A review of *Hyphodiscaceae*

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Abstract: In a recently published classification scheme for *Leotiomycetes*, the new family *Hyphodiscaceae* was erected; unfortunately, this study was rife with phylogenetic misinterpretations and hampered by a poor understanding of this group of fungi. This manifested in the form of an undiagnostic familial description, an erroneous familial circumscription, and the redescription of the type species of an included genus as a new species in a different genus. The present work corrects these errors by incorporating new molecular data from this group into phylogenetic analyses and examining the morphological features of the included taxa. An emended description of *Hyphodiscaceae* is provided, notes and descriptions of the included genera are supplied, and keys to genera and species in *Hyphodiscaceae* are supplied. *Microscypha cajaniensis* is combined in *Hyphodiscus*, and *Scolecolachnum nigricans* is a taxonomic synonym of *Fuscolachnum pteridis*. Future work in this family should focus on increasing phylogenetic sampling outside of Eurasia and better characterising described species to help resolve outstanding issues.

Key words: *Helotiales*, keys, *Leotiomycetes*, multi-gene phylogeny, new taxa, systematics, taxonomy.

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INTRODUCTION

Until the end of the 20th century, sparse molecular data in *Leotiomycetes* hampered attempts to elucidate evolutionary relationships among families and genera in the class. Consequently, the higher classification was comparatively stable but mostly influenced by morphological features. Families and orders in the class were generally broadly conceived and encompassed many genera. Twenty-four years ago, when the class was first recognised, it had four orders and 13 families (Eriksson & Winka 1998), and over the following decade six families were added (Lumbsch & Huhndorf 2010). Six years later, Baral (2016) modified the old concept of the class by resurrecting or erecting new families and proposing several phylogenetically supported clades as informal lineages. In his treatment, 10 orders and 42 families were included in *Leotiomycetes* based on available phylogenetic and morphological data. The additional orders were mainly due to the inclusion of small orders previously listed under *Pezizomycotina incertae sedis*. The modern classification of fungi is mostly based on molecular phylogeny. This has led to continuous changes and increased the number of recognized families in the past two decades (Cannon *et al.* 2018). Various molecular phylogenetic studies of *Leotiomycetes* have been published, the first such study by Wang *et al.* (2006), with Johnston *et al.* (2019) and Ekanayaka *et al.* (2019) being the most recent and comprehensive. Some authors have been conservative, avoiding disruptive changes in the higher classification of the class based on sequences alone, and have therefore only given informal names to some "clades" or "lineages" (*e.g.*, Wang *et al.* 2006, Han *et al.* 2014). More recently workers have circumscribed existing families or added new ones without making substantial changes to Baral's (2016) classification (Pärtel *et al.* 2017, Somrithipol *et al.* 2017, Johnston *et al.* 2019, Quijada *et al.* 2020, Johnston & Baschien 2020). On the other hand, Ekanayaka *et al.* (2019) made significant changes in the classification based solely on molecular data. In this new classification, nine new families were proposed for lineages that were detected mostly by other authors (Han *et al.* 2014, Baral 2016). Ekanayaka *et al.* also introduced a highly disruptive reassignment of families to orders and genera to families. These reassignments disagree with previous and subsequent classifications (Baral 2016, Johnston *et al.* 2019, Karakehian *et al.* 2019). Finally, it is important to point out that several new families (*i.e.*, Crous *et al.* 2017: *Neocrinulaceae* and *Vandijckellaceae* and Crous *et al.* 2018: *Porodiplodiaceae*) and genera (*i.e.*, Bien *et al.* 2020: *Capturomyces*, *Vexillomyces*, *Ramoconidiophora*, *etc.*) have been published based solely on information from asexual morphs, neglecting possible sexual morph connections.

Establishment of *Hyphodiscaceae* as a new family

The first large phylogeny of helotialean fungi did not include any DNA sequences from the genus *Hyphodiscus* (Wang *et al.* 2006), but in the same year the relationship between apothecial

Hyphodiscus hymeniophilus and conidial *Catenulifera rhodogena* was established using ITS, LSU rDNA and β-tubulin in a phylogenetic study of mainly asexual taxa (Untereiner *et al.* 2006). An ITS and LSU phylogeny of the genus *Hyphodiscus*, including the type species, *H. theiodeus,* and additional species, was published five years later (Hosoya *et al.* 2011). The species Hosoya *et al.* (2011) included were used by Han *et al.* (2014) who added the *RPB2* gene to their analyses in a large-scale phylogeny of *Hyaloscyphaceae* in the broad sense. Their analyses showed that *Hyphodiscus* was in a supported clade with *Hyphopeziza* and *Venturiocistella*. They called this clade "number four" (Han Clade 4) and emphasised the morphological heterogeneity among the genera within. *Hyphopeziza* is distinguished by hairs with a glassy wall with rough protrusions and thin-walled excipular cells. *Hyphodiscus* was described as fungicolous or lignicolous and included species having a gelatinised (as 'gelatinous') ectal excipulum, short hairs with coarse warts, and small unicellular ascospores (Han *et al.* 2014). Further morphological variation of the clade arises in *Venturiocistella* with long, dark brown, thick-walled, partially smooth spiny hairs (setae), along with short, lighter brown, thin-walled, warted cylindrical hairs (Baral 1993). Soon after this analysis, *Hyphodiscus* was included in a large-scale phylogeny of helotialean fungi based on ITS and LSU (Baral *et al.* 2015). There the genus was treated in *Hyaloscyphaceae* in agreement with the concept of the family in Baral (2016), rather than following the very narrow concept of *Hyaloscyphaceae* proposed by Han *et al.* (2014) who included only *Hyaloscypha* in the family. *Hyphodiscus* was later included in the large-scale phylogenies of Ekanayaka *et al.* (2019) and Johnston *et al.* (2019). Both papers used the name "Han Clade 4" for those genera related to *Hyphodiscus.* Johnston *et al.* (2019) used a 15-gene phylogeny to provide insight into the higher classification of *Leotiomycetes*. The results of this work agreed with those shown by Han *et al.* (2014) and to a large degree with the classification of *Leotiomycetes* proposed by Baral (2016). Han Clade 4 is supported and comprised of four genera as already shown in Johnston *et al.* (2019): *Hyphodiscus*, *Hyphopeziza*, *Gamarada* (known from the asexual morph only), and *Venturiocistella*. In the classification proposed by Ekanayaka *et al.* (2019), Han Clade 4 was taken up as a new family, *Hyphodiscaceae*, which included four further genera: *Fuscolachnum, Hyalopeziza, Scolecolachnum*, and *Soosiella* (known only from sterile mycelium). For the genus *Fuscolachnum* (type species *F. pteridis*) only *F. misellum* was included in their phylogenetic analyses. Without evidence of a close relationship between *F. misellum* and the type species, this placement seems premature. In their analyses they included three species of *Hyalopeziza*: *H. pygmaea*, *H. leuconica*, and *H. nectrioidea*. Unfortunately, they did not realize that Han *et al.* (2014) transferred *Hyalopeziza pygmaea* to their new genus *Hyphopeziza*, with *H. pygmaea* as the type species. Additionally, the other two species used in their analyses (*H. leuconica*, *H. nectrioidea*) are not related to *Hyphodiscaceae* (Ekanayaka *et al.* 2019, fig. 5). Thus, Ekanayaka *et al.* erroneously included *Hyalopeziza* in the *Hyphodiscaceae*. *Scolecolachnum*, erected by Guatimosim *et al.* (2016) for *S. pteridii*, (which in their ITS analysis formed a supported clade with *Hyphodiscus*, including the type species *H. theiodeus*) did have the type species included in Ekanayaka *et al.*'s (2019) analysis. They also described a new species in the genus *Scolecolachnum*, *S. nigricans*. The genus *Soosiella* in Johnston *et al.* (2019) falls in an unsupported clade with *Catenulifera luxurians*, *Hyphodiscus*, *Hyphopeziza*, *Gamarada*, and *Leptodontidium*, though only in their ITS phylogeny (only rDNA data were available) (additional file 6, fig. s2, Johnston *et al.* 2019). This relationship is roughly recapitulated in the Ekanayaka *et al.* (2019) analysis, though *Catenulifera* and *Gamarada* were excluded, and *Leptodontidium* was recovered in an isolated family *incertae sedis* in *Leotiomycetes*. To sum up, Ekanayaka *et al.* (2019) expanded the concept of Han Clade 4 (= family *Hyphodiscaceae*), agreeing partially with Johnston *et al.* (2019), to include the six genera *Fuscolachnum*, "*Hyalopeziza*", *Hyphodiscus*, *Soosiella*, *Scolecolachnum*, and *Venturiocistella*, with *Gamarada* not being included in their analyses.

Aim of this revision

In seeking to fill knowledge gaps, but also out of a competitive desire to erect new classes, orders and families or to reorganise the taxa included in these ranks, some workers have used only molecular data when reaching conclusions. This is despite the estimate that we know fewer than 10 % of the species diversity in *Leotiomycetes*, and have molecular data from only a small percentage of those taxa we know (excluding taxa known only from molecular data). A high number of genera have been shown to be polyphyletic and for many genera sequence data is lacking for the type species. Complicating the situation further, there are many misidentified DNA sequences in data repositories (Quijada 2018). Published sequence data is available for only *ca.* 30 % of the recognised genera in *Leotiomycetes*, and usually only a combination of the three standard rDNA loci exist (SSU, ITS or LSU) (Quijada 2018, Johnston *et al.* 2019). Changes in higher classification based solely on molecular data are strongly influenced by taxon sampling, the availability of sequences from type species, the gene regions chosen, the number and type of genes included (protein coding genes *vs* rDNA), and personal experience studying specimens and opinions about the boundaries of families and orders (Quijada 2018, Ekanayaka *et al.* 2019, Johnston *et al.* 2019). As an example, the latter two classification systems for *Leotiomycetes* based on phylogenetic data disagree in the number of families and orders and the organisation of the included taxa (Ekanayaka *et al.* 2019, Johnston *et al.* 2019). The aim of the present work is to provide background and a discussion of the different points of view regarding the family *Hyphodiscaceae sensu* Ekanayaka *et al.* (2019). Our goal is to reconcile current classifications and to present possible solutions for consideration in formulating future classification of *Leotiomycetes*.

MATERIAL AND METHODS

A bibliographic review was done by using Harvard University's online library catalog (HOLLIS), Web of Knowledge, GBIF, and Google Scholar. The information gathered was used to make a dataset that includes information about sexual and asexual morphs (morphology, biometry), ecology, and distribution. The dataset, as well as all the references reviewed, were used to emend the current concept of *Hyphodiscaceae*, discuss current problems in delimitation of species and genera (notes are provided for each genus), and to provide keys to identify genera and species. Macro- and micrographs, as well as drawings made by the authors, are used to illustrate the morphological variation inside each genus.

Fresh or dried material preserved at the fungaria FH, LE, S, TAAM, TUF, TUR, and TFC were used in this study, as were specimens from private collections, Stip Helleman (indicated with the prefixes and SBRH), Elisabeth Stöckli (indicated with the prefix ES), and Enrique Rubio (indicated with the prefix ERD). Hand sections and squash mounts were prepared to study

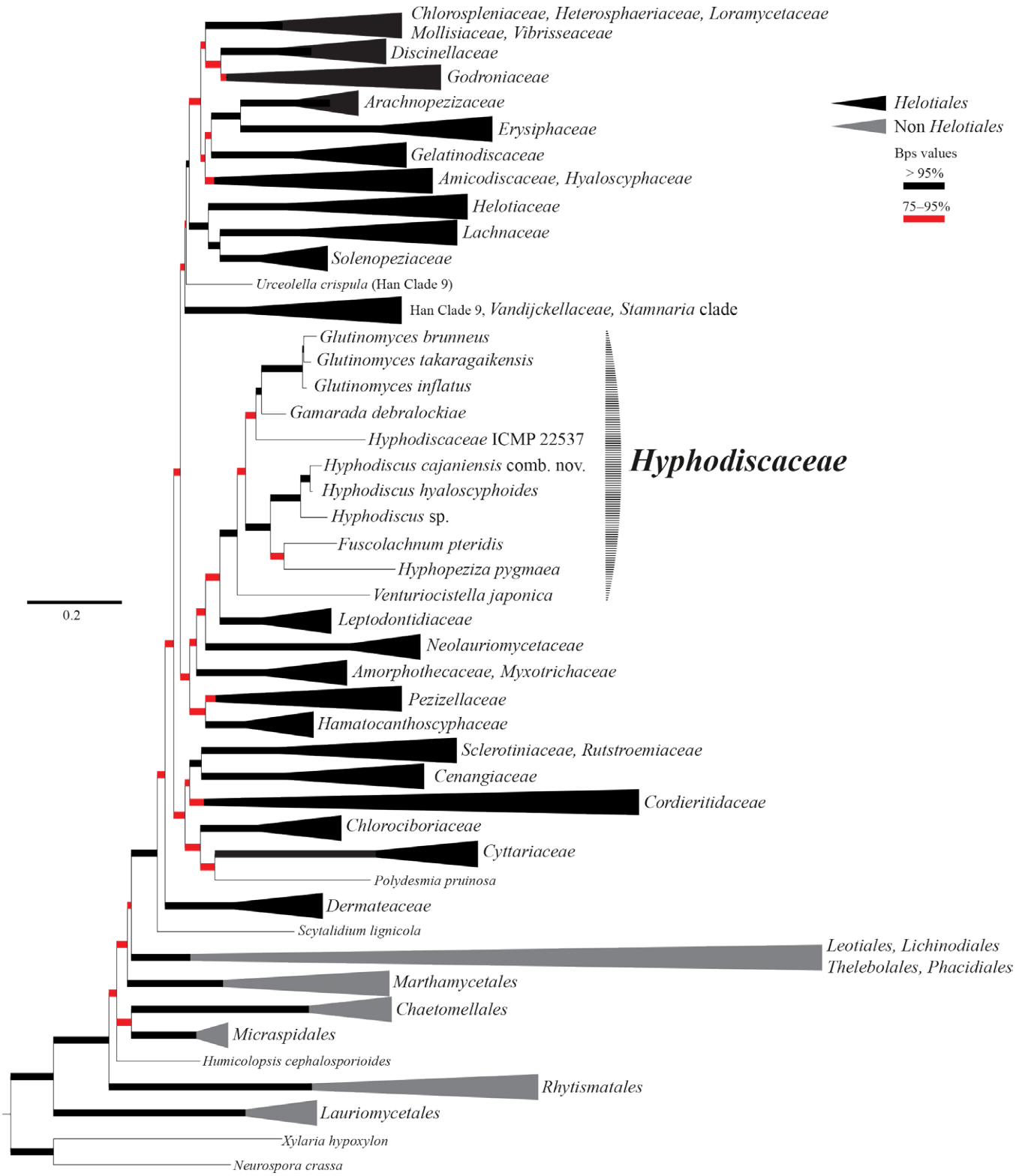

Fig. 1. Maximum-likelihood (ML) tree based on concatenated DNA (15-gene dataset) sequences for *Hyphodiscaceae*, plus the taxa treated by Johnston *et al.* (2019) and more recently acquired sequences. Source of DNA sequence data, concatenated alignments, partitions, models and informative sites are available at https://doi.org/10.7931/b1m9-kk21. The collapsed clades represent family-level or order-level taxa accepted in *Leotiomycetes*. Thick branches have bootstrap support (Bps) values >95 % in black and branches with bootstrap support values >75 % are in red.

micromorphological characters. Dried collections were rehydrated in 5–10 % potassium hydroxide (KOH). Samples were first studied in tap water, but other mounting media used include Melzer's reagent (MLZ) and IKI solution (LUG) (both used to check the amyloid reaction of hymenial structures), as well as Cotton blue (CB) and Congo red (CR) to stain cells walls. The formulas for reagents follow Huhtinen (1990). Sections for anatomical examination of ascomata were examined using an Olympus BX53 with bright field optics, Zeiss Axio Imager A1, Zeiss standard RA, or Motic B1 light microscope. The images of microstructures were captured with microscopes equipped with cameras (AxioCam MRc 5 digital camera, Nikon Coolpix 4500, USB Moticam 2500) or following Kosonen *et al.* (2020). All the measurements included in this review (descriptions, keys) are based on data from the literature or on data

Table 1. GenBank accession numbers for genera and species of *Hyphodiscaceae* used for the phylogenetic analyses with two concatenated loci (Fig. 2). Sequences in bold are new.

