wider at the middle portion and narrower at the apex, heavily encrusted, in older specimens very abundant and dominating in the trama, encrusted portion

4.5–11.5 μm wide. Basidia 12–16 \times 4–5.5 μm , clavate, with four sterigmata. Basidiospores 3.5–4.0(–4.5) \times 2.5–3.0(–3.5) μm , subglobose to oblong-ellipsoid, CB+.

Ecology and distribution: Causing a white rot on dead branches of unidentified angiosperms. Known from Brazil, Colombia, Costa Rica, and Venezuela. Almost year-round, collected from Jan to Aug and Nov.

Specimens examined: BRAZIL. RIO GRANDE DO SUL: São Francisco de Paula, Paradoiro Hampel, 19 Apr 2017, *M.C. Westphalen 564/17* (SP); SÃO PAULO: São Luis do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, Trilha do corcovado, 7 May 2015, *V. Motato-Vásquez, R.M. Pires & A. Gugliotta MV370* (SP); Trilha Poço do Pito, 14 Feb 2019, *M.C. Westphalen 670/19* (SP); Riberião Grande, Parque Estadual Intervalles, 4 Jun 2016, *V. Motato-Vásquez MV703* (SP); São Paulo, Parque Estadual das Fontes do Ipiranga, 16 Jan 2017, *V. Motato-Vásquez MV860* (SP). COLOMBIA. CUNDINAMARCA: km 16 in the road Mosquera-La Mesa, 3 Jun 1978, *L. Ryvar den 15438* (O); MAGDALENA: Parque Nacional

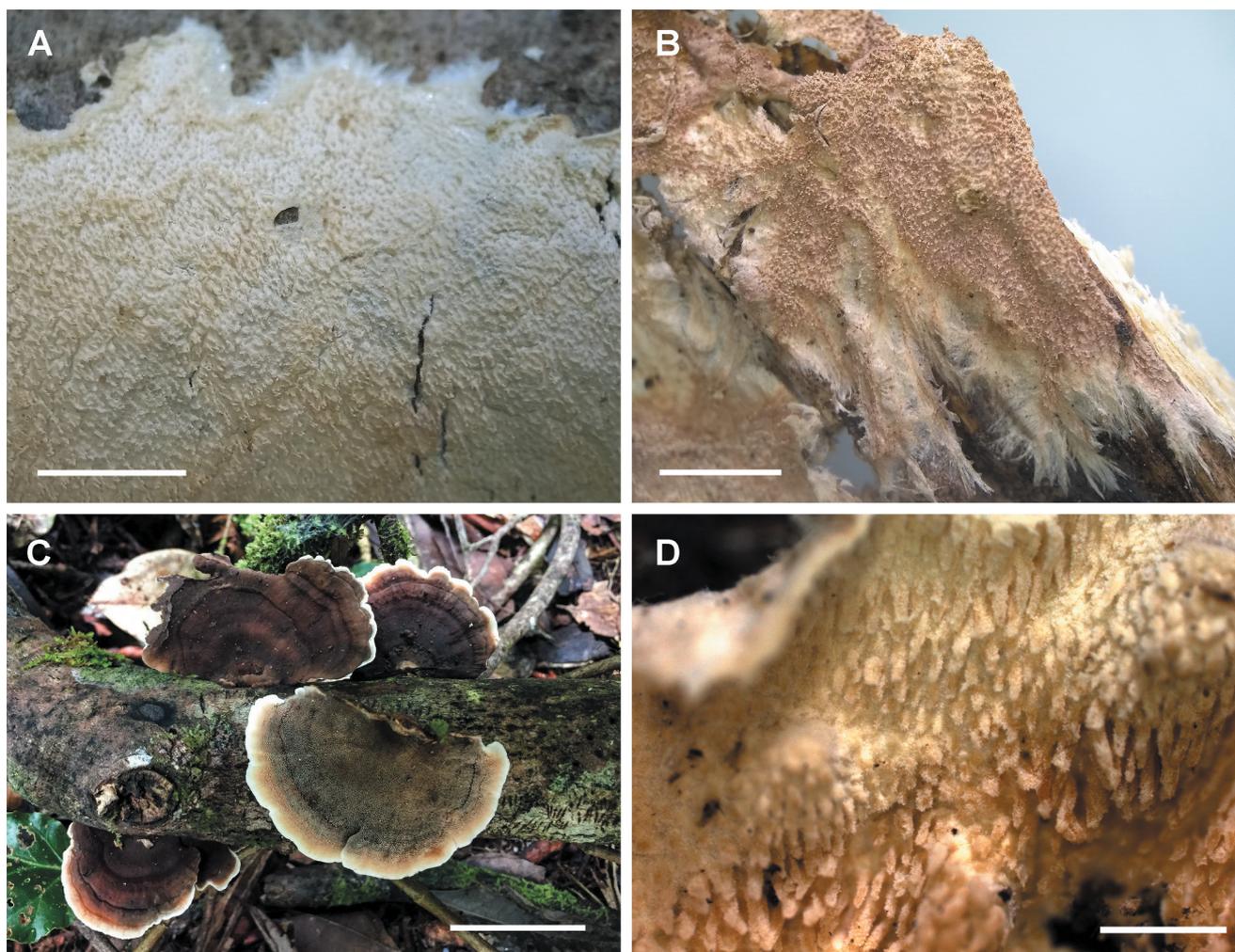


Figure 2. Basidiomes. A. *Cabalodontia delicata* (holotype 693/19). B. *Etheiroduon purpureum* (holotype MCW 642/18). C. *Metuloidea reniformis* (MCW 542/17). D. *Steccherinum larssonii* (holotype MCW 593/17). Bars: A, B = 3 mm; C = 3 cm; D = 1 mm.