Species	Isolate/herbarium number	ITS	LSU
Fuscolachnum inopinatum	**SBRH855**	**OL752697**	**OM203548**
Fuscolachnum misellum	SBRH799b	KX501124	KX501129
Fuscolachnum misellum	**SBRH943**	**OM203545**	**OM203549**
Fuscolachnum pteridis	**SBRH831**	**OM203547**	**n/a**
Fuscolachnum pteridis	**TUR215412**	**OM818501**	**OM818501**
Fuscolachnum* aff. *misellum	**SBRH927**	**OM203544**	**OM203550**
Fuscolachnum* aff. *misellum	**LE 305267**	**OM407389**	**n/a**
Gamarada debralockiae	T6G9	NXFV00000000	NXFV00000000
Glutinomyces brunneus	ta2uD7	LC218306	LC315171
Glutinomyces inflatus	TNS-F-80763	LC218289	LC315170
Glutinomyces takaragaikensis	TNS-F-80765	LC218290	LC315176
Glutinomyces vulgaris	TNS-F-80764	LC218288	LC315172
Hyphodiscus brachyconius	CBS 630.75	MH860958	MH872727
Hyphodiscus cajaniensis	M155	EU940189	EU940112
Hyphodiscus hyaloscyphoides	TNS-F-13588	AB546944	AB546945
Hyphodiscus hymeniophilus	**TAAM174997**	**ON241771**	**n/a**
Hyphodiscus hymeniophilus	**TUF117323**	**ON241772**	**n/a**
Hyphodiscus hymeniophilus	**TUF104970**	**ON241773**	**n/a**
Hyphodiscus hymeniophilus	TNS-F-31801	AB546948	AB546946
Hyphodiscus* cf. *hymeniophilus	**LE 305399**	**OM407386**	**n/a**
Hyphodiscus luxurians	**LE 304401**	**OM407387**	**n/a**
Hyphodiscus luxurians	**30BG69**	**OP585913**	**n/a**
Hyphodiscus otanii	TNS-F-7099	AB546949	AB546947
Hyphodiscus theiodeus	TNS-F-31803	AB546953	AB546952
Hyphodiscus ucrainicus	PZ124	MH134512	MH134511
Hyphopeziza pygmaea	KUS-F51564	JN033410	JN086713
Hyphopeziza pygmaea	TNS-F-17940	JN033448	JN086748
Microscypha arenula	**SBRH922**	**OM203546**	**n/a**
Scolecolachnum nigricans	MFLU 18-1817	MK584975	MK591973
Scolecolachnum pteridii	CPC 24666	KU597797	KU597764
Soosiella minima	MH_2012_1230	JX124327	JX124327
Venturiocistella japonica	TNS-F-18030	JN033447	AB546954
Venturiocistella sp.	KUS-F52028	JN033391	JN086694

modified according to the authors' personal observations. Because predominantly dead elements are described in the literature, we have tried for reasons of compatibility to avoid measurements of living elements in the keys. Therefore, using the keys necessitates mounting fresh specimens in reagents such as KOH or MLZ before taking measurements. The descriptions and abbreviations follow Baral (1992): † = dead state, * = living state. For studying the asexual morph of *Hyphodiscus hymeniophilus* the culture on malt extract agar (MEA) was used (Fig. 4 A1–5), deposited in the Tartu Fungal Culture Collection. The microstructures were mounted in tap water. The material was studied and photographed with Nikon 80i and Leica M205A microscopes.

The extant sequences and previously published multilocus phylogenies by Ekanayaka *et al.* (2019) and Johnston *et al.* (2019) were used as a basis for incorporating the new sequences and to evaluate the boundaries of *Hyphodiscaceae* (see Table 1 and Manaaki Whenua – Landcare Research Datastore https://doi.org/10.7931/b1m9-kk21, source of DNA sequences.xls). The molecular methods used to generate the new sequences varied depending on the origin of the collections. Total genomic DNA for the specimens from LE was extracted using the NucleoSpin® Plant II DNA Isolation Kit (Macherey-Nagel GmbH & Co. KG, Germany) following the manufacturers' protocols. The nuclear ribosomal internal transcribed spacer region (ITS1–5.8S–ITS2) was amplified and sequenced using primers ITS1F and ITS4 as described by White *et al.* (1990) and Larena *et al.* (1999). PCR products were purified with the Fermentas Genomic DNA Purification Kit (Thermo Scientific, Thermo Fisher Scientific Inc., MA, USA) according to the manufacturer's instructions. Purified PCR products were sequenced on an ABI model 3130 Genetic Analyzer (Applied Biosystems, CA, USA). For the collections deposited in S, DNA was obtained from fresh collections cultured on MEA plates in order to ensure ample living material for DNA extraction as described in Kosonen *et al.* (2020). DNA was isolated from fresh mycelium scraped from the agar

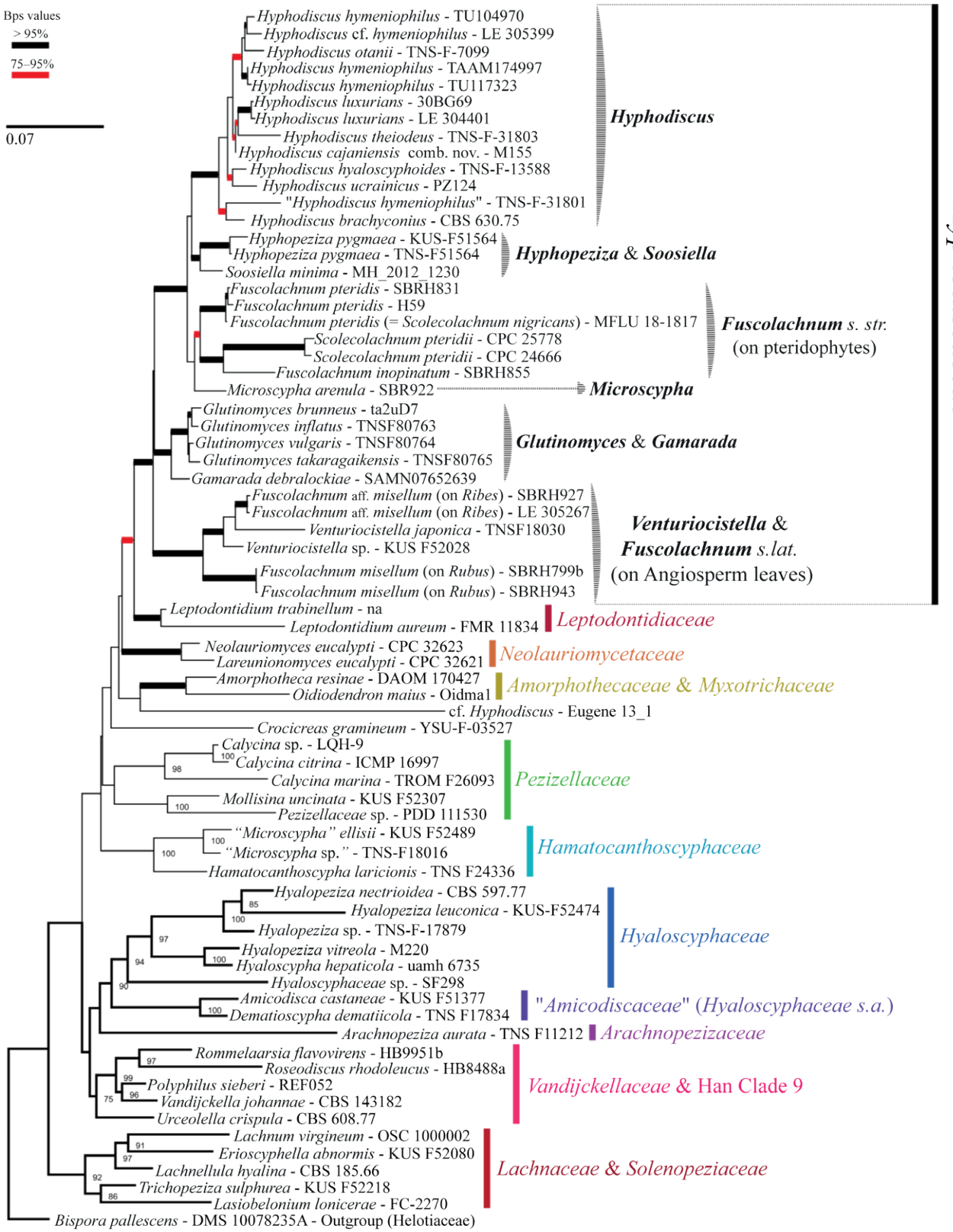

Fig. 2. Maximum-likelihood (ML) tree based on concatenated ITS+LSU sequences for *Hyphodiscaceae* and related families treated by Johnston *et al.* (2019) and Ekanayaka *et al.* (2019). *Lachnaceae*, *Solenopeziaceae* and *Bispora pallescens* (*Helotiaceae*) are used as outgroups. Collection information for sequenced specimens of *Hyphodiscaceae* is found in Table 1. Sequences and collection information of the other taxa treated are provided in Manaaki Whenua - Landcare Research Datastore, https://doi.org/10.7931/b1m9-kk21, source of DNA sequences.xls, along with the concatenated alignment used for this analysis. Thick black branches have bootstrap support (Bps) values >95 %, whereas branches in red indicate Bps >75–95 %.

plates. Fresh mycelium was mixed with a tiny amount of sterilised sea sand in an Eppendorf tube and ground with a pestle. DNA was extracted using the DNeasy® Plant Mini Kit (Qiagen), following the standard protocol for fresh plant material. The PCR protocols used to acquire the respective gene regions follow Kosonen *et al.* (2020). Concerning specimens deposited at TAAM and TUF, DNA was extracted from dried specimens using a High Pure PCR Template Preparation Kit (Roche, Basel, Switzerland). The rDNA

ITS region was amplified using the primers ITSOF (5'–ACTTGGT-CATTTAGAGGAAGT–3') (Tedersoo *et al.* 2008) and ITS4 (White *et al.* 1990). PCR was performed using PuRe Taq Ready-To-Go PCR beads (Amersham Pharmacia Biotech, Piscataway, NJ) following Pärtel *et al.* (2017). Cycling conditions included initial denaturation at 95 °C for 15 min; followed by 35 cycles of denaturation at 95 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 1 min; and a final extension step at 72 °C for 10 min. Purification of PCR products was conducted using Exo-Sap enzymes (Sigma, St. Louis, MO). The sequencing was performed by Macrogen Europe. SBRH collections were sent to Alvalab (Spain) for sequencing. Total DNA was extracted from dry specimens employing a modified protocol based on Murray & Thompson (1980). Amplification reactions (Mullis & Faloona 1987) included 35 cycles with an annealing temperature of 54 ºC. The primers ITS1F and ITS4 (White *et al.* 1990, Gardes & Bruns 1993) were employed to amplify the ITS rDNA region, and LR0R and LR5 (Vilgalys & Hester 1990, Cubeta *et al.* 1991) were used for the 28S rDNA region. PCR products were checked in 1 % agarose gels, and amplicons were sequenced with one or both PCR primers. Sequences were corrected to remove reading errors in chromatograms.

Two phylogenetic analyses were carried out. The first was based on the 15 genes treated by Johnston *et al.* (2019) with an expanded selection of taxa within *Hyphodiscaceae* and sister families. These include sequences from *Glutinomyces* spp. (Nakamura *et al.* 2018), *Hyphodiscus cajaniensis* (Stenroos *et al.* 2010, as *Microscypha* sp. A), sequences from *Leptodontidiaceae* (Hernández-Restrepo *et al.* 2017), sequences from *Neolauriomycetaceae* (Crous *et al.* 2018), and newly generated sequences from *Fuscolachnum pteridis* (specimen TUR 215412, collected by M. Pennanen), see Fig. 1 and data in Manaaki Whenua Landcare Research Datastore, Manaaki Whenua – Landcare Research Datastore, https://doi.org/10.7931/b1m9-kk21, source of DNA sequences.xls. The expanded dataset was reanalysed using the same methods as Johnston *et al.* (2019). Briefly, genes were aligned using MAFFT v. 7.450 (Katoh & Standley 2013), a maximum likelihood (ML) analysis of the concatenated alignments was run using IQ-TREE v. 1.6.12 (Nguyen *et al.* 2015; Chernomor *et al.* 2016), using models selected by ModelFinder (Kalyaanamoorthy *et al.* 2017) for each partitioned gene, and ultrafast bootstrap (BS) analysis with 1 000 replicates estimated branch support in the ML tree (Hoang *et al.* 2018). *Xylaria hypoxylon* and *Neurospora crassa* were used as outgroups. The second analysis focused on taxa and specimens within *Hyphodiscaceae* and closely related family-level clades where *Lachnaceae*, *Solenopeziaceae* and *Bispora pallescens* (*Helotiaceae*) are used as outgroups, based on concatenated ITS and LSU sequences, using the same methods as the first analysis. See Table 1 and Manaaki Whenua Landcare Research Datastore, https://doi.org/10.7931/b1m9-kk21, source of DNA sequences.xls, for the sequences used. The concatenated alignments for both analyses and the partitions and models used, are provided in the Manaaki Whenua Landcare Research Datastore (https://doi.org/10.7931/b1m9-kk21).

RESULTS

Phylogenetic issues with *Hyphodiscaceae sensu* Ekanayaka *et al.* and new results

Ekanayaka *et al.*'s (2019) proposal of the new family *Hyphodiscaceae* includes the family name, an Index Fungorum registration number, type genus, description with a Faces of Fungi identifier, and notes but not the included genera, which can be found only in their table 1 on p. 322. Phylogenetic results including this family are shown in their figs 1 (*Leotiomycetes*, clade 14 on p. 318) and 5, but the limits of the family are not indicated in fig. 5 or mentioned in the caption. The two phylogenies differ in taxon sampling, resulting support, and topology. In their fig. 1 (5-locus tree based on of LSU, SSU, ITS, *TEF* and *RPB2*) the family is not supported (–/69 %), whereas in their fig. 5 (ML analysis of ITS+LSU) it has strong support (98 %). The circumscription of the family presented in table 1 includes the genera *Fuscolachnum*, *Hyalopeziza*, *Hyphodiscus*, *Scolecolachnum*, *Soosiella*, and *Venturiocistella*. However, *Hyalopeziza* spp. appear in two different unlabelled family-level clades (*Hyaloscyphaceae* and *Hyphodiscaceae*) in their fig. 5, with *H. leuconica* and *H. nectrioidea* in a clade with *Hyaloscypha* and *Olla* (both placed in table 1 in *Hyaloscyphaceae*), and *H. pygmaea* in *Hyphodiscaceae*; this polyphyly is acknowledged on page 451. In cases of generic polyphyly, the generic concept should follow the placement of the type species, in this case *Hyalopeziza patula* (Clements & Shear 1931). Since no molecular data are available for this species, the genus may best be considered *incertae sedis* in *Helotiales* (which we prefer) or left as placed by previous authors in *Hyaloscyphaceae*. The inclusion of *Hyalopeziza* instead in *Hyphodiscaceae* in table 1 without any comment justifying this choice is strange and possibly suggests that *H. pygmaea* was considered a typical species of *Hyalopeziza*. This view has not been shared by previous authors; in fact, *Hyalopeziza pygmaea* was previously transferred to the monotypic genus *Hyphopeziza* because it differs genetically and morphologically from species considered typical of *Hyalopeziza* (see Han *et al.* 2014: fig. 2 clade 5 and p. 161). This study was cited by Ekanayaka *et al.* (2019), who accept the genus *Hyphopeziza* and include it in *Hyaloscyphaceae* in table 1. The placement of these two genera therefore appears to have been reversed in error.

Another mistake can be noted for the genus *Microscypha*. Only one sample of a *Microscypha* sp. (TNS-F-18016) is included in the list of sequences used in Ekanayaka *et al.* (2019), with three genes (ITS: JN033444, LSU: JN086745, *RPB2*: JN086837) employed according to their supplementary data (p. 475). The genus is included in the family *Hamatocanthoscyphaceae* in their table 1, and in their figs 1 (clade 14) and 5 this *Microscypha* sp. is in a supported clade with *Gremmenia infestans* (*Hamatocanthoscyphaceae*). In fig. 5, however, isolates of another *Microscypha* sp. (*M. cajaniensis* M155 and M147) fall inside the *Hyphodiscus* clade in *Hyphodiscaceae*. It appears that the authors used sequences from three different samples of *Microscypha* but listed only one in the supplementary data and did not comment on the lack of monophyly of the genus. None of the specimens included were identified as the type species of *Microscypha*, *M. arenula* (= *M. grisella*); no molecular data from that species had at that time been published. In the absence of data from the type species, and without an explanation for choosing to rely on a specimen identified only to genus to fix the placement of the genus, a statement on the correct position of *Microscypha* was premature.

by Ekanayaka *et al.* (2019: table 1) also misplace the genus *Glutinomyces* in *Hyaloscyphaceae*. These authors did not include any of the available sequences from species of this genus in their phylogenetic analyses; it was likely overlooked that Nakamura *et al.* (2018) previously placed the genus in Han Clade 4 (= *Hyphodiscaceae*).

Finally, in their multigene phylogeny (Ekanayaka *et al.* 2019: fig. 1, clade 14), *Scolecolachnum nigricans* stands separate

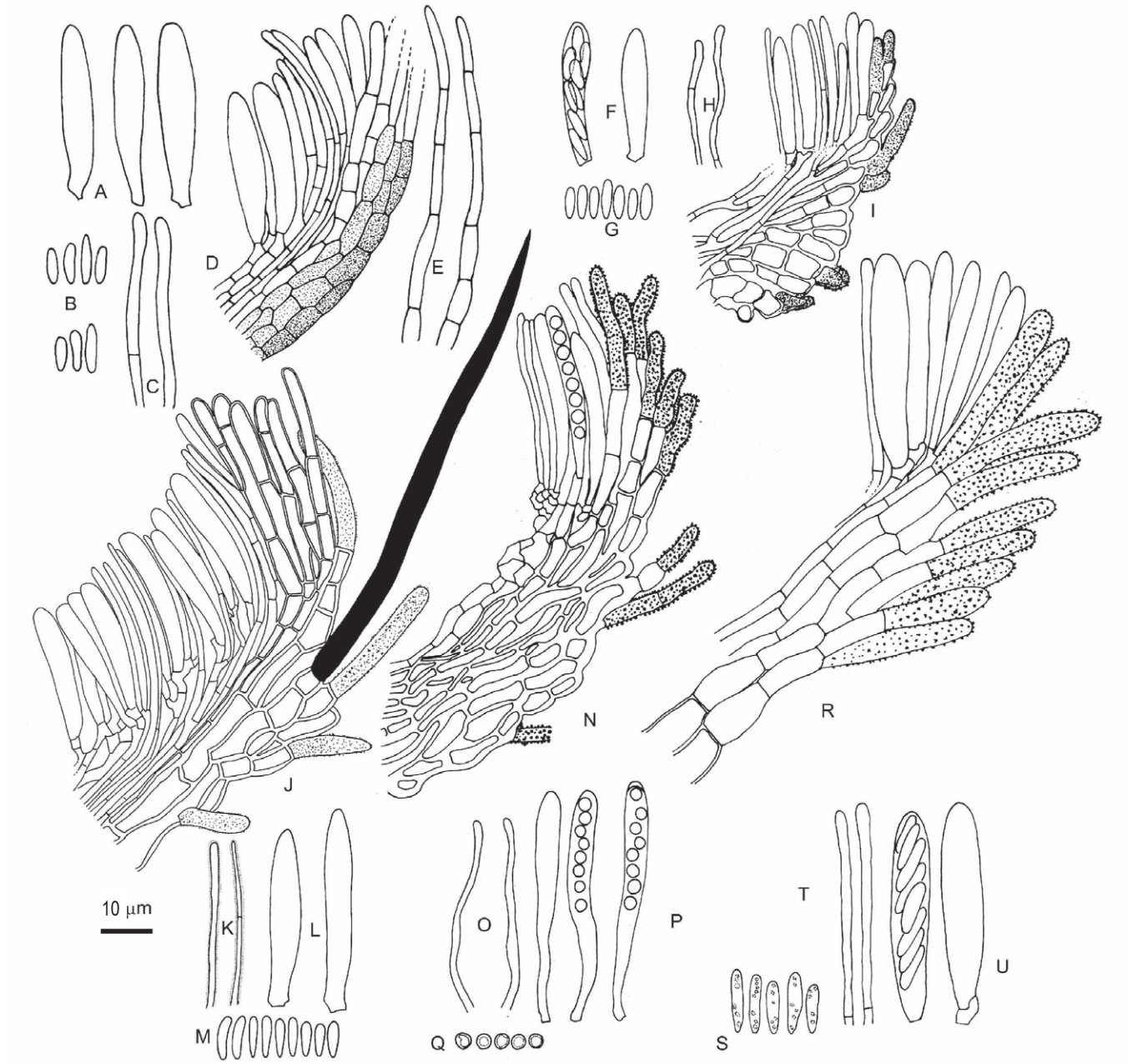

Fig. 3. Diagrammatic representation of the sexual morphs in *Hyphodiscaceae*: **A–E.** *Microscypha* (*M. arenula*, from Hosoya & Otani 1997a: fig. 9). **F–I.** *Hyphopeziza* (*H. pygmaea*, from Hosoya & Otani 1997b: fig. 4). **J–M.** *Venturiocistella* (*V. japonica*, from Hosoya & Harada 1999: fig. 2). **N–Q.** *Hyphodiscus* (*H. theiodeus*, from Hosoya 2002: fig. 8). **R–U.** *Fuscolachnum pteridis* (Hosoya, this publication). D, I, J, N & R. Transverse sections showing the margin and hairs morphology. A, F, L, P & U. Asci. B, G, M, Q & S. Ascospores. C, H, K, O & T. Paraphyses. **E.** Multiseptate hairs of *M. arenula.*

from *S. pteridii* which is in a supported clade with *Hyphodiscus hymeniophilus*. This agrees with Guatimosim *et al.*'s (2016) phylogenetic analyses which recovered the same relationship. The ITS+LSU analysis (Ekanayaka *et al.* 2019: fig. 5) yielded a different result, with *S. nigricans* and *S. pteridii* clustered in an unsupported clade sister to *Hyphodiscus*. This latter result was probably the reason why the authors placed *S. nigricans* in *Scolecolachnum*. The ITS sequences of *S. pteridii* and *S. nigricans* are only 91.73 % similar and the LSU sequences only 94.28 % similar, suggesting that *S. nigricans* was possibly erected in the wrong genus. The low genetic similarity mirrors the morphological differences between the two species, suggesting that placement of *S. nigricans* in *Scolecolachnum* is questionable.

In our new *Leotiomycetes*-wide multi-gene analysis (Fig. 1), we expanded the taxon coverage from Johnston *et al.* (2019), confirming a sister relationship between *Hyphodiscaceae* and *Leptodontidiaceae*, a relationship suggested in the ITS analysis from Johnston *et al.* (2019). *Neolauriomycetaceae* was sister to these two families, with all these relationships relatively poorly supported in the analysis presented here. The broader clade containing *Hyphodiscaceae* (Han Clade 4 in Johnston *et al.* 2019), *Amorphothecaceae*/*Myxotrichaceae*, and *Pezizellaceae* (included both *Pezizellaceae* and *Hamatocanthoscyphaceae* in Johnston *et al.* 2019), was again resolved.

Furthermore, our new analysis (Fig. 2) based on concatenated ITS and LSU sequences resolved a set of family-level clades that were generally consistent with the Fig. 1 analysis. Within *Hyphodiscaceae*, genus-level clades were mostly well resolved. Exceptions include *Fuscolachnum* where specimens placed in this genus fall into two clades, one also containing specimens identified as *Scolecolachnum*, the other also containing specimens identified as *Venturiocistella*. *Hyphodiscus* species are not consistently

resolved, with specimens identified as *H. hymeniophilus* especially spread across the genus-level clade. A specimen identified as the type species of *Microscypha*, *M. arenula*, clearly belongs in *Hyphodiscaceae*. Taxonomic thresholds predicted for the genus level were estimated at 94.3 and 98.2 % for ITS and LSU, respectively (Vu *et al.* 2019), therefore *Fuscolachnum pteridis* and *Scolecolachnum nigricans* appear to be conspecific and thus synonymous, with identities of 99.3 % for ITS and 99.2 % for LSU.

Current concept of *Hyphodiscaceae* and its emendation

Table 2 in Ekanayaka *et al.* (2019) lists morphological features of apothecia, excipula, paraphyses, asci, and ascospores for each family of *Leotiomycetes.* This listing closely corresponds to the new families described in the text. For the family *Hyphodiscaceae*, the table and text regarding sexual morphs on pp. 332 and 345 reads "Ascomata apothecial, cupulate or discoid, sessile or short stalked, sometimes gelatinised. Margins covered with hairs. Hairs white or brownish, cylindrical, granulate, sometimes septate. Ectal excipulum of *textura angularis*, *intricata* or *prismatica*. Medullary excipulum of *textura intricata* to *angularis*. Paraphyses hyaline, filiform, septate, slightly enlarged at the apices. Asci 8-spored, cylindric-clavate, amyloid or non-amyloid, sometimes arising from croziers. Ascospores hyaline, 0–3-septate, ellipsoid." These diagnostic morphological features of the family are so general that they could apply without conflict to several families in *Leotiomycetes*, including *Helotiaceae*, *Hyaloscyphacae*, *Lachnaceae*, and *Pezizellaceae* (Baral 2016). The family thus needs to be better defined by studying the morphology of the subordinate taxa.

When comparing this broad family concept and previously published descriptions of the genera placed in it, there are still some morphological and ecological disagreements. These discrepancies extend even to the type genus, *Hyphodiscus*. Ekanayaka *et al.* (2019: 345) gave the substrate of members of *Hyphodiscaceae* as dead plant material, whereas prior authors noted that certain species of *Hyphodiscus* are regularly found growing on other fungi (Hosoya 2002: 56, Raitviir 2004: 73) and living liverworts (Huhtinen *et al.* 2010). Ekanayaka *et al.* (2019: 332, 345) also described the ascus apex as amyloid or non-amyloid in *Hyphodiscaceae*, but there are several species with a hemiamyloid reaction (Hosoya 2002, 2011, Raitviir 2004, Quijada *et al.* 2015). The shape of ascospores in *Hyphodiscaceae* is described as "ellipsoid" (Ekanayaka *et al.* 2019: 332, 345), but *Hyphodiscus* has species with globose, elongate-ellipsoid, subfusoid, clavate-fusoid, and fusoid ascospores (Raitviir 2004, Huhtinen *et al.* 2010, Quijada *et al.* 2015). *Hyphopeziza* has ascospores that can be elliptic-clavate to cuneiform (Han *et al.* 2014), *Venturiocistella* species can have cuneiform, clavate, and fusoid ascospores (Hosoya & Harada 1999, Raitviir 2004), and the type species of *Scolecolachnum* has "filiform, initially somewhat clavate, becoming subcylindrical" ascospores (Guatimosim *et al.* 2016). The ascospores are also said to be 8 per ascus (Ekanayaka *et al.* 2019: 332, 345), when at least one species in the family has been observed with only four spores per ascus (Huhtinen *et al.* 2010). The family concept presented by Ekanayaka *et al.* (2019) similarly does not cover all hair morphological variation in the other genera included in the family. The hairs are described only as "granulate" by Ekanayaka *et al.* (2019: 345), when previous authors have noted not just granules, but coarse or spiny warts on the hairs of certain species of *Hyphodiscus* (Raitviir 2004, Quijada *et al.* 2015). Species of *Hyphopeziza*, *Scolecolachnum*, and *Venturiocistella* also have a much higher diversity of hair shapes which Ekanayaka *et al.* (2019) did not mention, but hair features are the key, in conjunction with excipular features, to differentiate among genera in this family. *Hyphopeziza* species can have conical or lageniform hairs with smooth walls (Raitviir 2004: 56, Han *et al.* 2014), the type species of *Scolecolachnum* has smooth-walled hairs (Guatimosim *et al.* 2016), and *Venturiocistella* species have spiny, smooth, basally warted hairs together with entirely warted hairs (Baral 1993, Hosoya & Harada 1999). None of this is captured by the Ekanayaka *et al.* (2019) family description. Finally, *Scolecolachnum* was said to have an ectal excipulum of *textura epidermoidea*, which is also not represented in Ekanayaka *et al.*'s (2019) family description.

In addition to the inaccurate circumscription of the family *Hyphodiscaceae*, there are other signs that Ekanayaka *et al.* (2019) held mistaken understandings of the taxonomic concepts of the fungi they were reassigning. When discussing *Scolecolachnum nigricans*, Ekanayaka *et al.* (2019) stated that "our new species is similar to the genus *Hyalopeziza*, especially *H. pygmaea* [= *Hyphopeziza pygmaea*] and *H. digitipila* by having small cupulate, blackish apothecia, granulate hairs, filiform paraphyses, cylindric-clavate asci with croziers, ellipsoid to fusoid ascospores". This statement is not only undiagnostic, since many genera have cupulate apothecia with filiform paraphyses and cylindric-clavate asci with croziers, but also incorrect. Most species in *Hyalopeziza* have whitish apothecia (including *H. digitipila*; Raitviir 2004) and the only species in *Hyphopeziza* has been variously described as "gray when fresh becoming white when dry" (Han *et al.* 2014) and "pale yellowish to pale ochraceous" (Raitviir 2004), but not blackish. Moreover, none of these species have granulate hairs like *S. nigricans*, but rather have hairs that are smooth or have appendages (*Hyalopeziza*; Raitviir 2004) or are entirely warty (*Hyphopeziza*; Han *et al.* 2014). In fact, the genus *Hyalopeziza* strongly differs from *S. nigricans*, by long hyaline hairs (cylindrical, tapering, conical, lageniform) with smooth, thick, glassy walls that do not dissolve in KOH (Raitviir 2004).

Because the morphological description provided by Ekanayaka *et al.* (2019) for the family *Hyphodiscaceae* does not include all the morphological variation inside this family and seems to rely on faulty understanding of its subordinate taxa, we here give an emended description and add a circumscription for the asexual morphs.

Hyphodiscaceae Ekanayaka & K.D. Hyde ***emend.*** Quijada & Baral

Systematic position: *Hyphodiscaceae*, *Helotiales*, *Leotiomycetes*, *Pezizomycotina*, *Ascomycota*, *Fungi*.

Type genus: *Hyphodiscus* Kirschst.

Other genera included: *Fuscolachnum* J.H. Haines, *Gamarada* D.J. Midgley & Tran-Dinh, *Glutinomyces* Nor. Nakam., *Hyphopeziza* J.G. Han, Hosoya & H.D. Shin, *Microscypha* Syd. & P. Syd., *Scolecolachnum* Guatim., R.W. Barreto & Crous, *Soosiella* Hujslová & M. Kolařík, and *Venturiocistella* Raitv.

Sexual morph: *Apothecia* superficial, 0.1–1 mm diam, solitary or scattered to gregarious, discoid to cupulate, sessile with broad or narrow attachment to substipitate or sometimes shortly stipitate, slightly contracted to closed when dry; disc smooth, bright (white-beige-yellow-green-orange-reddish-brownish) or dark (grey-brown-black); margin and receptacle downy to hairy, concolourous with

the disc, or margin differentiated by a paler-brighter colour, hairs solitary or united in small fascicles (teeth-like), sometimes very short and macroscopically unobservable; receptacle frequently concolourous with the hymenium but with a darker base. *Medullary excipulum* of *textura angularis* to *t. porrecta*, thin-walled, non-gelatinised, hyaline to pale ochre-brown, usually poorly developed, not changing colour in KOH or LUG. *Ectal excipulum* of *textura globulosa-angularis* or *prismatica-porrecta* at flanks, and *t. angularis-prismatica-porrecta* towards margin; thin-walled or often ± thick-walled (refractive, slightly to strongly gelatinised), hyaline, yellowish, pale or dark brown, colour not changing in KOH, CR or LUG, except for *H. auricolour* which turns deep violaceous in KOH. *Hairs* morphologically variable, sometimes with two types of hairs; primary hairs can be cylindrical, clavate to lageniform, (10–)20–60(–150) µm length, 0–3(–4)-septate, cells at septa constricted or not; walls hyaline to light or dark brown, thin to slightly thickened, pigment and wall not dissolving or changing in KOH, CR or LUG, entire length or rarely only apical cell densely ornamented with round tubercules or granules (warts), rarely smooth (*Microscypha*), without intracellular guttules, with or without amorphous exudates, without crystals; secondary hairs (if present) conical to lageniform, much longer than primary hairs, (25–)50–125(–250) µm long, aseptate, walls dark brown to blackish-brown, thick-walled, upper part smooth and with subacute-pointed apex, ornamented with granules only in their broad lower part. *Asci* cylindric-clavate, (4–)8-spored, ascospores occupying less than ⅓ to about ½ of the length of the living asci, *obliquely (1–)2(–3)-seriate, 1–2-seriate in dead asci, occupying more than ½ of their length, in fascicles if forming filiform spores; apex *rounded-obtuse, thin-walled, †obtuse-conical to papillate and ± thick-walled, inamyloid or with eu- or hemiamyloid (rr or rb) apical ring; arising from simple septa or often croziers. *Ascospores* hyaline, thin- and smooth-walled, variable in shape (globose, ellipsoid, cylindrical, allantoid, clavate, fusoid, filiform); straight, inequilateral or slightly to medium curved; aseptate, rarely 1(–3)-septate; eguttulate or with a few to many minute- to medium-sized guttules (LBs) in each half or toward the ends. *Paraphyses* filiform to cylindrical, not exceeding the living asci, straight or slightly flexuous, hyaline, without refractive vacuolar guttules (VBs), rarely with low- to medium-refractive VBs, unbranched or dichotomously branched near base, rarely bifurcate at apex; apical cell usually longer than lower cells, uninflated to slightly-medium lanceolate-clavate, with smooth, hyaline, thin walls (but firm-walled and dark-brown in *Microscypha fuscoparaphysata*). **Asexual morph** (as far as known): *Colonies* slow-growing, mostly pale coloured (white, red, yellowish), but some greyish brown, pale brown or dark brown. Hyphae septate, branched, hyaline to brown, occasionally producing (sub)globose, intercalary or terminal, hyaline or brown chlamydospore-like cells. *Conidiogenous cells* solitary lateral phialides or micro- to macronematous, mononematous, simple conidiophores consisting of a stalk and one to three terminal phialides with conspicuous cylindrical, cup- to funnel-shaped or flaring collarettes. *Conidia* one-celled, usually short-cuneiform to guttuliform with a truncate base, hyaline, smooth, produced in chains or in slimy masses.