Tayrona, Estacional Cañaveral, 14 Jun 1978, L. Ryvar den 15894 (O); Sierra Nevada de Santa Marta, Entre Palo el Campano y Minca, 21 Jun 1978, L. Ryvar den 16338 (O). COSTA RICA. Puntarenas, Coto Brus, Sabalito, Zona Protectora Las Tablas, Camino a Cotoncito, 3 Nov 2004, K.H. Larsson 12601 (O); Organization for Tropical Studies Station, 4 Nov 2004, K.H. Larsson 12639 and 12672 (O); San José, Reserva Los Santos, Cerro de la Muerte, San Gerardo de Dota, 18 Jul 2001, K.H. Larsson 11554 (O). VENEZUELA. ARAGUA: Rancho Grande, Parque Nacional H. Pittier, 30 Aug 1999, K.H. Larsson 11032 (O).

Other specimens examined: Cabalodontia queletii. PORTUGAL. ESTREMADURA: Setúbal, Serra da Arrábida, Mata do Vidal, 27 Jan 1982, I. Melo et al. 1573 (O). *Steccherinum oreophillum.* USA. ARIZONA: Treasure Park, Pinaleno Mountains, Coronado National Forest., Graham County, 31 Aug 1973, J. Page Lindsey 300 (holotype BPI)

Remarks: Cabalodontia delicata is characterized by the very thin and fragile, whitish basidiomes with short teeth. Microscopically, it presents subglobose to oblong-ellipsoid basidiospores, somewhat variable in size and shape. *Cabalodontia queletii* is very similar, differing mainly in the thicker and more robust basidiomes and longer short-cylindrical basidiospores ($5-6 \times 3-3.5 \mu\text{m}$) (Eriksson et al. 1984). In our phylogenetic analyses, one of the specimens studied (MCW 564/17) presents a few noticeable differences in *tefl* and sequences (~20 bp). However, morphologically, it is identical to the other specimens examined of *C. delicata*; therefore, we chose to keep it under the same name. Most of the specimens studied were collected in high-altitude areas.

Etheiroduon purpureum Westphalen, sp. nov. FIGS. 2B, 4 MycoBank MB836504

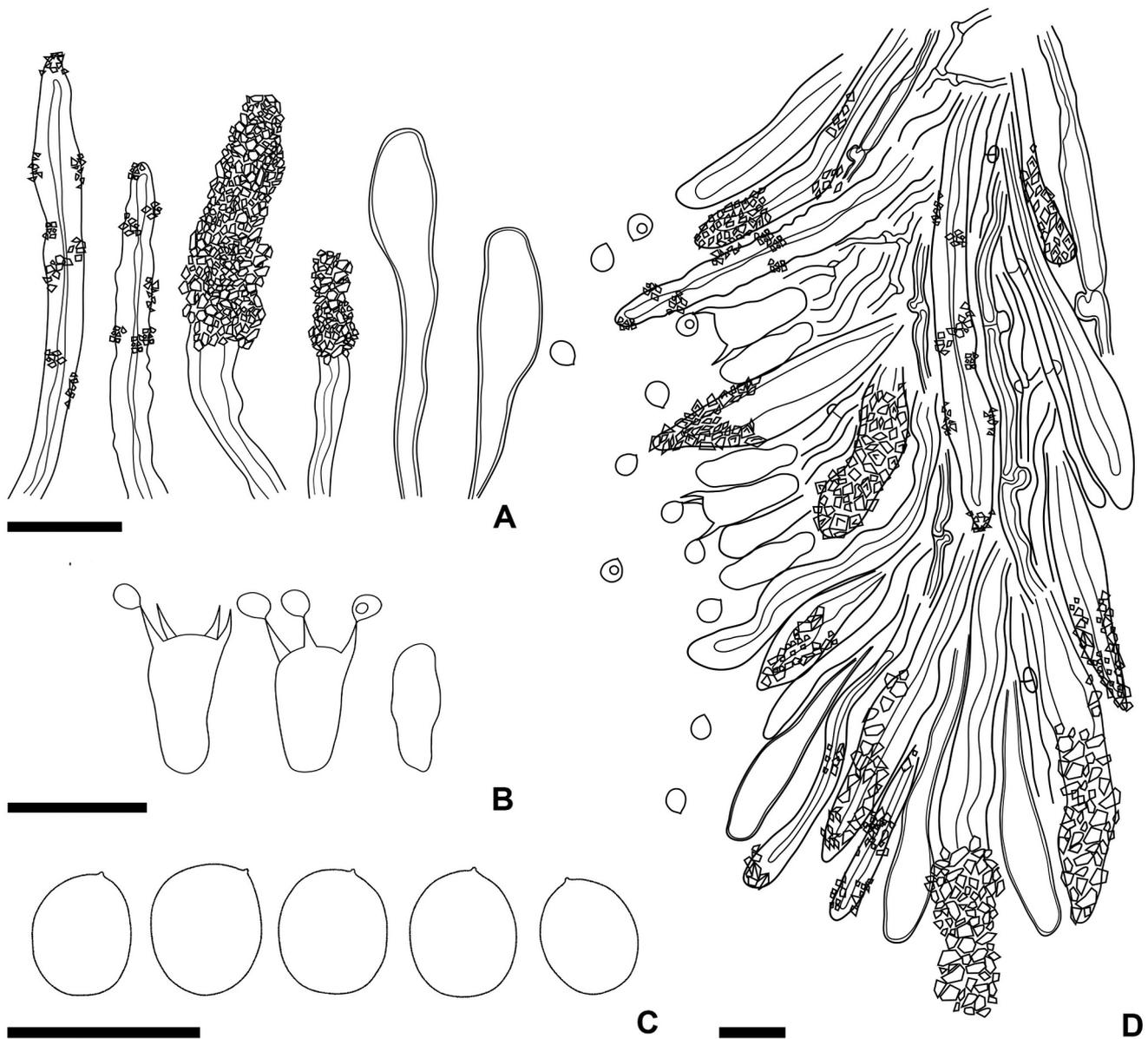


Figure 3. *Cabalodontia delicata* (holotype MCW 693/19). A. Cystidia. B. Basidia and basidioles. C. Basidiospores. D. Microscopic section of the basidioma. Bars: A, B, D = 10 μ m; C = 5 μ m. Drawings by Viviana Motato-Vásquez.

Typification: BRAZIL. RIO GRANDE DO SUL: São Francisco de Paula, Floresta Nacional (FLONA), 14 May 2018, *M.C. Westphalen* 642/18 (**holotype** SP).

Etymology: *purpureum* (Latin), purple, referring to the color of the basidiomes when fresh.

Diagnosis: Characterized by the annual, purplish basidiomes with strongly fimbriate margins, elliptical to sub-cylindrical basidiospores, dimittic hyphal structure, and thin-walled encrusted cystidia. Differs from *E. frimbriatum* by the slightly narrower and longer basidiospores.

Description: Basidiomes annual, resupinate, adnate, detachable, soft and papery; purplish gray when fresh, becoming somewhat discolored to ochraceous when

dried; very thin, up to 0.75 mm thick; margins strongly fimbriate to rhizomorphic, grayish white, up to 1 cm wide. Hymenophore odontoid to warty, teeth 7–10 per mm and up to 0.25 mm thick, somewhat irregular, with protruding encrusted cystidia giving a pulverulent appearance. Subiculum very thin, grayish white, homogenous and somewhat cottony and loose, up to 0.5 mm thick.

Hyphal system dimittic. Generative hyphae thin- to thick-walled, often dichotomously branched, hyaline to slightly yellowish, 3–4 μ m wide. Skeletal hyphae thick-walled to solid, straight to somewhat tortuous, mostly unbranched, yellowish to pale brownish, 3.5–4.5 μ m wide, CB+. Cystidia thin- to slightly

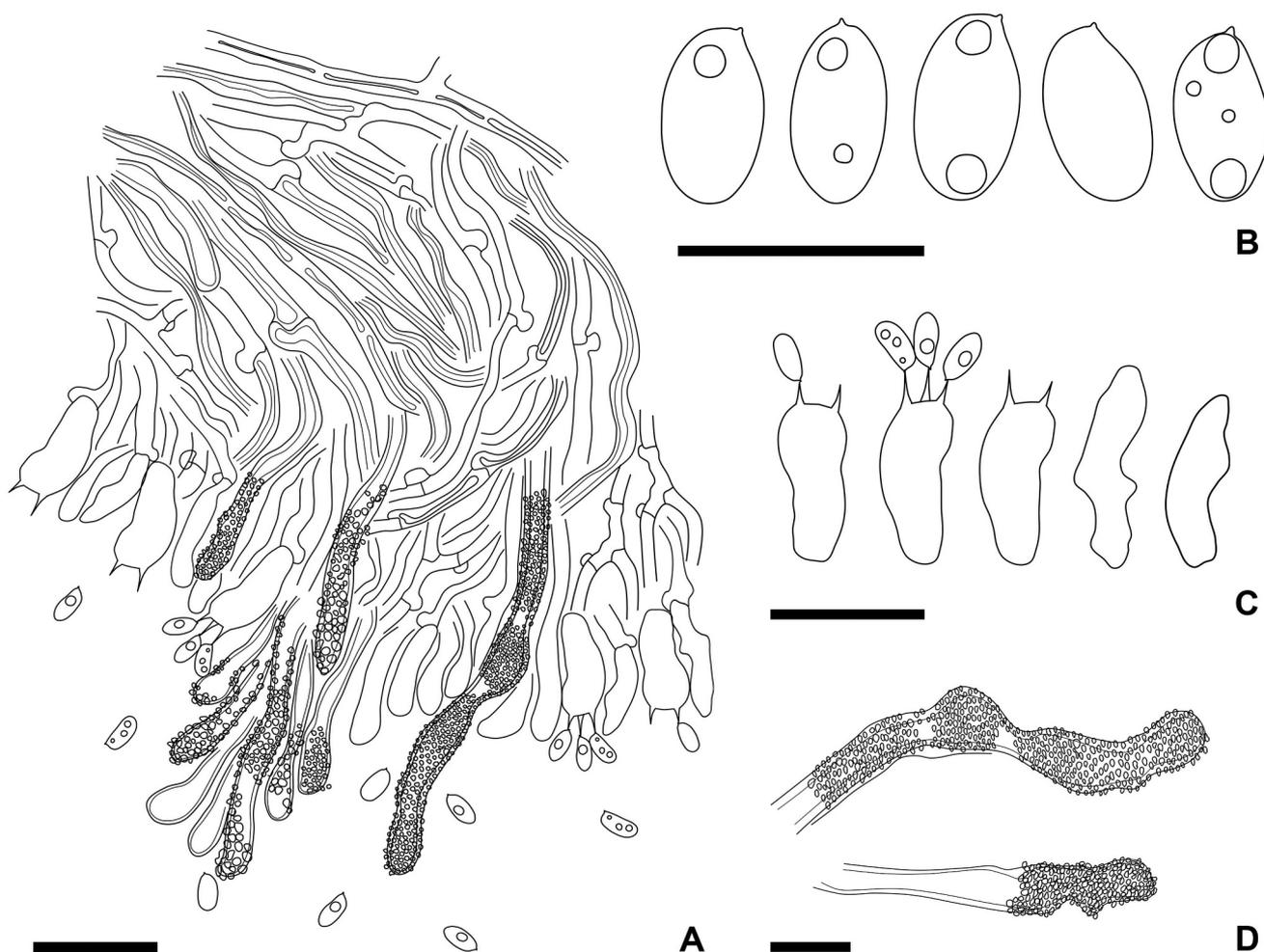


Figure 4. *Etheirodu purpureum* (holotype MCW 642/18). A. Microscopic section of the basidioma. B. Basidiospores. C. Basidia and basidioles. D. Cystidia. Bars: A, C, D = 10 µm; B = 5 µm. Drawings by Viviana Motato-Vásquez.

thick-walled, clavate to tortuous, smooth or more commonly covered with crystals, 5–9 µm wide in the encrusted portion. Cystidioles sometimes present in the hymenium among the cystidia, fusoid. Basidia 10–15 × 4–5.5 µm, clavate, with four sterigmata. Basidiospores 4.0–4.5 × 2.0–2.5 µm, elliptical to sub-cylindrical, hyaline, thin-walled, often with small oil drops, CB+.