Material examined: ***Fuscolachnum inopinatum***: **Germany**, Neuhaus am Rennweg, 50.503169°N 11.112246°E, 824 m ASL, on *Lycopodium* sp., 15 Oct. 2015, P. Püwert, SBRH855. **Norway**, Rjukan, Kvitavatn umradet, 59.879645°N 8.742626°E, 960 m ASL, on *Lycopodium* sp., 31 Jul. 2012, *S. Helleman*, SBRH734. ***Fuscolachnum pteridis***: **Finland**, Pohjois-Karjala, Outokumpu, Rikkaranta, Eskola, 62.7717°N 28.75825°E, on *Pteridium aquilinum*, 23 May 2015, *M. Pennanen*, MP150538/TUR215412. **France**, Deux Sevres, Foret de l'Hermitain, 46.318250°N 0.148890°W, on *Pteridium* stems, 23 May 2014, *M. Hairaud & A. Gaillard*, SBRH831. **The Netherlands**, Dorst, brick factory remnants, 51.589532°N 4.890632°E, *Pteridium* stems, 5 Jul. 2003, *L. Rommelaars*, SBRH304. **Spain**, Asturias, Castrillón, La Curtia, 43.542413°N 5.967827°W, 102 m ASL, on rachis of *Pteridium aquilinum*, 10 Apr. 2020, *E. Rubio*, ERD-4066; Quirós, Las Llamargas, 43.130818°N 5.950335°W, 975 m, on rachis of *Pteridium aquilinum*, 14 Jul. 2019, *E. Rubio*, ERD-4073. **Switzerland**, Jura, Les Genevez, La Tourbière, 47.24170°N 7.09645°E, 1 020 m ASL, on dead *Pteridium* stems, 12 Jun. 2018, *E. Stöckli*, ES 201840. **UK**, Cumbria, Hardknott Roman fort, 54.402104°N 3.203593°W, on dead *Pteridium* stems, 8 Jul. 2015, *S. Helleman*, SBRH833; Cumbria, 3 km SE of Osmotherly, 54.342614°N 1.264159°W, on dead *Pteridium* stems, 21 Jul. 2015, *S. Helleman*, SBRH834; Two Bridges, Dartmoor, Wistmans wood, 50.575786°N 3.961405°W, dead *Pteridium* stems, 30 May 2000, *S. Helleman*, SBRH 110. ***Fuscolachnum cf. misellum***: **Finland**, Pohjois-Karjala, Outokumpu, Rikkaranta, Eskola, 62.769806°N 28.757419°E, 124 m ASL, on dead *Ribes nigrum* leaves, 6 Jul. 2017, *M. Pennanen*, SBRH927. ***Fuscolachnum misellum***: **Germany**, NRW Sauerland, Balve, Balver Wald, 51.348448°N 7.829166°E, 434 m ASL, on dead *Rubus fruticosus* leaves still attached, 30 Dec. 2018, *S. Helleman*, SBRH943. **The Netherlands**, Boxmeer Schraalzand, 51.632230°N 5.938311°E, on *Rubus fruticosus* leaves, 9 May 2014, *S. Helleman*, SBRH799. **Russia**, Pskov Oblast, Loknyansky District, Bashovo, 56.64999°N 30.16472°E, on overwintered leaves of *Ribes nigrum* in a garden, 14 May 2012, *E. Popov*, LE 305267; Leningrad Oblast, Priozersky District, Otradnoye station of Komarov Botanical Institute, on overwintered leaves of *Rubus idaeus* in litter, 28 May 2004, *E. Popov*, LE 304526. **Spain**, Llanera, Villabona de Asturias, 43.461370°N 5.828154°W, 167 m ASL, on overwintered leaves of *Rubus* sp., 18 May 2009, *E. Rubio*, ERD-4797; Lena, alto de La Cobertoria, 43.155225°N 5.891653°W, 868 m ASL, on overwintered leaves of *Rubus* sp., 19 Jun. 2020, *E. Rubio*, ERD-8399. **Switzerland**, Jura, Les Genevez, Les Veaux, 47.24389°N 7.09282°E, 1 019 m ASL, on dead *Rubus* sp. leaves, 8 May 2015, *E. Stöckli*, ES 201535. ***Hyphodiscus auricolour***: **Russia**, Krasnoyarsk Krai, Taymyrsky Dolgano-Nenetsky District, Khatanga, 71.98°N 102.47°E, on *Larix dahurica*, lower side of a fallen trunk, 23 Aug. 1967, *P. Põldmaa*, TAAM032381 (as *Cistellina auricolour* Raitv., **holotype**). ***Hyphodiscus otanii***: **Spain**, Asturias, Somiedo, Saliencia, road to La Farrapona, 43.061370°N 6.099003°W, 1 575 m ASL, on wood of *Sorbus aucuparia*, 25 May 2019, *E. Rubio*, ERD-7921. ***Hyphodiscus hyaloscyphoides***: **Japan**, Aomori Prefecture, Hakkoda, 40.70525°N 140.871222°E, on *Betula ermanii* var. *ermanii* wood, 25 May 2006, *T. Hosoya*, TNS-F-13588. ***Hyphodiscus cf. hymeniophilus***: **Japan**, Nagano Prefecture, Wada-mura, 36.161796°N 138.169522°E, on decaying coniferous wood, 13 Feb. 1992, *T. Hosoya*, TNS-F-31801. **Russia**, Karachay-Cherkessia, Teberdinsky Nature Reserve, Teberda river valley, 43.41303°N E 41.72314°E, 1 380 m ASL, on wood of *Populus tremula*, 10 Aug. 2009, *E. Popov*, LE 305399. ***Hyphodiscus hymeniophilus***: **Estonia**, Harju County, Anija Comm, by Mustjõe River, 59.2825°N 25.46222°E, 55 m, on basidiomata of *Neoantrodia serialis*, 6 Sep. 2013, *U. Ojango*, TUF117323; Hiiu County, NW of Mägipe, Kõpu Nature Reserve, 58.9283°N 22.190°E, 35 m ASL, on rotten basidiomata of *Neoantrodia serialis*, 26 Apr. 1999, *E. Parmasto*, TAAM174997; Jõgeva County, Alam-Pedja Nature Reserve, Võiviku Reservate, 58.49373°N 26.23458°E, 37 m ASL, on basidomata of *Corticiaceae* indet. growing on *Populus tremula* rotten trunk, 24 Oct. 1998, *E. Parmasto*, TAAM174487a (sexual morph)/TFC190382 (asexual morph on MEA); Tartu County, Elva Comm, Mälgi, Sillamatsi, 58.259583°N, 26.358633°E, 65 m ASL, on rotten basidiomata, 6 Oct. 2017, *K. Põldmaa*, TUF104853. **Spain**, Canary Islands, Tenerife, Piedra Chinobre, 28.3330°N 161029°W, 900 m ASL, on *Hymenochaete* sp., 7 Apr. 2013, *L. Quijada & C. Quijada* (TFCMic. 24046); Vueltas de Taganana, 28.3236°N 16.1342°W, 763 m ASL, on wood of *Phyllis nobla*, 23 Jun. 2014, *L. Quijada* (TFCMic. 21421); Los Batanes, 28.3258°N 16.1759°W, on *Erica arborea*, 2 Sep. 2014, *L. Quijada* (TFC Mic. 24497). ***Hyphodiscus luxurians***: **Russia**, Republic of Mordovia, Temnikovsky District, Mordovsky Nature Reserve, 54.79043°N 43.39827°E, old stromata of *Xylariaceae* indet., 30 Apr. 2013, *S. Bolshakov*, LE 304401. ***Hyphodiscus smaragdinus***: **Spain**, Asturias, Somiedo, La Malva, 43.104955°N 6.258827°W, 659 m ASL, on hardwood (*cf. Acer pseudoplatanus*), 12 Feb. 2011, *E. Rubio*, ERD-5251. ***Hyphodiscus cf. stereicola***: **Germany**, Thuringia, Ilm-Kreis, between Bücheloh and Cottendorf, near "Humbach ponds", 50.73139°N 11.01028°E, 417 m ASL,

on hygric dead wood of *Fagus sylvatica* of a branch, 20 Apr. 2018, *I. Wagner*, TUF104970. **Russia**, Karachay-Cherkessia, Teberdinsky Nature Reserve, Nizhny Arkhyz, 43.67405°N 41.43485°E, 1 210 m ASL, on rotten wood of *Fagus orientalis*, 22 Aug. 2009, *E. Popov*, LE 305400. ***Hyphodiscus pinastri***: **Spain**, Canary Islands, Santa Cruz de Tenerife, Monte de La Esperanza, the vicinity of Pico de las Flores, 28.4313°N 16.3905°W, *ca.* 1 000 m ASL, on twig of *Pinus canariensis*, 31 Mar. 2001, *E. Beltran-Tejera*, TAAM182359 (**isotype**). ***Hyphodiscus theiodeus***: **Netherlands**, Noordlaren, Noordlaarder bos, 53.119000°N 6.653273°E, on dead *Sorbus aucuparia* close to old *Peniophora* sp, 20 Oct. 2012, *S. Helleman*, SBRH738. **Switzerland**, Jura, Saignelégier, Goumois, 47.26230°N 6.95506°E, 536 m ASL, on old *Peniophora* sp. on dead *Corylus avellana*, *E. Stöckli*, ES 201770. ***Hyphopeziza pygmaea***: **Japan**, Aomori Prefecture, Towada-shi, Horyo, 40.586583°N 141.018528°E, on a leaf of *Quercus mongolica* var. *grosseserrata*, 25 May 2006, *T. Hosoya*, TNS-F-17940; Akita Prefecture, Tazawa Lake, 16 May 1995, TNS-F-56879/TRL 1189 [line drawing, Fig. 3 F–I]. **Spain**, National Park Cabañeros, no exact locality, on the lower side of fallen leaves of *Quercus faginea*, 12 May 1996, *A. Raitviir*, TAAM137705. ***Microscypha arenula***: **Finland**, Pohjois-Karjala, Outokumpu, Rikkaranta, Eskola, 62.769806°N 28.757419°E, on the underside of leafs of *Pteridium aquilinum*, 6 Jul. 2017, *M. Pennanen*, SBRH922. **Germany**, Brandenburg, on *Pteridium aquilinum*, 20 Jul. 1919, P. Sydow (FH00464271). **The Netherlands**, Dorst brick factory, 51.589532°N 4.890632°E, on *Pteridium* fronds, 5 Jul. 2003, *L. Rommelaars*, SBRH302. **Spain**, Lena, puerto de Pajares, estación invernal El Brañillín, 42.984550°N 5.774126°W, 1339 m ASL, on fronds of *Pteridium aquilinum*, *J. Mateos*, ERD-8386; Somiedo, Coto de la Buena Madre, 43.080044°N 6.237699°W, 1 000 m ASL, on an unknown pteridophyta, 2 Jun. 2018, *E. Rubio*, ERD-4866. ***Venturiocistella pini***: **The Netherlands**, Boxmeer, brestbos, 51.651038°N 5.930254°E, on *Pinus* bark, 23 Oct. 2001, *S. Helleman*, SBRH187; Nieuw-Bergen, Driessens Ven, 51.598583°N 6.072948°W, on *Pinus* bark on the ground, 11 Nov. 2006, *S. Helleman*, SBRH426. ***Venturiocistella diversipila***: **The Netherlands**, Boxmeer, brestbos, 51.650685°N 5.925136°W, on *Betula* leaf, 1 Nov. 2002, *S. Helleman*, SBRH264. **Spain**, Comunidad de Madrid, Alcalá de Henares, "finca La Oryga" by Rio Henares, 40.49859°N 3.33211°W, 590 m ASL, on *Populus alba* decaying leaf, 25 Nov. 1991, *R. Galán & A. Raitviir*, TAAM136194. **Switzerland**, Jura, Les Genevez, Les Embreux, 47.26303 °N 7.11684°E, 1 017 m ASL, on dead *Betula* leaves, 14 Oct. 2017, *E. Stöckli*, ES 201784. ***Venturiocistella japonica***: **Japan**, Aomori Prefecture, Towadako-machi, Oirase, Chisuji-no-taki, 40.586583°N 141.018528°E, on *Cercidiphyllum japonicum* leaf, 20 May 2006, *Y. Harada & K. Tanaka*, TNS-F-18030; Iwate Prefecture, Shizukuishi-cho, Ohmura, 10 May 1994, *T. Hosoya & T. Kutono*, TNS-F-100239 (**holotype**) [line drawing, Fig. 3 J–M]. ***Venturiocistella ulicicola***: **Spain**, Asturias, Salas, La Espina, turbera de La Molina, 43.380173°N 6.330087°W, 654 m ASL, on wood of *Ulex europaeus*, 11 Apr. 2015, *E. Rubio*, ERD-6422. ***Venturiocistella uliginosa***: **Russia**, Buryatia, Barguzinsky District, *ca.* 3 km NO of Ust-Barguzin, close to the Barguzin River, 53.4340°N 109.1002°E, 450 m ASL, on fallen leaves of *Vaccinium uliginosum*, 15 Jul. 1971, *B. Kullman*, TAAM065303 (**holotype**).

Key to identify *Hyphodiscaceae* genera based on the sexual morph:

1. Two hair types on receptacle: I) short cylindric-clavate, with rounded to obtuse apex, hyaline or brownish, thin- or slightly thick-walled, 0–2(–4)-septate, surface overall warted; II) long, spiny, conical to lageniform, usually with subacute apex, aseptate, dark brown, thick-walled, aseptate, surface warted only in basal region (setae) ..... *Venturiocistella*

1'. Only one hair type on receptacle: cylindric-clavate to lageniform, 0–3-septate; walls hyaline to brown, thin- to slightly thick-walled or solid-glassy, surface smooth or ornamented with roundish granules or warts; apical cells of hairs about as wide as lower cells, also enlarged (clavate) or subacute-pointed; if two types of hairs are present, none of them is spiny (non setae-like; observed in the *Fuscolachnum misellum* aggregate) 2

2. Hairs cylindrical-conical to lageniform, hyaline, non-septate (occasionally 1-septate near the base), ± bulbous base thin-walled, remaining part ± thick-walled to entirely solid-glassy, surface granulate; paraphyses sometimes with coarsely warted and glassy apex ..... *Hyphopeziza*

2'. Hairs cylindric-clavate, hyaline or brownish, 0–3-septate, thin- to slightly thick-walled, non-glassy, surface smooth or ornamented with roundish granules or warts; paraphyses never hair-like 3

3. Hairs hyaline to pale brownish, walls smooth; excipulum not gelatinised, excipular cells hyaline-pale brownish, thin-walled 4

3'. Hairs hyaline to dark brown, walls ornamented with granules or warts; excipulum slightly to strongly gelatinised, excipular cells hyaline or pale to dark yellowish-brown, rarely bluish-green or reddish, thick-walled 5

4. Hairs 13–16 µm long, hyaline, smooth, aseptate; average asci †11–18 µm wide; ascospores †44–57 × 2–3 µm, 3-septate; on leaves of ferns ..... *Scolecolachnum s. str.*

4'. Hairs on average >15 µm long, hyaline to pale brownish, smooth, 0–3-septate; average asci width <10 µm; ascospores up to 21 µm long, 0–3-septate, sometimes constricted at septa; on wood or leaves of angiosperms ..... *Microscypha*

5. Excipulum not or only slightly gelatinised; hairs brown, without exudate, cylindrical, usually not swollen at apex, 0–3(–6)-septate, ornamentation composed of small, densely, overall distributed warts (sparsely and coarsely granulated in *F. hainesii*); on leaves of bryophytes, ferns, gymnosperms, and angiosperms ..... *Fuscolachnum*

5'. Excipulum ± strongly gelatinised, rarely thin-walled; hairs hyaline or to pale brown, often covered by yellow exudate that change to green in KOH and disappears slowly, cylindric-clavate, frequently ± enlarged toward the apex, 0–2-septate, ornamentation often composed of ± large, sparsely to densely distributed warts, overall or only in apical cell, sometimes whole hair lenght smooth; mostly on wood of angiosperms or gymnosperms (often on fungi, including lichens), also on bryophytes ..... *Hyphodiscus*

Notes on *Fuscolachnum*: Selected publications chronologically arranged are Desmazières (1847, 1850), Saccardo (1889), Höhnel (1918), Kirschstein (1938), Holm & Holm (1977), Huhtinen (1985), Haines (1989), Baral (1993), Huhtinen & Söderholm (1997), Chlebicki & Suková (2005), Huhtinen *et al.* (2010), Dougoud (2011), and Baral (2015). Haines (1989) erected the genus in the family *Hyaloscyphaceae* (tribe *Lachneae*) to accommodate six species.