Ecology and distribution: Causing a white rot on fallen logs of unidentified angiosperms. Known from Brazil and Venezuela. Collected from Feb to May.

Specimens examined: BRAZIL. RIO GRANDE DO SUL: Cambará do Sul, PARNA da Serra Geral, Trilha para o Cãnion Fortaleza, 29 Apr 2012, *J.M. Baltazar* 2755 (ICN); Parecí, 1931, *J. Rick s.n.* (PACA, lectotype of *Odontia rosea* Rick). VENEZUELA. ARAGUA: Rancho Grande Res. Station, Parque Nacional H. Pittier, 22 Feb 2000, *L. Ryvar den* 42280 (O).

Other specimens examined: *Etheirodu fimbriatum*. CZECHIA. Lázně Bohdaneč, Bohdanečský rybník

Nature Reserve, 210 m above sea level (a.s.l.), 26 Apr 2015, *L. Zibarová* (HR97926); Vraclav, 290 m a.s.l., 4 Mar 2016, *T. Tejklová et al.* (HR98811). SPAIN. CANARY ISLANDS: Tenerife, Monte de las Mercedes, 18 Jan 1974, *L. Ryvar den* 12402 (O). UK. BUCKINGHAMSHIRE: Great Missenden, 1 Jul 1925, *E.J.H. Corner* 429529 (E). *Irpex microdon*. BRAZIL. RIO GRANDE DO SUL: São Salvador, 18 Mar 1943, *J. Rick s.n.* (**holotype** PACA).

Remarks: Our morphological analyses showed that neotropical specimens primarily identified as *Etheirodu fimbriatum* (Pers.) Banker featured narrower and longer basidiospores when compared with European specimens characterized by ellipsoid basidiospores (3.5–4.0 × 2.0–2.5 µm). Our phylogenetic analyses (FIG. 1) confirmed that the neotropical specimens nest in the genus *Etheirodu* in a separate lineage from *E. fimbriatum*. This is the second species confirmed in the genus so far and differs only by basidiospores shape and size. Both species are similar

in gross morphology, with purplish basidiomes when fresh, strongly fimbriate margins, small irregular teeth, and hymenophore with a pulverulent aspect. However, *E. fimbriatum* is known only from Europe, and *E. purpureum* is known only from the Neotropics.

Searching among potential older names that could be used for our specimens, we examined the lectotype of *Odontia rosea* Rick and concluded that it is conspecific with *E. purpureum*. However, the name *O. rosea* Rick is an illegitimate homonym of *Odontia rosae* Bres. We also examined the type of *Irpex microdon* Rick (Rick 1959), considered a synonym of *S. ciliolatum* by Baltazar et al. (2016). *Irpex microdon* features loosely adnate, cream-colored basidiomes, fimbriate margins, small teeth, and a somewhat irregular hymenophore with a pulverulent aspect, thin-walled cystidia, and yellowish hyphae. *Steccherinum ciliolatum* differs from *I. microdon* in having subceraceous basidiomes that crack when dried and that are firmly attached to the substratum, a regular hydroid hymenophore with longer well-developed teeth, and thick-walled cystidia (Maas Geesteranus 1974). The micromorphological features of *Irpex microdon* relate it more to *Etheirodon*. However, it differs from *E. purpureum* by the cream-colored basidiomes and narrower basidiospores (very few could be observed). Since only one specimen of *Irpex microdon* is available and it is in a somewhat bad condition, more collections are needed to clarify its taxonomic status.

Metuloidea reniformis (Berk. & M.A. Curtis) Westphalen & Motato-Vásq., comb. nov. **FIG. 2C**
MycoBank MB836505

Basionym: *Hydnum reniforme* Berk. & M.A. Curtis, J Linn Soc Bot 10:325. 1868.

≡ *Steccherinum reniforme* (Berk. & M.A. Curtis) Banker, Mem Torrey Bot Club 12:127. 1906.

≡ *Mycoleptodon reniformis* (Berk. & M.A. Curtis) Pat., Essai Tax Hyménomyc (Lons-le-Saunier):117. 1900.

≡ *Irpex reniformis* (Berk. & M.A. Curtis) Saaren. & Kotir., Polish Bot J 47:106. 2002

Description and illustrations: Maas Geesteranus (1974) and Campos-Santana and Loguercio-Leite (2010).

Ecology and distribution: Basidiomes annual, causing a white rot in fallen logs of angiosperms. Widespread in the Neotropics. Collected from Feb to Oct, probably year-round.

Specimens examined: BRAZIL. RIO GRANDE DO SUL: Nova Roma, Ponte Velha, 5 Apr 2017, *M.C. Westphalen* 523/17 (SP); Caxias do Sul, Gruta da 3a Léguas, 6 Apr 2017, *M.C. Westphalen* 532/17 (SP); São Francisco de Paula, Hotel Parador Hampel, 19 Jun 2017,

M.C. Westphalen 569/17 (SP); Maquiné, Fundação Estadual de Pesquisa Agropecuária, 27 Jun 2017, *M.C. Westphalen* 583/17 (SP); São Francisco de Paula, FLONA, 8 Jul 2017, *M.C. Westphalen* 585/17 (SP); Sarandi, P.E. Papagaio Charão, 8 Oct 2017, *M.C. Westphalen* 619/17 (SP); SÃO PAULO: Cananea, Ilha do Cardoso, Trilha das Antas, 24 Mar 2015, *V. Motato-Vásquez* MV323 (SP); Peruíbe, Estação Ecológica Juréia-Itatins, 14 Feb 2017, *V. Motato-Vásquez* MV895 (SP); São Luís do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, 5 Jun 2017, *M.C. Westphalen* 550/17 (SP); Parque Estadual da Cantareira, 24 Apr 2017, *M.C. Westphalen* 542/17, 544/17, and 549/17 (SP). COSTA RICA. Alajuela, San Ramón, Jul-Sep 1894, *L.D. Gómez* 24292 (O). VENEZUELA. MIRANDA: Universidad Simon Bolivar, Sartenejas, 10 Apr 1995, *L. Ryvardeen* 37552 (O); Mt. Avila, above Caracas, 2 Feb 2006, *L. Ryvardeen* 46997 (O).

Remarks: *Metuloidea reniformis* was originally described in *Hydnum* (Berkeley and Curtis 1868) and later transferred to *Steccherinum* (Banker 1906), where it has been widely accepted. Maas Geesteranus (1974) compared *S. reniforme* with *S. rawakense* (Pers.) Banker, proposing morphological features to separate them, including characteristics of the pileus surface, context, and shape of cystidia. We examined several specimens with variable morphology, often with intermediary characteristics between the two species as recognized by Maas Geesteranus (1974). Molecular data obtained from the specimens examined showed that they are all conspecific with identical ITS sequences and nested in the genus *Metuloidea*. Since *Hydnum rawakense* was described from the Rawak Island (New Guinea) and *H. reniforme* from Cuba, we concluded that all specimens studied with a neotropical distribution correspond to *H. reniforme*. Although the name *H. rawakense* has priority over *H. reniforme*, we do not expect that these two geographically separated species should be conspecific. *Metuloidea reniformis* exhibits considerable morphological plasticity, especially macroscopic characteristics such as thickness basidiomes, presence of hairs in the pilear surface, and thickness of teeth. Studies of collections from the South Pacific are needed to verify the phylogenetic position, distribution, and morphology of *H. rawakense*, mainly to resolve whether this species should be also transferred to *Metuloidea*.

Metuloidea reniformis is characterized by the sessile and thin basidiomes (up to 3 mm) with hydroid hymenophore, small, short-cylindrical basidiospores (3.5–4.0 × 1.5–2.0 µm), ventricose to clavate, thick-walled cystidia, often apically encrusted and thin-walled, clavate septocystidia, and a di-trimitic hyphal system with

yellowish, branched skeletal hyphae. Whereas some of the specimens collected have very small basidiomes, up to 2–2.5 cm wide, others reach 6–7 cm across. Most of the collections studied presented a markedly zonate pileus surface, in shades of brown, but some azonate ones were also seen. In addition, the fresh basidiomes, as well as the cultures we obtained, present a very sweet and pleasant, coumarin-like smell, which was also registered for most species of *Metuloidea*. In our phylogenetic analyses, *M. reniformis* was recovered as sister to *M. cinnamomea*, the only other neotropical species in the genus, and *M. murashkinskyi*, another hydroid

species in the genus but with an east Asian distribution. Morphologically, *M. reniformis* and *M. murashkinskyi* are very similar, but the latter differs by the somewhat thicker basidiomes and clavate cystidia similar to those of *Steccherinum* s. str.

Steccherinum larssonii Westphalen & Motato-Vásq., sp. nov. **FIGS. 2D, 5**

MycoBank MB836506

Typification: BRAZIL. SÃO PAULO: Santo André, Rebio do Alto da Serra de Paranapiacaba, 25 Aug 2017, M.C. Westphalen 593/17 (**holotype** SP).