The following description of the genus is based on the literature

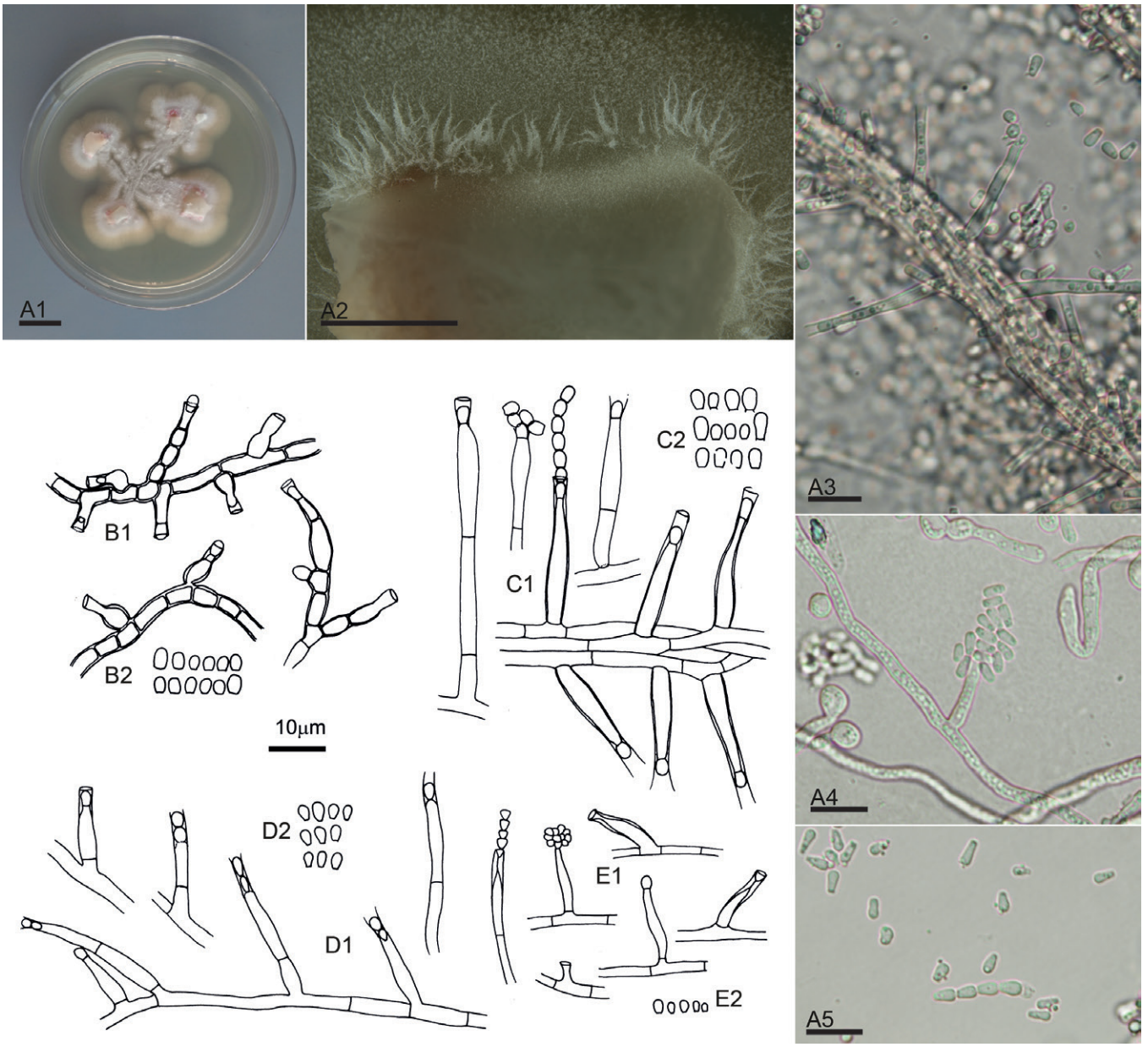

Fig. 4. Asexual morphs. **A1–5.** *Hyphodiscus hymeniophilus* culture strain TFC190382. A1. Petri dish after 17 d; A2. Tufted colonies on MEA; A3. Funiculose hyphae and phialides with collarettes and conidia in water; A4. A conidiogeneous cell with conidia, on the left a chlamydospore; A5. A conidial chain and conidia in water. **B–E.** A conidiogenous structure and conidia of different species of *Hyphodiscus*. B1, B2 = *H. theiodeus*; C1, C2 = *H. otanii*; D1, D2 = *H. rhodogena*; E1, E2 = *H. hyaloscyphoides*. Scale bars: A1 = 1 cm; A2 = 2 mm; A3–-5 = 10 µm.

cited as well as our own observations: Apothecia cupulate, 0.1–0.4 mm diam, sessile or short-stipitate; hymenium pale to dark cinereous-brownish; receptacle light grey to dark brown or fuscous-black, covered with ± appressed hairs; margin whitish or paler than hymenium and/or receptacle, fringed by hairs or looking lacerate because of hair aggregation (Fig. 5 A, F, K); ectal excipulum composed of *textura angularis-prismatica* (*-porrecta*), not or slightly gelatinised, cells brownish, thin- to firm-walled; hairs cylindrical, 17–40(–83) × 4–8 µm [but in *F. necator* (20–)40–110 µm], light to dark brown, thin- to firm-walled, without exudates, not swollen at apex, 0–3-septate, septa ± equidistantly spaced, ornamentation composed of small, spherical or vertically elongated granules, dense and evenly distributed (Fig. 5 B1, B2, B5, G2–5), but of sparse, coarse, conical warts in *F. hainesii*. All species with one type of hair except for the *Fuscolachnum misellum* aggregate (Fig. 5 G6–8) which comprises collections with hair dimorphism (though not spiny hairs as in *Venturiocistella*); asci cylindric-clavate, †(17–)20–35(–48) × 4–6(–8.5) µm (but in *F. necator* †72–83 × 6–11 µm), (4–)8-spored, apex obtuse-subacute to slightly truncate, positive in LUG (*Calycina*-type), hemiamyloid (rb) or euamyloid (Fig. 5 E2, E6, H3–5), base arising from croziers (simple septate in *F. necator*); ascospores ellipsoid-cuneate-clavate, straight-inequilateral or slightly curved, 4–10(–14) × 1–2(–3.5) µm (*F. necator*: 20–34 × 2–3.5 µm), aseptate (up to 3-septate in *F. necator*), frequently without or with tiny, hyaline-greyish, sparse or sometimes abundant small guttules (LBs), or with two large LBs (in *F. inopinatum*); paraphyses filiform-cylindrical, not exceeding the asci, sparsely septate, simple or branched at lower septa, apical cell longer than lower cells, up to 2.5 µm wide, without or, in *F. pteridis,* with globose to elongated, low- to medium-refractive guttules (VBs, refractivity enhanced in LUG, Fig. 5 D).

Figure 5 shows the morphology of the type species (*F. pteridis*, A–E) and two other species: *F. misellum* agg. (F–J) and *F. inopinatum* (K). Eight species and one variety have been included

Fig. 5. Detailed morphology of the genus *Fuscolachnum*. **A–E.** *F. pteridis*. A1. Fresh apothecia; A2. Dry apothecia; B1. Transverse section at margin and upper flank; B2, B5. Hairs at flanks and margin; B3, B4. Ectal excipular cells at flanks; C. Living ascospores; D. Dead paraphyses in LUG, with guttules (VBs) enhanced in contrast; E1, E3, E5. Living mature asci; E2, E6. Immature asci in LUG with euamyloid ring (dead in E6); E4. Base of asci with croziers. **F–J.** *F. misellum*. F1–3. Adult and young apothecia (fresh, rehydrated in F2); G1–8. Details of ectal excipulum and different morphologies of hairs observed; H1. Dead asci KOH-pretreated and LUG (with blue apical ring); H2 & H7. Living young and mature asci with biseriate ascospores in water; H3–5. Hemiamyloid apical ring in LUG showing blue and reddish reactions; H6. Base of asci with croziers; I1, I2. Living ascospores; J1. Dead paraphyses (in KOH); J2. Living paraphyses. **K.** Macrophotos of *F. inopinatum* showing its short and black stipe. Collections: *F. pteridis* = A1, B1–3, C, D, E3, E4 (ERD-4066); A2, E5, E6 (ERD-4073); B4, B5, E1, E2 (ES 201840). *F. misellum* (on *Rubus*) = F1, G4, G5, H2, H3, I1, J2 (ERD-8399); F4, G6–8, H4–7, I2 (ERD-4797); F3 (SBRH943). *F. misellum* (on *Ribes*) = F2, G1–3, H1, J1 (LE 305267). Scale bars: A1, A2, F1–4 = 200 µm; B1, G1 = 50 µm; G6 = 25 µm; B2–5, C, D, E1–4, G2–5, G7, G8, H1, H2, H7, I1, I2, J1, J2 = 10 µm; E5, E6, H3–6 = 5 µm.

in the genus: *F. boreale*, *F. dumorum*, *F. hainesii*, *F. inopinatum*, *F. labradoricum*, *F. misellum*, *F. necator*, *F. pteridis*, and *F. pteridis* var. *tumidipila*. One of these, *F. dumorum*, has been transferred to *Brunnipila* (Baral 2015). Species of *Fuscolachnum* are usually saprotrophs on the dead, decaying leaf litter of various vascular plants and have been classified as terrestrial epiphytic saprobes and litter saprotrophs (Wijayawardene *et al.* 2017, Põlme *et al.* 2020). Three species occur on the leaves of angiosperms: *F. labradoricum* on *Rhododendon groenlandicum* (Huhtinen 1985), *F. hainesii* on *Dryas grandis* (Huhtinen & Söderholm 1997), and the *F. misellum* aggregate with one clade on *Rubus* (the host listed in the original description; Desmazières 1847) and one on *Ribes* in our analyses (Fig. 2), though other authors have also reported its presence on *Acer* (Haines 1989). One species, *F. boreale*, occurs on the leaves of a gymnosperm (*Juniperis communis*, Holm & Holm 1977). One species, *F. inopinatum*, occurs on species of *Lycopodium* (Kirschstein 1938, Haines 1989). Another species, *F. pteridis*, occurs on leaves and rarely stems of Northern Hemisphere ferns in the genera *Athyrium*, *Dryopteris, Onoclea*, *Osmunda*, and *Pteridium* (Desmazières 1847, Dennis 1949, Haines 1989, Höhnel 1918). Interestingly, the two species occurring on pteridophytes cluster in our analyses (Fig. 2) in a marginally supported clade with another pteridicolous species, *Scolecolachnum pteridii*; another pteridicolous member of the family, *Microscypha arenula*, clusters near this clade, but without support. A final, unusual species (*F. necator*) was described from a bryophyte (Huhtinen *et al.* 2010); it is unusual in many ways, as is evidenced in the generic description above, and we discuss it further below. Most of these species are shared between at least two continents: four species have been reported from both Europe and North America, one from Europe and Asia, and one (*F. pteridis*) from Europe, Asia, and North America. Only two species display continental endemism so far: *F. labradoricum* has only been reported from North America, and *F. necator* has only been reported from Europe (Table 2).

Not much work has been done since Haines erected the genus *Fuscolachnum* in 1989; only two species, *F. hainesii* (Chlebicki & Sudová 2005) and *F. necator* (Huhtinen *et al.* 2010), have been added to the genus since. Both species could fit in the concept of the genus although there are some deviant morphological features. The biometry of *F. necator* is exceptional, with much longer hairs, asci and ascospores to the point that the length of all three structures only overlap with other species in *Fuscolachnum* at the extreme ends of their ranges. It is the only species in which the ascospores become septate with age, and the hair morphology resembles that in the genus *Brunnipila*, with shorter cells at the hair apex. Although the hair septation pattern is variable in *Fuscolachnum*, cells are usually equidistantly septate or apical cells are longer than lower cells (Fig. 5 B2–5, G2–8). These morpho-biometric features together with the ecology of the species (a possible necrotrophic parasite growing on a bryophyte; Huhtinen *et al.* 2010) indicate that molecular study is needed to clarify its generic placement. An interesting deviation is also found in *F. hainesii*: the drawing provided by the authors (Chlebicki & Suková 2005) shows a different ornamentation pattern in the hairs, with sparse conical protrusions of the cell wall instead of the typical granulate ornamentation of the wall surface. The published photo does not show these protrusions, but it is of too low resolution to see fine details. Chlebicki & Suková (2005) compared this foliicolous species with *F. misellum*, another species growing on leaves of *Rosaceae* (Table 2).

Fuscolachnum misellum was originally described by Desmazières (1847), as *Peziza misellum*, from Europe on *Rubus* leaves. The original description states, "covered by short blackish hairs, more abundant towards the margin, where they are replaced by also short and white hairs forming like a little areola around the cup". This description could be misinterpreted and lead one to think that two types of hairs occur in the same apothecium. Haines (1989) reviewed a "possible isotype" and other collections (including North American material on *Acer* leaves), emended the description, and provided drawings. The hairs do vary in colour and length depending on their placement on the receptacle, and like other species of *Fuscolachnum* (Fig. 5 A1, A2, F2–4), *F. misellum* does have a whitish hairy margin, confirming and clarifying Desmazières' (1847) description. Here we augment our description with some recent collections of *F. misellum* from Europe found on leaves of *Rubus* and *Ribes* (Figs 2, 5 F–J) and also consider previous descriptions. Our molecular results (Fig. 2) show that *F. misellum* is heterogeneous, with one clade composed of specimens growing on *Rubus* leaves (*Rosaceae*), and another of specimens on *Ribes* leaves (*Grossulariaceae*). Both clades are intermixed with species of *Venturiocistella* with high support (Fig. 2, "*Venturiocistella* & *Fuscolachnum misellum*"). Despite significant molecular differences, the two *F. misellum* clades, on *Ribes* and on *Rubus* (Fig. 5) are morphologically so similar that we could not determine any morphological or biometrical differences. ERD-8399, another well documented collection on *Rubus* leaves without molecular data, is also morphologically indistinguishable from these sequenced specimens (Fig. 5 F1, F3, G4, G5, H2, H3, I1, J2). A different morphotype on *Rubus* leaves identified as *F. misellum* (ERD-4797) is shown in Fig. 5 (F4, G6–8, H4–7, I2). In this sample we can differentiate two types of hairs (long-dark *vs* short-hyaline), both being ornamented and septate, with the apical cell usually longer than the lower cells, sometimes appearing aseptate. The morphology of this collection resembles *Venturiocistella*, but all hairs are thin-walled and septate, unlike the spiny hairs in *Venturiocistella* species. Spore size is also quite different between these two morphotypes (Fig. 5 I1, I2). No specimens from North America collected on *Acer* leaves were examined for comparison. We conclude that *F. misellum* is an aggregate of several different species and encourage the acquisition of more molecular and morphological data.

Fuscolachnum pteridis, the type species of the genus, is placed close to *Microscypha* (Fig. 2, *Fuscolachnum s. str.* on ferns clade), distant from the *Venturiocistella-F. misellum* clade. Our molecular analysis shows that even *Fuscolachnum s. str.* is polyphyletic, with *Scolecolachnum pteridii* nested between *F. pteridis* and *F. inopinatum* in a marginally supported clade. As noted before, these species and their unsupported sister, *Microscypha arenula* (= *M. grisella*) all grow on pteridophytes. In results section 5 (Phylogenetic issues in Ekanayaka *et al.* 2019), we proposed that *Scolecolachnum nigricans* could have been misplaced in *Scolecolachnum*; our molecular results indicate that it is not even a distinct species, just a redescription of *F. pteridis* (Fig. 2). Ekanayaka *et al.* (2019) included in their analysis only one sequence of *Fuscolachnum misellum* (SBRH799b), which led to the erroneous conclusion and comparison of their collection (MFLU 18-1817) with *Scolecolachnum pteridii* described by Guatimosim *et al.* (2016). Although *S. pteridii*, *F. pteridis* (including *S. nigricans*) and *F. inopinatum* grow on pteridophytes and cluster together with moderate support (75–95 % Bps), they are morphologically well distinguished. *Scolecolachnum pteridii* was described with hyaline smooth hairs and filiform, 3-septate ascospores, whereas all species recognised in *Fuscolachnum* have ornamented ± brown hairs, and only one has elongated 1–3-septate ascospores (*F. necator*). Based on our molecular analysis and ecological traits

we believe *Scolecolachnum* should probably be synonymised with *Fuscolachnum*; poor taxon sampling in *Fuscolachnum* and other genera in *Hyphodiscaceae* is possibly affecting the position of these taxa in our analyses, and we therefore prefer to not propose new combinations until more morphological and molecular data are gathered for both genera.