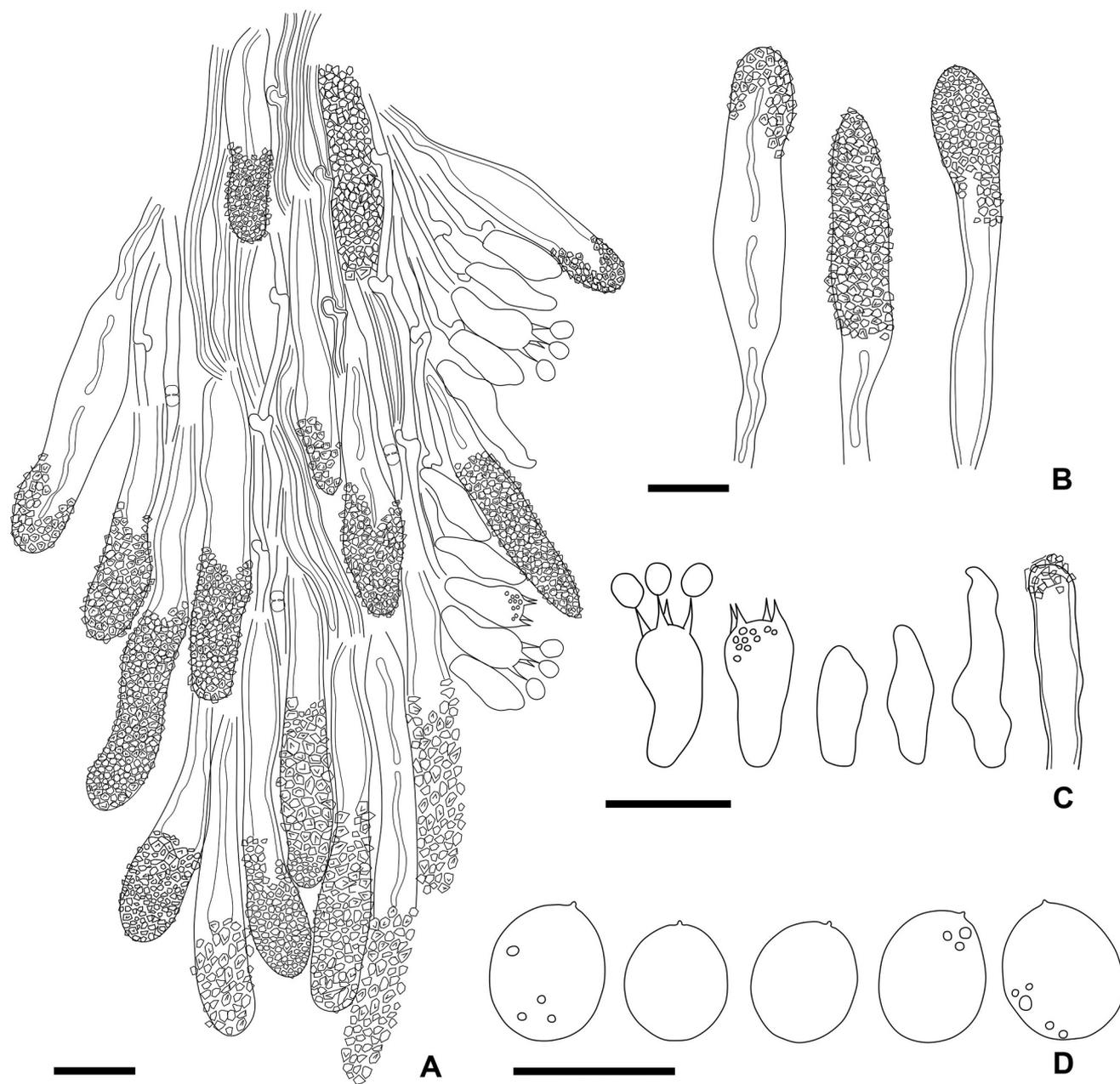


Figure 5. *Steccherinum larssonii* (holotype MCW 593/17). A. Microscopic section of the basidioma. B. Cystidia. C. Basidia, basidioles, and cystidioles. D. Basidiospores. Bars: A, B, C = 10 µm; D = 5 µm. Drawings by Viviana Motato-Vásquez.

Etymology: *larssonii*, named in honor of the Swedish mycologist Karl-Henrik Larsson.

Diagnosis: Characterized by the cream to salmon basidiomes, resupinate or with lifted margins, small teeth, broadly ellipsoid basidiospores, dimitic hyphal system, and encrusted skeletocystidia. It can be separated from other species in the genus by the combination of the basidiomes aspect and tooth and spore size.

Description: Basidiomes resupinate to effused-reflexed, easily detached from the substratum, somewhat papery and flexible when fresh, becoming corky when dried; pilei when present forming at the margins, very small, up to 7 mm wide; pilear surface pale brown to straw-colored, faintly zonate and somewhat sulcate; sterile margins entire, very thin to absent, up to 0.5 mm wide, on resupinate parts sometimes slightly fimbriate and up to 1 mm wide. Hymenophore hydroid, cream to pale pinkish-orange, teeth up to 0.75 mm long and 0.2 mm wide, with obtuse to acute apices, 4–6 per mm. Subiculum cream to white, homogeneous, up to 0.25 mm thick.

Hyphal system dimitic. Generative hyphae clamped, hyaline, thin- to slightly thick-walled, 2–4 μm wide, unbranched to moderately branched, CB+. Skeletal hyphae thick-walled to almost solid, hyaline in the trama and subiculum, slightly yellowish in the pileus surface, tortuous and mostly unbranched, 2.5–5 μm wide, CB+. Clavate cystidia of two types: (i) thin-walled to slightly thick-walled, present at the dissepiments, smooth or with a crown of crystals, 4–6.5 μm wide; and (ii) skeletocystidia originating in the trama, projecting into the hymenium and beyond it, heavily encrusted, up to 10 μm wide. Cystidioles 12–19 \times 4–5 μm , present in the hymenium, fusoid. Basidia 13–17 \times 3.5–5 μm , clavate, with four sterigmata. Basidiospores 3.5–4.0(–4.5) \times 3.0–3.5 μm , subglobose to obovoid, hyaline, thin-walled, smooth, CB+.

Ecology and distribution: Causing a white rot on fallen logs of unidentified angiosperms. Known from Brazil, Costa Rica, and Mexico. Collected from Feb to Nov, probably year-round.

Specimens examined: BRAZIL. SÃO PAULO: Santo André, Rebio do Alto da Serra de Paranapiacaba, 25 Aug 2017, *M.C. Westphalen* 594/17 (SP); *ibid.*, 17 Nov 2017, *M.C. Westphalen* 621/17 (SP); São Paulo, Parque Estadual das Fontes do Ipiranga, 18 Feb 2019, *M.C. Westphalen* 676/19 (SP). COSTA RICA. Puntarenas, Monte Verde, Reserva Bosque Nuboso de Santa Elena, 13 Jul 2001, *K.H. Larsson* 11326 (O); San José, Reserva Los Santos, Cerro de la Muerte, San Gerardo de Dota, 18 Jul 2001, *K.H. Larsson* 11622 (O). MEXICO. VERACRUZ: Veracruz, Cofre de Perrote,

Mpio. Xico, Los Gallos, 18 Sep 1985, *L. Ryvardeen* 23000 and 23024 (O).

Other specimens examined: *Steccherinum bourdotii*. CZECHIA. Brno, Štýřice, bank of the Svatka River, 175 m a.s.l., 28 Sep 2019, *M. Tomšovský* MT 10/19 (BRNM); Prague, Hvězda Game Park, 330 m a.s.l., 26 Apr 2016, *T. Tejklová & L. Zibarová* (HR99893); Prague, Divoká Šárka Nature Reserve, 265 m a.s.l., 22 Nov 2016, *T. Tejklová* and *L. Zibarová* (HR102002). *Steccherinum perparvulum*. BRAZIL. SÃO PAULO: Campinas, Moji-Guaçu, Fazenda Campininha, 29–30 Jan 1987, *D. Pegler, K. Hjortstam & L. Ryvardeen* 24589 (**holotype** O).

Remarks: *Steccherinum larssonii* is characterized by the resupinate to effused-reflexed basidiomes forming very small, brownish to straw-colored pilei on the margins. Microscopically, it features subglobose to ovoid basidiospores and abundant cystidia. Phylogenetically, it forms a sister species with *S. bourdotii* described from France (Saliba and David 1988), which differs by the larger, well-developed pilei, longer teeth (up to 2–2.5 mm long), and larger basidiospores (4.0–5.0 \times (3.0–)3.5–4.0 μm). We examined other species described under *Steccherinum* from Brazil, such as *S. perparvulum* Hjortstam & Ryvardeen, but this species is characterized by the slightly smaller teeth (130–500 μm long) and smaller basidiospores (2.5–3 \times 1.5–2.5 μm) (Hjortstam and Ryvardeen 2008). *Steccherinum subochraceum* Bononi & Hjortstam has very similar microscopic features to *S. larssonii* but differs by the much larger teeth (1.5–2 mm long) and resupinate basidiomes with effused margins (Hjortstam and Bononi 1986).

KEY TO GENERA WITH HYDNOID-LIKE SPECIES IN THE RESIDUAL POLYPOROID CLADE

1. Basidiomes pileate, effused-reflexed to stipitate..... 2
- 1'. Basidiomes resupinate, adnate, or with lifted margins..... 6
2. Hyphal structure dimitic with a monomitic context and skeletal hyphae restricted to the trama...
..... *Mycorrhaphium*
- 2'. Hyphal structure dimitic to trimitic throughout the basidiomes..... 3
3. Hymenophore hydroid to odontoid, with regular teeth, thick-walled encrusted cystidia present... 4
- 3'. Hymenophore poroid to irpicoid when mature, cystidia thin-walled and smooth or absent..... 5
4. Basidiomes brownish, with a characteristic sweet and pleasant smell when fresh, skeletal hyphae yellowish to brownish and strongly branched.....
..... *Metuloidea*

- 4'. Basidiomes cream to salmon, without a characteristic sweet smell, skeletal hyphae hyaline and unbranched..... *Steccherinum*
5. Upper surface glabrous, context simple, basidiospores up to 4 µm long, cystidia absent.....
..... *Antrodiella*
- 5'. Upper surface tomentose, context duplex, often with a dark line below the tomentum, basidiospores longer than 4 µm, cystidia present.....
..... *Cerrena*
6. Basidiomes with strongly fimbriate to rhizomorphic margins, in shades of purple when fresh
..... *Etheirodon*
- 6'. Basidiomes with entire margins, not in shades of purple..... 7
7. Cystidia thick-walled and encrusted 8
- 7'. Cystidia thin-walled and smooth..... 9
8. Basidiomes whitish, fragile and brittle, cystidia wider in the middle portion with a narrower apex, hyphal structure monomitic.....
..... *Cabalodontia*
- 8'. Basidiomes cream to pinkish, corky to subceraceous, cystidia clavate, wider at the apex, hyphal structure dimitic..... *Steccherinum*
9. Basidiomes brittle and fragile, hyphae not agglutinated..... *Pseudolagarobasidium*
- 9'. Basidiomes denser, hyphae agglutinated in dried specimens..... *Radulodon*

DISCUSSION

This study presents important additions to the knowledge of the hydroid species of *Steccherinaceae*, with inclusion of new data on poorly known genera previously unregistered from the Neotropics. In our phylogenetic analyses, the species studied were recovered in four main clades, representing the following genera.

Cabalodontia

Type: Cabalodontia queletii (Bourdot & Galzin) M. Piątek, Polish Bot J 49:3. 2004.

This genus was originally described by Piątek (2004) including five species: *C. bresadolae* (Parmasto) Piątek, *C. cretacea* (Romell) Piątek, *C. livida* (Fr.) Piątek, *C. queletii*, and *C. subcretacea* (Litsch.) Piątek. Later, Miettinen et al. (2012) confirmed by phylogenetic evidence that only the type species, *C. queletii*, belongs to *Cabalodontia*, and that all other species nested in different genera. Our study expands *Cabalodontia* by including two other species: *C. albofibrillosa*, from Asia, and the new species *C. delicata*, from the Neotropics. All three known species in the genus are rather similar

morphologically and distinguished mostly by slight differences in the teeth and the basidiospore size and shape. *Cabalodontia* differs from *Steccherinum* by the more fragile and brittle basidiomes, usually whitish, and a monomitic hyphal structure. Furthermore, the cystidia in *Cabalodontia* are mostly thinner at the apices and wider at the middle portion (somewhat resembling metuloid cystidia), whereas in *Steccherinum* they are always clavate.

In our phylogenetic analyses, sequences available on GenBank identified as *Steccherinum oreophilum* (from Alaska and Finland) nested in *Cabalodontia*. *Steccherinum oreophilum* was originally described from Arizona (Lindsey and Gilbertson 1977). The original description suggests that this species differs from others in *Cabalodontia* by the dimitic hyphal system and the pileate basidiomes (effused-reflexed to sessile). However, a morphological review of the type specimen showed that basidiomes of this species consist of very small and fragile pilei, forming small protuberances concurring on the substratum, somewhat similar to other species in *Cabalodontia*. In addition, transitory hyphae are shown in the drawings of the original description, very similar to those present in *C. queletii*. The cystidia found on the type of *S. oreophilum* are also identical to the ones found in species of *Cabalodontia*, only differing in arising from the skeletal hyphae, whereas in *C. delicata* the cystidia arise from thickened generative hyphae with longer aseptate segments. For now, we choose not to propose the combination of *S. oreophilum* in *Cabalodontia*, since its phylogenetic placement has not been widely explored. Further studies should include sequences from the type locality and a broad morphological review of specimens from different regions to verify the geographic distribution of *S. oreophilum*.

Cabalodontia is morphologically and phylogenetically related to *Junghuhnia*, but the relationship between the two genera is still unclear. *Junghuhnia crustacea* (Jungh.) Ryvar den, the only species currently confirmed in the genus, differs from *Cabalodontia* by the poroid hymenophore, dimitic hyphal structure, and clavate cystidia. In our phylogenetic analyses, two other species, *Steccherinum robustius* and *S. laeticolor*, appeared as the sister clade to *J. crustacea*. Both species are hydroid, with basidiomes in shades of salmon and orange, easily detachable from the substratum, and with a dimitic hyphal system, features more in common with *Steccherinum* s. str. Moreover, all *Cabalodontia* species are white to cream, do not detach from the substratum when dried, and are mostly monomitic. Although *Junghuhnia* has priority over

Cabalodontia, we believe that considering them as synonyms would create further confusion, as the genus would be too heterogeneous and its boundaries and relation with *Steccherinum* would be unclear. Therefore, with the data currently available, we choose to keep *Cabalodontia* as a separate genus from *Junghuhnia*, which can be more easily recognized in the field by its morphology.