Key to accepted species of *Fuscolachnum* based on sexual morphs:

1. Average ascospore length greater than 10 µm 2
1'. Average ascospore length less than 10 µm 3

2. Asci 23–32 × 4–6 µm, 4-spored, ascospores 10–14 × 1–1.5 µm, oligoguttulate, aseptate, on leaves of *Rhododendron* ..... *F. labradoricum*
2'. Asci 72–83 × 6–11 µm, 8-spored, ascospores 20–34 × 2–3.5 µm, multiguttulate, finally 1–3-septate, on *Polytrichum* ..... *F. necator*

3. Average ascospore length less than 7 µm, on leaves of angiosperms (*Acer*, *Rubus*, *Ribes*) ..... *F. misellum*
3'. Average ascospore length greater than 7 µm, on leaves/stems of angiosperms, gymnosperms, ferns and lycopods 4

4. On leaves and stems of cryptogams (ferns, lycopods), ascospores 5.6–10.5 × 1.5–3.2 µm 5
4'. On leaves (and twigs) of phanerogams (angiosperms, gymnosperms), ascospores 7–10 × 1.5–2 µm 6

5. Apothecia sessile, asci 17–36 × 4–6.7 µm, ascospores clavate, mainly 1.5–2 µm wide, with only minute LBs, on ferns ..... *F. pteridis*
5'. Apothecia stipitate, asci 31–48 × 4.7–8.5 µm, ascospores ellipsoid, mainly 2–3 µm wide, with two large LBs, on lycopods ..... *F. inopinatum*

6. Hairs 20.5–33 × 5.2–6.2 µm, with sparse conical protrusions, ascospores 9–10 × 1.5 µm, with a few medium-sized LBs, on leaves of *Dryas* ..... *F. hainesii*
6. Hairs 40–70 × 4–5 µm, densely rough-warted, ascospores 7–9 × 2 µm, eguttulate, on leaves and twigs of *Juniperus* ..... *F. boreale*

Notes on *Hyphodiscus*: Selected publications chronologically arranged are: Karsten (1861), Cooke & Ellis (1878), Ellis (1883), Boudier (1888), Höhnel (1903), Kirschstein (1906, 1938), Graddon (1974), Gams & Holubová-Jechová (1976), Raitviir (1979), Baral & Krieglsteiner (1985), Zhuang (1988), Schmid & Schmid (1990), Baral (1993), Raitviir & Galán (1994), Kondratyuk & Galloway (1995), Lumley *et al.* (2001), Hosoya (2002), Raitviir (2004), Bogale *et al.* (2010), Huhtinen *et al.* (2010), Hosoya *et al.* (2011), Pärtel & Põldmaa (2011), Johnston *et al.* (2014), Baral (2015), Quijada *et al.* (2015), Suija *et al.* (2018), and Ekanayaka *et al.* (2019).

The genus *Hyphodiscus* was erected by Kirschstein (1906) with only one species, *H. gregarius*. Zhuang (1988) found *Lachnellula theiodea* (≡ *Peziza theiodea*) to be conspecific with *H. gregarius.* Because *P. theiodea* has priority over *H. gregarius* (Hosoya 2002, Zhuang 1988), the combination *Hyphodiscus theiodeus* was proposed. Baral (1993) included two more species: *H. viridipilosus* and *H. hymeniophilus*. In his revision of *Hyaloscyphaceae*, Raitviir (2004) proposed a new species, *H. pinastri*, and two new combinations, and gave a key to the seven species he included. Today, a total of 17 species names have been published in *Hyphodiscus*, but only 14 are accepted (Index and Species Fungorum, 2022). Three species are known from only their asexual morphs isolated in pure culture, which were formerly allocated in the genus *Catenulifera* (Seifert *et al.* 2011). Here we describe the morphology of the sexual morph using 11 species: *H. auricolour*, *H. delitescens*, *H. hyaloscyphoides*, *H. hymeniophilus*, *H. incrustatus, H. luxurians*, *H. otanii*, *H. pinastri*, *H. smaragdinus*, *H. theiodeus*, and *H. ucrainicus*, and propose below one new combination, *H. cajaniensis* (≡ *Microscypha cajaniensis*). *Hyphodiscus viridipilosus* was found to be a later synonym of *H. smaragdinus* (Baral pers. comm., Species Fungorum 2022). *Hyphodiscus stereicola* belongs to *Cordieritidaceae* based on molecular data. For details about the asexual morphs, see the description of the family *Hyphodiscaceae* above.

Here we characterise the sexual morph of *Hyphodiscus* as: *apothecia* 0.1–0.5(–1) mm diam, discoid-turbinate to cup-shaped, sessile to subsessile (rarely short-stipitate), disc smooth, bright (white-beige-yellow-green-orange-reddish-brownish) or dark (grey-brown-black) coloured (Fig. 6 A1–11); margin pruinose to minutely downy, rarely hairy (Fig. 5 A10, A11) or with small irregular teeth (*H. delitescens*); margin usually differentiated, concolourous with the disc or lighter coloured (whitish); receptacle concolourous, darker towards the base, in *H. smaragdinus* with bluish-green tint. *Ectal excipulum* composed of *textura* (*angularis*-)*prismatica*-*porrecta*, usually strongly gelatinised (*t. oblita*), hyaline, yellowish, pale or dark brown (Fig. 6 B1–4) to greenish brown or reddish, not changing with reagents (but *H. auricolour* turns deep violaceous in KOH); cells thick-walled (glassy, refractive) and without guttules. *Hairs* cylindric-clavate, (8–)15–35(–50) × 2.5–5(–7) µm, hyaline or coloured (brown, bluish-green, red) because of pigments in the walls or warts, often covered with yellow KOH-soluble exudates that turn green before disappearing, 0–2(–3)-septate, not or slightly constricted at septa (Fig. 6 D1, D5), apical cell frequently longer than lower cells and enlarged toward the apex, ornamentation frequently composed of thick warts, sometimes rod-like granules (spiny solidifications), sparse to dense along the whole length or only at the apex (Fig. 6 D1–6). *Asci* cylindric-clavate, †(19–)25–50(–60) × (3.5–)4–7(–8.5) µm, 8-spored (but sometimes 4-spored in *H. delitescens*), apex obtuse-subacute to truncate, positive in LUG (*Calycina*-type), hemiamyloid (rr/rb) or euamyloid (bb, Fig. 6 E2, F1, F2, F5), base arising from croziers. *Ascospores* globose to ellipsoid-fusoid-clavate, straight to inequilateral, (2–)4–6(–10.5) × 1–3(–3.5) µm, aseptate, rarely finally 1-septate (*H. cajaniensis* and *H. ucrainicus*), frequently with some guttules (LBs) near each end (Fig. 6 G1–5), secondary spores (budding of overmature ascospores) only described in *H. cajaniensis*. *Paraphyses* cylindrical, not branched or rarely branched at lower septa, not

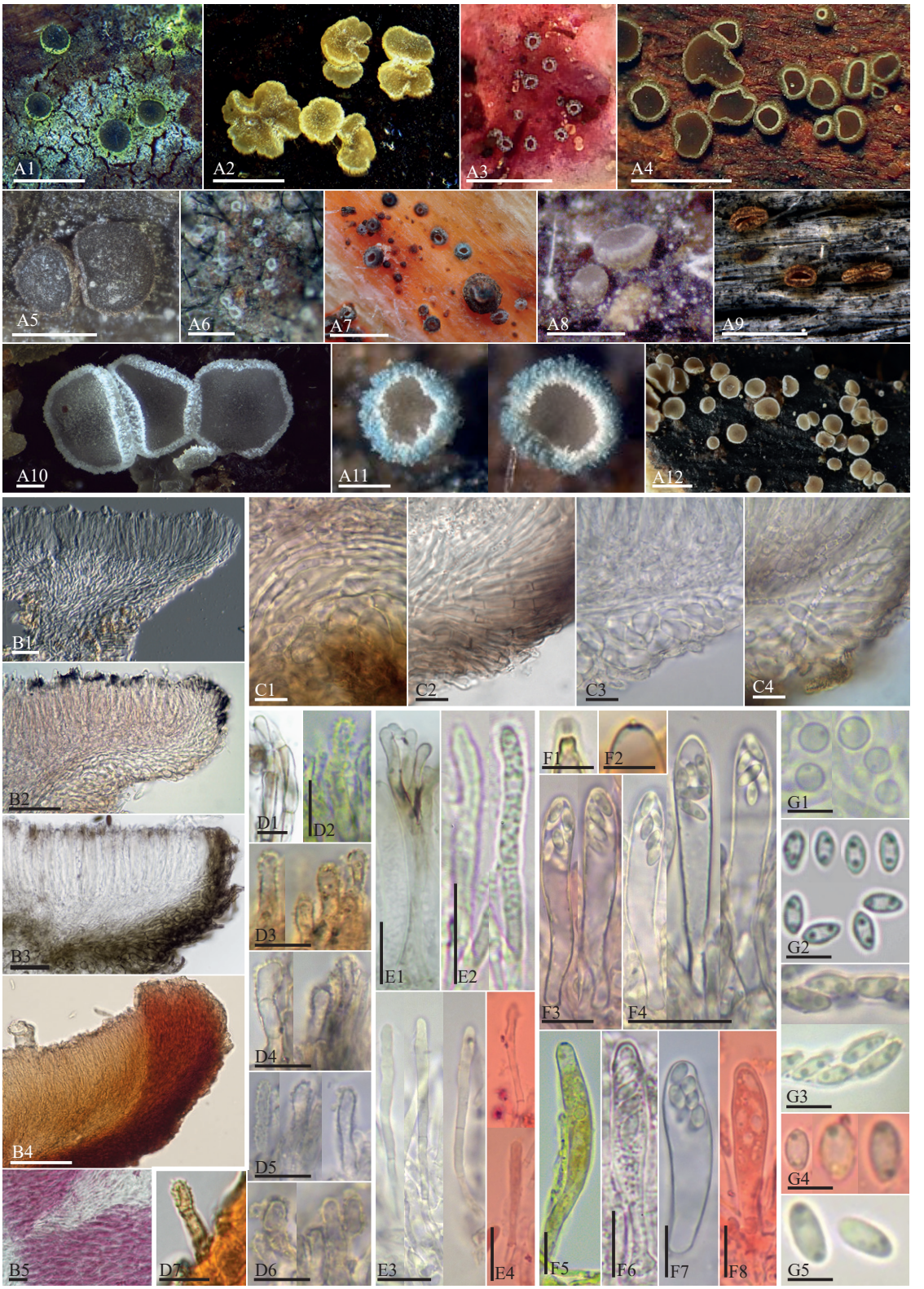

Fig. 6. Detailed morphology of the genus *Hyphodiscus*. **A.** Fresh and rehydrated apothecia showing the morphological variation in the genus. **B.** Transversal sections of apothecia showing hyaline *vs* pigmented tissues. B5. Purple reaction of tissues in KOH in *H. auricolour*. **C.** Details of ectal excipular cells at flanks, noted the thick-walled (glassy) cells embedded in gel. **D.** Hair morphological variation; note coloured hairs in D1 (*H. luxurians*) and D7 (*H. auricolour*) mounted in water; all hairs are ornamented with warts except D1 which has mostly smooth walls with sparse warts. **E.** Paraphyses. E1–3. Living paraphyses showing exudates, and cells with and without globose vacuolar bodies (guttules); E4. Dead paraphyses in CR showing septa and long apical cells. **F.** Morphological details of asci. F1, F2. Hemiamyloid and amyloid reaction of the ascus apex in LUG and after pretreatment with KOH; F3, F4, F7. Turgid living asci with ascospores biseriately arranged; F5, F8. Dead asci. **G.** Different morphologies of ascospores; noted the lipid bodies (usually two dark guttules inside each ascospore). Species in the figure: *H. auricolour* = A9, B4, B5, D7; *H. otani* = A7, E2, F6, G2; *H. hyaloscyphoides* = A6, B1; *H. hymeniophilus* = A1–4, B2, C2, C4, D3, D4, D6, E3, F1–4, F7, F8, G3–5; H; *H. luxurians* = A5, B3, D1, E1; *H. smaragdinus* = A11; *H. theiodeus* = A8, D2, F5, G1; *Hyphodiscus* sp. = A10, A12, C1, C3, D5, E4 Collections: *H. auricolour* = A9, B4, B5, D7 (TAAM032381). *H. otanii* = A7, E2, F6, G2 (ERD-7921). *H. hyaloscyphoides* = A6, B1 (TNS-F-13588). *H. hymeniophilus* = A1, C4, D6, F2, F7, F8, G4, G5 (TFCMic. 21421); A2, B2, C2, D3, D4, E3, F1, F3, F4, G3 (TFCMic. 24046); A3 (TU104853); A4 (TU104970). *H. luxurians* = A5, B3, D1, E1 (AP20042013). *H. theiodeus* = A8, D2, F5, G1 (ES 201770). *H. smaragdinus* = A11 (ERD-5251). *H.* sp. = A10, C3, D5, E4 (TFC Mic. 24497); C1 (LE235721). Scale bars: A1–7, A9, A12 = 500 µm; A8, A10, A11 = 100 µm; B1–4 = 50 µm; B5, C1–4, D2–7, E1–4, F5, F6, G1–5 = 10 µm; D1, F1–3, F7, F8 = 5 µm.

exceeding the asci, 1–2 septate, apical cell longer than lower cell(s), up to 2.5 µm wide, without or with long cylindrical or globose, low-refractive guttules (VBs, Fig. 6 E2, E4).

Members of *Hyphodiscus* are mainly found as saprotrophs on decaying wood and often on corticioid fungi. Two species are hepaticolous: the ascomata of *H. delitescens* have been found on living and senescent leaves of *Bazzania trilobata* (Huhtinen *et. al*. 2010), and *H. cajaniensis* is a possible saprobe on *Ptilidium pulcherrimum* and *Lophozia* sp., with the two known records on the dorsal side of the stems. Fungicolous members of the genus are more or less restricted to specific fungal groups. *Hyphodiscus ucrainicus* is specialised on lichens (*Cladonia* spp.), with a parasymbiotic lifestyle (Kondratyuk & Galloway 1995). The type species of the genus, *H. theiodeus* was found frequently on basidiomata of *Peniophora* spp. and other corticioid fungi, as well as on wood (*Fagus*, *Rhamnus*) (Höhnel 1903, Zhuang 1988, Hosoya 2002, Raitviir 2004, GBIF 2022). *Hyphodiscus hymeniophilus* is well recognisable in the field due to its ability to produce a red to pink pigment on the substrate, usually the hymenophore of polypores (*Fomitopsis*, *Neoantrodia*, *Stereum*, *Trametes*) (Karsten 1861, Schmid & Schmid 1990, Raitviir 2004, Quijada *et al.* 2015, Mycoportal 2022). *Hyphodiscus incrustatus* has been recorded from *Polyporus* spp. basidiomata (Ellis 1883, Raitviir 2004), and the asexual morph of *H. brevicollaris* has been isolated from decaying *Phellinus* sp. Three lignicolous species are so far only known from conifers: *H. otanii*, *H. auricolour*, and *H. pinastri* (Raitviir 1979, Hosoya 2002, Raitviir 2004, GBIF 2022). The other wood saprobes appear to prefer hardwood: *H. brachyconius* (*Fagus*), *H. hyaloscyphoides* (soaked wood of *Betula*) and *H. smaragdinus* (*Acer*, *Fagus*, *Salix*) (Gams & Holubová-Jechová 1976, Kirschstein 1938, Graddon 1974, Baral 1993, Hosoya *et al.* 2011). One wood saprobe was described only as growing on decaying wood (*H. luxurians*, Bogale *et al.* 2010)

The genus *Hyphodiscus* has not been monographed since Raitviir (2004). All 12 species included in our sexual morph concept share a similar morphology with variation in ascospores, asci and hair biometry and morphology, iodine reaction, and apothecial pigmentation, depending on the species. *H. auricolour* is the only species with a reddish excipulum and hairs, the pigment changing to violet when treated with KOH (Raitviir 2004). Some species of *Proliferodiscus* similarly show a purple KOH-reaction of the hyaline tissue. *H. auricolour* is known only from the type, and it lacks molecular data, so its generic placement needs to be verified. All *Hyphodiscus* species with a sequence form a well-supported monophyletic clade (Fig. 2), which clusters sister to *Hyphopeziza*, *Soosiella*, *Fuscolachnum s. str.*, and *Microscypha*. *Hyphodiscus* differs from those genera with a known sexual morph by its usually strongly gelatinised excipular cells (glassy appearance), short-clavate coarsely warted hairs (long cylindrical in *H. smaragdinus*), usually with an apical cell longer than lower cells, and frequent presence of pigmented exudates. *Fuscolachnum* is morphologically the most similar genus, but its excipular cells are not or only slightly gelatinised, and brown hairs are ornamented with small granules, dense and evenly distributed, usually with septa equally spaced and not enlarged at the apical cell. Most species of *Microscypha* differ from *Hyphodiscus* in their non-gelatinised excipulum and smooth hairs.

Two species previously included in *Microscypha* have ornamented hairs, *M. lonicerae* and *M. cajaniensis*. Huhtinen *et al.* (2010) placed their species in *Microscypha* based on comparison with *M. lonicerae*, which is a deviant species within *Microscypha*, and was not accepted by Raitviir (2004) as a member of the genus. In the same publication, Huhtinen *et al.* (2010) erected *Hyphodiscus delitescens*, which was the first species of the genus described as growing on bryophytes, although two years before, Kauserud *et al.* (2008) mentioned an unidentified species of *Hyphodiscus* in association with bryophytes. Later, Zhang *et al.* (2013) found *Hyphodiscus* spp. as endophytes of mosses as well. The morphology of *M. cajaniensis* fits quite well within the present concept of *Hyphodiscus*, and its molecular data (Fig. 2) support this placement. The relationship with mosses is consistent with the other members of the genus mentioned above.