Etheiroduon

Type: Etheiroduon fimbriatum (Pers.) Banker, Bull Torrey Bot Club 29:441. 1902.

Etheiroduon was originally described by Banker (1902) to include *Odontia fimbriata* Pers. The genus is characterized by resupinate basidiomes with fimbriate-rhizomorphic margins, presence of encrusted thin-walled cystidia, and a dimitic hyphal structure. Unlike *Steccherinum* and *Cabalodontia*, which are characterized by conspicuous and well-developed cystidia, in *Etheiroduon* the cystidia are thin- to only slightly thick-walled and can be interpreted as inflated hyphal ends covered with crystals. Many authors have identified *E. fimbriatum* in different parts of the world, usually including it in *Steccherinum* (Maas Geesteranus 1974; Lindsey and Gilbertson 1977; Dai 2011). However, Miettinen et al. (2012) showed that *E. fimbriatum* nests outside of *Steccherinum* s. str. and can be differentiated by the irregularly aculeate hymenophore and strongly fimbriate and rhizomorphic margins. This study confirms the occurrence of a new neotropical species in the genus described here as *E. purpureum*. Both species are very similar and can only be distinguished by basidiospore shape and size and geographic distribution.

A sequence used in this study and identified as *E. aff. fimbriatum* (FP102075) available in GenBank (KY948950) does not represent any of the two species currently included in *Etheiroduon*, suggesting an additional species in the genus. Since this sequence was obtained from material collected in the United States (Illinois), further studies, including morphological data of collections from the same locality, are necessary to solve the identity of this species.

Metuloidea

Type: Metuloidea tawa (G. Cunn.) G. Cunn., Bull New Z Dept Sci Indust Res 164:250. 1965.

Metuloidea is characterized mostly by brownish pileate basidiomes, the di-trimitic hyphal system with branched, yellowish skeletal hyphae, and a strong sweet smell in fresh specimens (also present in mycelium cultures). The genus resembles *Steccherinum* morphologically, whose species are generally resupinate to effused-reflexed, not brown-colored and lack the sweet smell reported in almost all

the species of *Metuloidea* (Miettinen and Ryvardeen 2016). The cystidia are highly variable in species of *Metuloidea*, ranging from clavate, similar to species in *Steccherinum* s. str. (*M. murashkinskyi*), to ventricose (in *M. reniformis*), whereas in *M. cinammomea* the cystidia are absent, presenting only encrusted hyphal ends in the pore mouths. *Metuloidea* is also a classic example of a genus that includes both poroid and hydroid species, which is common among the Steccherinaceae (Miettinen et al. 2016). It is possible that the genus includes other species that are morphologically related to *M. reniformis*, such as *S. rawakense* and *S. subrawakense* Murrill, but more morphological and molecular data are required to determine the phylogenetic position of this species. Four ITS sequences from the United State (Tennessee and Indiana) identified as *Metuloidea* sp. available on GenBank (MK564571, MK564605, MF686528, and MF686531) seem to be conspecific with *M. reniformis*, having about only four base changes. Further studies are needed to confirm whether these specimens present morphological differences from the neotropical collections; if not, we can conclude that *M. reniformis* has a wider distribution in America.

Steccherinum

Type: Steccherinum ochraceum (Pers.) Gray, A natural arrangement of British plants 1:651. 1821.

Steccherinum is a large genus with a worldwide distribution. Currently, it includes many hydroid and poroid species (Miettinen et al. 2012; Miettinen and Ryvardeen 2016; Westphalen et al. 2018). Morphologically, the genus is homogeneous, presenting a dimitic hyphal system, small basidiospores, and encrusted skeletocystida. The species usually can be differentiated by very few characters, such as pore or tooth size and shape, basidiome coloration, and basidiospore size. However, phylogenetically, many species can be recognized, some of these composing species complexes in the genus. For example, *S. ochraceum*, originally described from Europe, has been widely registered around the world and certainly constitutes a species complex. We examined several specimens identified as *S. ochraceum* from the Neotropics and found that none of these fit the concept of *S. ochraceum* s. str. All of the neotropical specimens represent several different species, possibly still undescribed, yet very similar to each other. More studies are being carried out to try to solve this and further extend the knowledge on neotropical species of *Steccherinum*.

In this study, we present a new neotropical species, described as *S. larssonii*. Microscopically, the basidiospores are almost identical to *S. subochraceum*, *S. bourdotii*, and

S. basibasidium Banker. However, these three species have much larger teeth, and the pilei are larger and more developed in *S. bourdotii* and *S. basibasidium*. By contrast, macroscopically, *S. larssonii* is almost identical to *S. perparvulum*, differing mostly in basidiospore size and shape. This shows that a careful morphological examination is necessary to separate species in the genus.

ACKNOWLEDGMENTS

The authors are grateful to the curators of BPI, E, HR, ICN, O, PACA, and SP herbaria for the loan of types and original collections. The authors especially thank Dr. Karl-Henrik Larsson (O) for the loan of several specimens of *Steccherinum*, which were an invaluable addition to this study, and their colleagues Mariana Drewinski, MSc, and Melissa Palacio, MSc, for the macrophotographs of the new taxa. The Instituto Florestal (Brazil) granted permission to work in protected areas. The authors would also like to thank the reviewers and the executive editor, Brandon Matheny, for their time and all the improvements suggested in the manuscript.

FUNDING

M.C.W. would like to thank FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo, Brazil; grant numbers 2016/10031-9 and 2017/50341-0) for funding. V.M.-V. received financial support from Coordenação de Aperfeiçoamento Pessoal de Nível Superior (CAPES/Brazil) and International Association for Plant Taxonomy (IAPT) and a Rufford Foundation Small Grant for Nature Conservation. M.T. was supported by the project “Phytophthora Research Centre” funded by the Czech Ministry for Education, Youth and Sports and the European Regional Development Fund, grant number CZ.02.1.01/0.0/0.0/15_003/0000453.

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