Our phylogenetic results also suggest a possible conspecificity of *H. hymeniophilus* and *H. otanii*, given that *H. hymeniophilus* is taken as a species comprising different genotypes. However, *H. hymeniophilus* has distinctly narrower ascospores than *H. otanii* and grows preferentially on old perennial basidiocarps which it stains red, whereas *H. otanii* was on decorticated unstained wood. Two collections with almost identical ITS sequences (TNS-F-31801, TNS-F-31802), identified in GenBank as *H. hymeniophilus*, clustered in a marginally supported clade with *H. brachyconius* in our analysis (Fig. 2), sister to the remaining *Hyphodiscus* spp. More documented collections of *H. hymeniophilus* are needed to clarify its morphological and molecular boundaries.

Hyphodiscus luxurians was previously known only from its asexual morph, but a new sequence included in our analysis was obtained from apothecia and fully matches the type in the ITS region; its sexual morph morphology is shown here for the first time (Fig. 6 A5, B3, D1, E1).

Hyphodiscus cajaniensis (Huhtinen) Quijada, T. Kosonen & Huhtinen, ***comb. nov.*** MycoBank MB 845186.
Basionym: *Microscypha cajaniensis* Huhtinen, Nova Hedwigia 90: 419. 2010.

Based on the ITS–LSU sequence *Hyphodiscus cajaniensis* is firmly nested in *Hyphodiscus* (Fig. 2). The morphology of *Hyphodiscus cajaniensis* agrees with the concept of *Hyphodiscus* used here as well as in previous literature.

Key to accepted species of *Hyphodiscus* based on sexual morphs:

1. Average ascus length > 40 µm 2
1'. Average ascus length < 40 µm 5

2. Hairs rust-coloured, 30–50 × 2.3–2.7 µm, disc orange, ascus apical ring euamyloid, ectal excipulum and hairs deep violaceous in KOH, on gymnosperm wood ..... *H. auricolour*
2'. Hairs hyaline or pale brownish, not changing colour in KOH, 10–35 µm long, ascus apical ring hemiamyloid 3

3. Ascospores globose, fungicolous (on *Peniophora*, *etc.*) ..... *H. theiodeus*
3'. Ascospores ovate to ellipsoid-clavate 4

4. Asci 50–65 µm long, hairs 5–7 µm wide, on gymnosperm wood ..... *H. pinastri*
4'. Asci 30–50 µm long, hairs 2–5 µm wide ..... *H. hymeniophilus* (see below)

5. Ascospores 3–4 × 1.5–2 µm, with two prominent guttules, apothecial exterior with green tint (but changing to dull ochraceous with age), asci 25–35 × 4–5 µm, apical ring euamyloid, on angiosperm wood ..... *H. smaragdinus* (= *H. viridipilosus*)
5'. Average ascospore length > 4 µm 6

6. Average ascus length < 30 µm, apical ring euamyloid 7
6'. Average ascus length > 30 µm, apical ring hemiamyloid 9

7. On liverworts, apothecia white, hairs up to 50 µm long, asci 4-spored ..... *H. delitescens*
7'. Not on liverworts, apothecia yellowish, hairs up to 30 µm long, asci 8-spored (asci/ascospores morphology and biometry overlap) 8

8. Fungicolous (on fruitbodies of *Basidiomycota*), apothecia yellowish-cream, up to 0.15 mm diam ..... *H. incrustatus*
8'. Lichenicolous (*Cladonia*), apothecia yellowish to orange, up to 0.27 mm diam ..... *H. ucrainicus*

9. Apothecia up to 0.15 mm diam, grey-brown, asci 30–45 × 5–8.5 µm, ascospores 4.5–9 × 1–3 µm, on hepatics in Europe ..... *H. cajaniensis*
9'. Apothecia 0.2–7 mm diam, fungicolous or on hard/softwoods 10

10. Apothecia 0.2–0.27 mm diam, white, asci 5–7 µm wide, ascospores 4–8 × 2–3.5 µm, on angiosperm wood ..... *H. hyaloscyphoides*
10'. Apothecia 0.2–0.7 mm diam, ochraceous, greyish-blackish, yellowish, reddish, asci 4.5–5.5 µm wide, fungicolous or on hard/softwood 11

11. Ascospores 4–6 × 1.5–2 µm, fungicolous on old fruitbodies of *Basidiomycota*, substrate stained red ..... *H. hymeniophilus*
11'. Ascospores 3–4(–5.5) × 2–2.5 µm, on gymno- and angiosperm wood, substrate not stained red ..... *H. otanii*

Notes on *Hyphopeziza*: Selected publications chronologically arranged are Svrček (1985), Huhtinen (1987), Hosoya & Otani (1997b), and Han *et al.* (2014). This monotypic genus was erected by Han *et al.* (2014) during their revision of *Hyaloscyphaceae*. The type species, *H. pygmaea* was previously placed in *Trichopeziza*, *Hyalopeziza*, *Hyaloscypha* and *Unguicularia*. The name *Hyphopeziza* was created in reference to its resemblance to both *Hyalopeziza* and *Hyphodiscus*. It grows on angiosperm leaves (*Quercus*, *Carpinus*) in Europe and Asia (Japan, Korea) (Table 2, Huhtinen 1987, Hosoya & Otani 1997b, Han *et al.* 2014). According

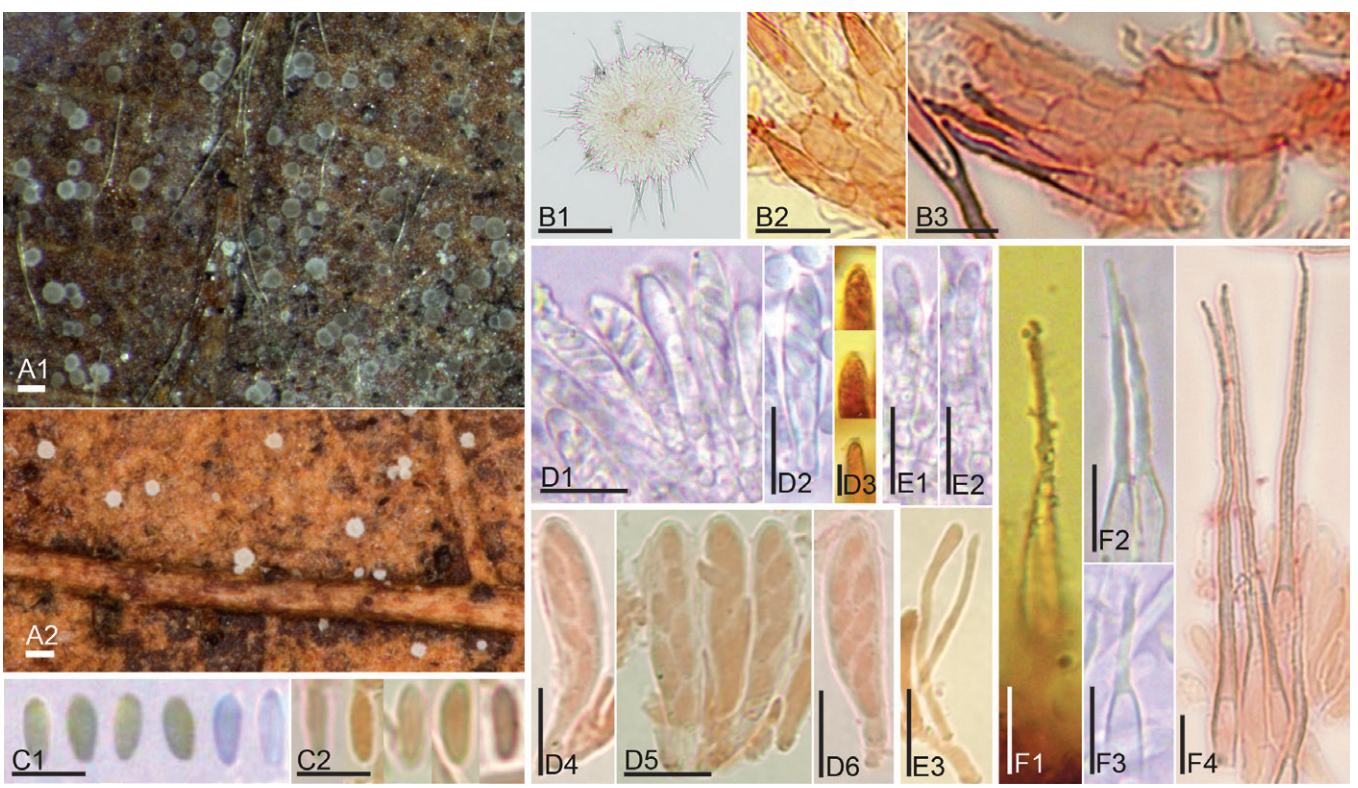

Fig. 7. Detailed morphology of the genus *Hyphopeziza*. **A.** Fresh apothecia. **B.** Details of tissues. B1. Whole apothecia on top view showing long hairs in the margin; B2, B3. Ectal excipular cells at flanks and margin in CR. **C.** Ascospores. **D.** Asci. D1, D2. Living asci; D3. Hemiamyloid and amyloid reaction of the ascus apex; D4–6. Dead asci showing ascus base. **E.** Paraphyses. **F.** Hairs. F1. Ornamented hair in MLZ; F2–4. Long glassy walls of the hairs in water and CR. Collections: B1–3, C2, D4–6, E3, F4 (TAAM137705). A1 (TNS-F-17940); A2, C1, D1–3, E1, E2, F1–3 (F.G. 692); B1–3, C2, D4–6, E3, F4 (TAAM137705). Scale bars: A1, A2 = 500 µm; B1–3 = 100 µm; D1, D2, D4–6, E1–3, F1–4 = 10 µm; C1, C2, D3 = 5 µm.

to Han *et al.* (2014) the genus is characterised by white-greyish, minutely pubescent apothecia, 0.5–1 mm in diam The ectal excipulum is hyaline to pale brown *textura* (*globulosa*-) *angularis* to *t. prismatica*, slightly gelatinised, cells thin- to slightly thick-walled. Hairs are cylindrical-conical to lageniform, hyaline, non-septate (occasionally 1-septate near the base); walls thick, granulate and glassy, not changing after addition of KOH or other reagents. Asci are cylindric-clavate, 8-spored, amyloid and arising from croziers. Ascospores elliptic-clavate, hyaline, aseptate and without guttules. Paraphyses cylindrical, hyaline, apical cell clavate-lanceolate and also becoming coarsely warty and glassy like the hairs (Figs 3A, 7). Ekanayaka *et al.* (2019) included *Hyphopeziza pygmaea* in their studies as *Hyalopeziza pygmaea*; some of this confusion likely led them to consider *Hyalopeziza* polyphyletic and to place the genus *Hyalopeziza* in *Hyphodiscaceae*, while simultaneously placing *Hyphopeziza* in *Hyaloscyphaceae*. For more details on this problem, see section 2 (Establishment of *Hyphodiscaceae* as a new family) and section 5 (Phylogenetic issues and new results) above. Our results place *Hyphopeziza* sister to *Soosiella* in a supported clade within *Hyphodiscaceae* (Fig. 2). This relationship was pointed out by Johnston *et al.* (2019). *Soosiella* is only known in a sterile mycelial morph, producing macroscopically yeast-like colonies, and growing very slowly. It was isolated from acidic soils in Czech Republic (Hujslová *et al.* 2014). Hosoya & Otani (1997b) briefly described cultures of *Hyphopeziza*, but they did not find yeast-like colonies described by Hujslová *et al.* (2014). Given that the cultures of *Soosiella* and *Hyphopeziza* are both sterile they are difficult to compare. We do not believe *Soosiella* to be congeneric with *Hyphopeziza* because the taxa were isolated from different substrates (leaves *vs* acidic soil). Discovery of a sexual morph for *Soosiella* would allow the two genera to be better compared.

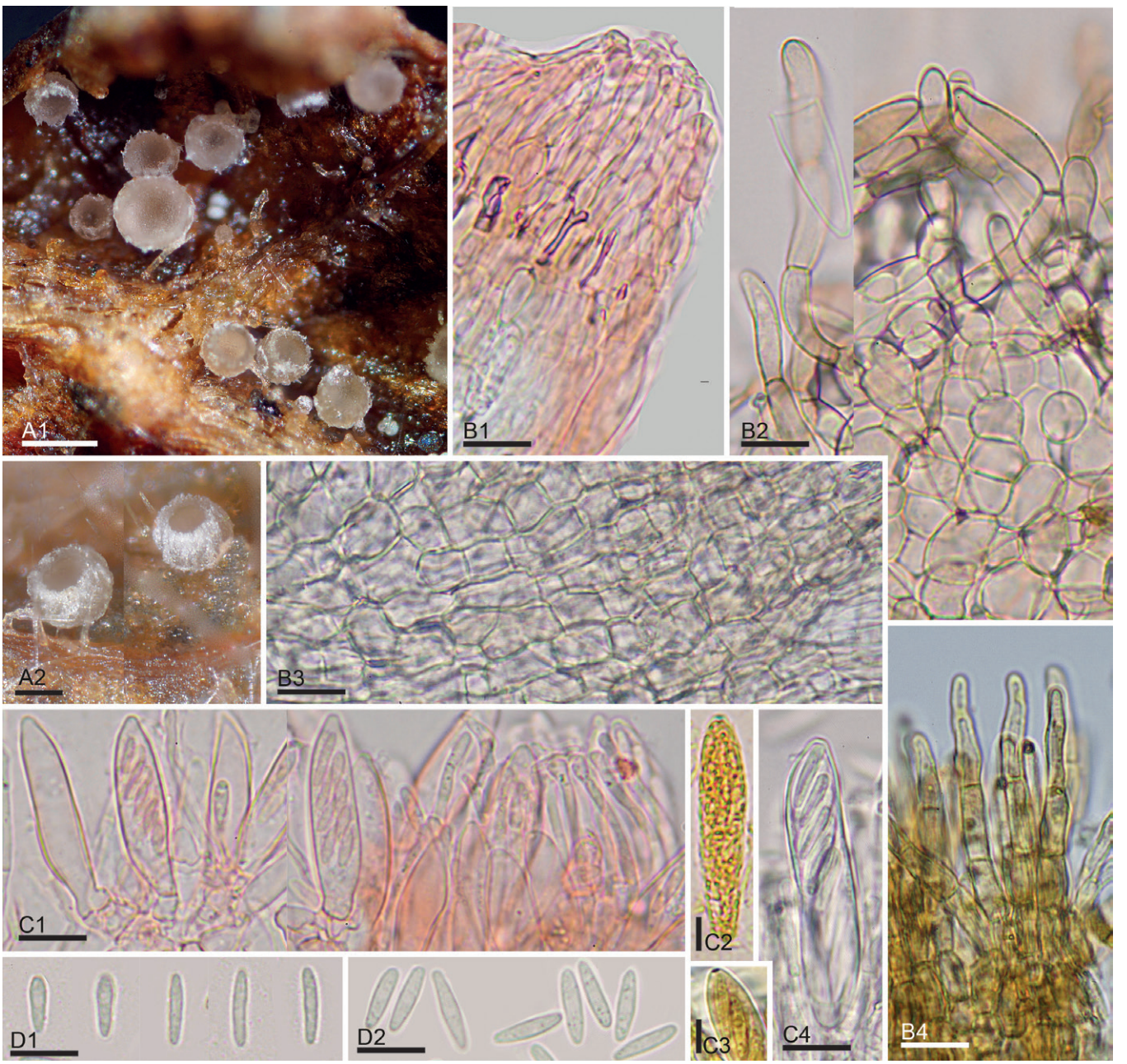

Fig. 8. Detailed morphology for *Microscypha arenula*. **A.** Fresh apothecia. **B.** Details of living excipular cells and hairs. **C.** Asci. C1. Dead asci (with croziers) and paraphyses in CR, C2, C3. Euamyloid reaction of the ascus apex (C2 dead ascus, C3 living ascus); C4. Living ascus in tap water. **D.** Living ascospores in tap water. Collections: A1, B3, B4, C3, C4, D2 (ERD-8386); A2, B1, B2, C1, C2, D1 (ERD-4866). Scale bars: A1, A2 = 500 µm; B1–4, C1, C4, D1, D2 = 10 µm; C2, C3 = 5 µm.

Notes on *Microscypha*: Publications chronologically arranged are Allescher (1898), Moesz (1926), Velenovský (1934), Killerman (1935), Dennis (1949), Graddon (1967), Svrček (1967), Dennis (1971), Bøhler (1974), Svrček (1976), Dennis (1978), Clark (1980), Kirk & Spooner (1984), Svrček (1987: 198), Huhtinen (1990: 53), Hosoya & Otani (1997a), Vesterholt (2000), Chrispijn & Douwes (2004), Raitviir (2004), Ayel & Van Vooren (2005), Huhtinen *et al.* (2010), Thompson (2013), Han *et al.* (2014), Ren & Zhuang (2016), Koizumi & Nara (2017), and Ekanayaka *et al.* (2019). The genus *Microscypha* was monotypic when it was erected by Sydow & Sydow (1919) for the species *M. grisella*, based on *Helotium grisellum*. Svrček (1976) combined *Peziza arenula* in *Microscypha*, and this name is currently considered an earlier synonym of *M. grisella* (*e.g.*, Hosoya & Otani 1977a, as *Micropodia*; Raitviir 2004), although Dennis (1949) considered this synonymy only to apply to Boudier's (1909) concept of the species (as *Micropodia arenula*) and not necessarily to the species as meant by Albertini and Schweinitz (1805). Nine species had been at various points included in *Microscypha* until Raitviir (2004) revised the genus: *M. arenula*, *M. candida*, *M. cejpii*, *M. ellisii*, *M. enrhizus*, *M. grisella*, *M. incerta*, *M. lonicerae*, and *M. monticola*. Raiviir (2004) only accepted four species, *M. arenula*, *M. enrhizus*, *M. cejpii*, and a new species he described, *M. fuscoparaphysata*. Raitviir (2004) synonymised *M. candida* with *M. arenula*, but this appears incorrect as the description and drawing provided by Moesz (1926) suggest a species of *Incrupila*, possibly *I. aspidii*, which grows on the same host (*Polystichum*) and has a very similar morphology and biometry, except for possessing strongly curved hairs shown in Moesz's drawing. A restudy of the type of *M. candida* should clarify whether the hairs are covered by crystalline matter instead of roundish particles as figured by Moesz. Raitviir (2004) also placed *M. monticola* in synonymy with *M. cejpii*. *Microscypha ellisii* was excluded from the genus by Weber (1992, to *Psilachnum*) and Raitviir (2004, to *Calycina*); in our analyses, a specimen identified as *M. ellisii* was resolved in *Hamatocanthoscyphaceae* (Fig. 2). *Microscypha lonicerae* was not mentioned by Raitviir (2004), and *M. incerta* was synonymised by Huhtinen (1990) with *Hyaloscypha vitreola*. Since Raitviir's revision only two additional species have been described: *M. cajaniensis* and *M. septospora* (Huhtinen *et al.* 2010, Ren & Zhuang 2016). When Huhtinen *et al.* (2010) described *M. cajaniensis*, they compared it to *M. lonicerae*. The inclusion of these two species in *Microscypha* widened the generic concept from solely smooth-haired species to include species with granulate hairs. Our phylogenetic results (Fig. 2) placed *M. cajaniensis* in *Hyphodiscus*, and its morphology fits the concept of that genus quite well (see Notes on *Hyphodiscus*, Fig. 2). Along with its divergent morphology, this makes us doubt the generic placement of *M. lonicerae*. We treat *M. lonicerae* as a doubtful species that needs to be re-studied to clarify its generic position within *Helotiales*.

Microscypha is circumscribed here to include five species: *M. arenula*, *M. cejpii*, *M. enrhizus*, *M. fuscoparaphysata*, and *M. septospora*. The following generic concept was based on previous reports and our own observations. Species in *Microscypha* have small apothecia of 0.2–0.5(–1) mm diam, discoid-cupulate, sessile or short-stipitate; a bright coloured hymenium and whitish to pale yellow to greyish brownish exterior; margin and exterior finely pubescent or hairy (Fig. 8 A1, A2). The ectal excipulum is composed of *textura* (*globulosa*-) *angularis* to *t. prismatica*, not gelatinised, hyaline or pale brown (Fig. 8 B2, B3), not changing with reagents; cells thin-walled and without inclusions. Hairs are cylindrical to slightly clavate, 25–60 × 2–5 µm, hyaline or pale brown, 0–3-septate; solitary or agglutinated like pyramidal teeth surrounded by an amorphous hyaline gel (Fig. 8 B1); with or without constrictions at the septa, walls smooth (Fig. 8 B1, B2, B4). The asci are cylindric-clavate, (21–)40–60 × (3–)4–8 µm (but *M. septospora* 73–84 × 6.8–7.5 µm), 8-spored, apex obtuse-subacute, apical ring hemi- or euamyloid, of *Calycina*-type (Fig. 8 C2, C3), base arising from croziers. Ascospores are narrowly cylindrical to clavate-fusoid, straight to inequilateral, (3.5–)6–11(–14) × 1–2.5 µm, aseptate (*M. septospora* 18–20.5 × 2.5–3.3 µm, 3-septate) without or with some tiny sparse inclusions (Fig. 8 D1, D2). The paraphyses are cylindrical, not branched, not exceeding the asci, 0–1(–2) septate, apical cell longer than lower cells, up to 2 µm wide, without or with some sparse vacuolar bodies, surrounded by a hyaline gel (Fig. 8 C1); paraphyses of *M. fuscoparaphysata* differing by slightly swollen, thick-walled, dark brown, sometimes bifurcate apices (Raitviir 2004).

The accepted species of *Microscypha* have been found in Europe and Asia on angiosperm or fern leaves, except *M. septospora* which was described from rotting wood (Table 2). The genus is considered a litter saprotroph or terrestrial saprobe (Wijayawardene *et al.* 2017, Põlme *et al.* 2020). *Microscypha arenula* grows on decayed fern leaves (rarely stems) of *Pteridium aquilinum* and *Matteucia struthiopteris*. It is the most commonly reported species of the genus with a widespread distribution, having been reported from Europe (Austria, Czech Republic, Denmark, France, Finland, Germany, Netherlands, Norway, Sweden, UK) but also from Asia (Japan) (Karsten 1873, Rehm 1885, Phillips 1890, Rehm 1896, Zahlbruckner 1908, Petrak n.d., Dennis 1949, Bøhler 1974, Svrček 1976, Dennis 1978, Clark 1980, Kirk & Spooner 1984, Hosoya & Otani 1997a, Vesterholt 2000, Raitviir 2004, Chrispijn & Douwes 2004, Ayel & van Vooren 2005, Thompson 2013). Two species grow on decayed fallen angiosperm leaves in Europe: *M. cejpii* has been reported on *Salix* and *Alnus* from Czech Republic and Finland and *M. enrhizus* on *Ilex aquifolum* from the UK (Velenovský 1934, Graddon 1967, Clark 1980, Vesterholt 2000). The foliicolous Asian *M. fuscoparaphysata* grew on unidentified deciduous leaves in Tajikistan (Raitviir 2004). Finally, *M. septospora* was collected on rotten wood in China (Ren & Zhuang, 2016).

Microscypha species are not commonly found by mycologists. The exception is *M. arenula*, which has been reported under many different generic names (*Helotium*, *Micropodia*, *Mollisia*, *Peziza*, *Pyrenopeziza*, *Urceola*) and studied by various authors (Karsten 1873, Rehm 1885, Phillips 1890, Rehm 1896, Dennis 1949, Bøhler 1974, Svrček 1976, Dennis 1978, Ellis & Ellis 1997, Hosoya & Otani 1997a, Vesterholt 2000, Raitviir 2004, Thompson 2013). Our generic concept is, in keeping with Raitviir (2004), more homogeneous than that of previous authors and includes only species with similar excipular structure and hair type. The different ecology (leaves *vs* wood) is correlated with biometric deviations: the lignicolous *M. septospora* has longer asci and ascospores which do not overlap in size with any of the foliicolous species, and it is the only species with 3-septate ascospores. The paraphyses of *M. fuscoparaphysata* are extraordinary in having thick-walled brown, sometimes bifurcate paraphyses (Raitviir 2004). Unfortunately, there are no recent collections or molecular data available for these two species.

As we mentioned in section 5 (Phylogenetic issues and new results), Ekanayaka *et al.* (2019) included *Microscypha* in the family *Hamatocanthoscyphaceae* based on sequences of a *Microscypha* sp. (TNS-F-18016). Han *et al.* (2014) used the same collection as well as a specimen of *Microscypha ellisii* (KUS-F52489) in their molecular analyses and found the same close relationship with

Hamatocanthoscypha laricionis; we also resolve this relationship (Fig. 2). Han *et al.* (2014) characterised their *Microscypha-Hamatocanthoscypha* clade as having hairs that only slightly taper to an obtuse end. Whether KUS-F52489 was correctly identified as *M. ellisii* is difficult to say, particularly because another collection treated there under the same name (KUS-F52663) differs by almost 3 % in the ITS. The transfer of *M. ellisii* to *Psilachnum* by Weber *et al.* (1992) was confirmed in an analysis in Baral & Haelewaters (2015), where KUS-F52663 clustered supported with *Psilachnum chrysostigma*, whereas *P. staphyleae* and *Psilachnum* sp. clustered elsewhere. The type species of *Psilachnum*, *P. lateritioalbum*, recently uploaded in GenBank, clustered together with *P. chrysostigma* and *P. ellisii* (unpublished analysis). Our phylogenetic analysis (Fig. 2) includes for the first time the type species, *M. arenula*, and shows that the position of *Microscypha* is correct within *Hyphodiscaceae* (support > 95 %).

Microscypha differs from other genera in the family by its thin-walled excipular cells from which cylindrical, hyaline to pale brown, septate, smooth hairs arise. The morphologically most similar genus is *Scolecolachnum*, which has shorter aseptate hairs and wider asci (Guatimosim *et al.* 2016). No other species accepted by us (*M. candida*, *M. enrhizus*, *M. fuscoparaphysata*, *M. septospora*) has DNA sequence data, therefore we cannot show how consistent the generic concept is.

Key to accepted species of *Microscypha* based on the sexual morph:

1. Average ascus length > 50 µm 2
1'. Average ascus length < 50 µm 4

2. Asci 73–84 × 6.8–7.5 µm, ascospores 18–20.5 × 2.5–3.3 µm, 3-septate, on unidentified wood in Asia ..... *M. septospora*
2'. Asci shorter than 70 µm, ascospores shorter than 18 µm, on fallen leaves of angiosperms 3

3. Apothecia sessile, hairs 50–60 × 3–4 µm, ascospores narrowly cylindrical, 9–14 × 2–2.5 µm, paraphyses simple, hyaline, on *Salix* and *Alnus* in Europe ..... *M. cejpii*
3'. Apothecia sub- to short-stipitate, hairs 30–40 × 2.5–3.5 µm, ascospores clavate-fusoid, 6–10 × 1.5–2 µm, paraphyses apically slightly swollen, with dark brown thick-walls, in Asia ..... *M. fuscoparaphysata*

4. Asci 40–45 × 4–5 µm, hairs hyaline, 25–60 × 2–3 µm, 3-septate, ascospores 6–9 × 1.5–2 µm, on fallen leaves of angiosperms in Europe ..... *M. enrhizus*
4'. Asci 24–40 × 5–8 µm, hairs pale brown, 25–60 × 2–5 µm, 0–3-septate, ascospores 6–14 × 1.5–2 µm, on dead leaves of ferns in Europe and Asia ..... *M. arenula*

Notes on *Scolecolachnum*: The genus was recently established during a survey of fungi associated with ferns in Brazil (Guatimosim *et al.* 2016). It was erected for a single newly described species, *Scolecolachnum pteridii*, based on two collections on fronds of *Pteridium arachnoideum*. We follow the circumscription of the genus given by the authors, with some modifications (Fig. 9). The genus has cupulate sessile apothecia with whitish to cream-coloured disc and a concolourous hairy receptacle. The ectal excipulum is composed of hyaline *textura intricata* (previously reported as *epidermoidea*, Guatimosim *et al.* 2016), covered with 13–16 µm long (but we estimate up to *ca.* 80 µm by using the photos Fig. 9 A1), hyaline (but also brownish, Fig. 9 B1 indicated with black arrow), cylindrical, aseptate, thin-walled, smooth hairs at the margin and upper flank. Asci cylindric-clavate, 8-spored, euamyloid, arising from croziers (Fig. 9 C3, erroneously as "without croziers"). Ascospores 44–57 × 2–3 µm, filiform, straight, inequilateral or very slightly curved, hyaline, 0–3-septate, with sparse small guttules. Paraphyses filiform, hyaline, simple, not exceeding the asci.

The genus was monotypic until Ekanayaka *et al.* (2019) added *Scolecolachnum nigricans*. In the Notes on *Fuscolachnum* we explain that *S. nigricans* is a synonym of *Fuscolachnum pteridis*. *Microscypha* is morphologically most similar to *Scolecolachnum*, the latter differing in wider asci and longer ascospores than any species in the genus *Microscypha*. Only *M. cejpii*, *M. enrhizus*, and *M. monticola* have smooth, hyaline, cylindrical hairs like *Scolecolachnum*. None of them grows on ferns or have septate

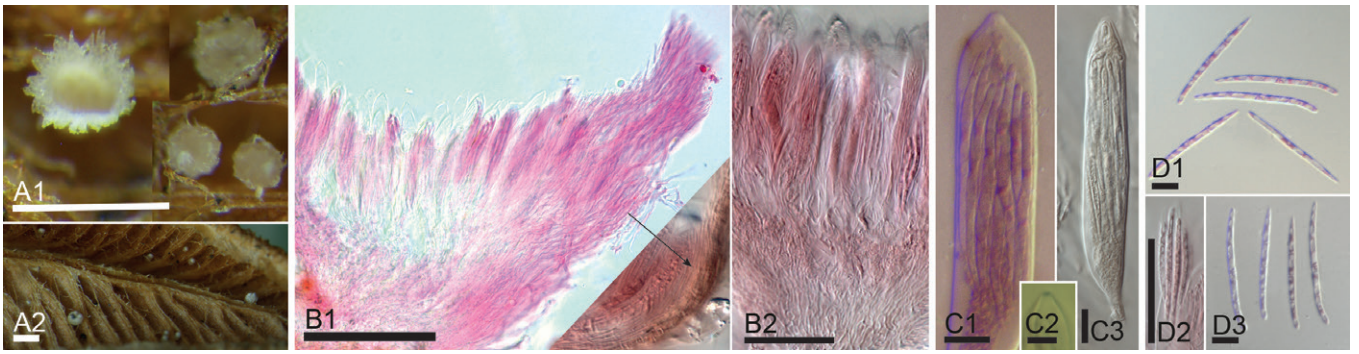

Fig. 9. Morphological details of *Scolecolachnum pteridii*. **A.** Apothecia. **B.** B1. Transversal section, showing detail of the brownish flank of the ectal excipulum in the right corner; B2. Asci and paraphyses, medullary excipulum. **C.** Asci with ascospores. C2. Amyloid reaction of apical ring. **D.** Ascospores. Collection: A1–D3 (VIC 42921, from Guatimosim *et al.*: fig. 8 and E. Guatimosim *pers. comm.*). Scale bars: A1, A2 = 500 µm; B1 = *ca.* 100 µm; D2, B1(inset) = 50 µm; B2 = *ca.* 50 µm; C1–3, D1, D3 = 10 µm.

ascospores, however. Our phylogenetic analysis (Fig. 2) shows that *Scolecolachnum pteridii* is placed sister to *Fuscolachnum inopinatum* and more distantly related to *F. pteridis*, with this latter relationship lacking strong support. Although this points to a possible congenicity between *Scolecolachnum* and *F. pteridis*, the type species of *Fuscolachnum* (both share the same ecology), and the differences especially in hair morphology makes us doubt whether they are congeneric. For the time being, *Scolecolachnum* is retained as monotypic until studies on fresh collections of *S. pteridii* can be performed to produce a better description of the hairs. Increased taxon sampling for *Fuscolachnum* and possibly *Microscypha* may also aid in better understanding the molecular phylogenetic boundaries of *Fuscolachnum* and *Scolecolachnum*.

Notes on *Venturiocistella*: Publications chronologically arranged are Ellis & Everhart (1888), Höhnel (1907), Dennis (1963), Eriksson (1970), Graddon (1974), Raitviir (1979), Remler (1979), Graddon (1980), Spooner (1987), Baral (1993), Galán & Raitviir (1994), Hosoya & Harada (1999), Raitviir (2004), and Kutorga *et al.* (2012). Baral (1993) provided an overview of the genus and explained in detail its history. The morphological concept below is based on the above references and personal studies. Apothecia of *Venturiocistella* are very small, 0.1–0.3(–0.5) mm diam (excluding hairs), sessile or short-stipitate (Fig. 10 B1, B2), with a pale whitish-grey-brownish disc, the receptacle is greyish-brownish, covered with long black spiny hairs except at the uppermost margin, which is whitish-greyish and sometimes lacerate-toothed when the short hairs are aggregated in groups (Fig. 10 A1, A3–5); ± dry apothecia are closed resembling a hairy pyrenomycete (Fig. 10 A2). Ectal excipulum composed of *textura angularis-prismatica*, cells hyaline to brownish, thin- to thick-walled, cortical cells from which the hairs emerge partially also granulated on the outside like the hairs. The hair dimorphism is the most distinctive feature of the genus (Fig. 10 B2–6): (1) long conical spiny hairs, up to 250 µm, dark-brown, non-septate, stiff, thick-walled, warted only in the lower part, apex blunt to mostly tapered or pointed; (2) much shorter cylindrical hairs, up to 70 µm, hyaline or brownish, ± straight, thin or slightly thick-walled, overall warted, 1–2(–4)-septate, apical cell not inflated, sometimes slightly tapered. Asci cylindric-clavate, †17–60 × 4.5–8 µm, in some species with hemiamyloid (rr) outer ascus wall, apex slightly to strongly conical, always with apical ring reacting positive in LUG, hemiamyloid (rr or rb) or euamyloid (bb) (Fig. 10 C2–5), base arising from croziers or sometimes simple septa. Ascospores cylindric-clavate to fusoid, straight to slightly (to medium) curved, *5–24 × 1.5–3 µm, aseptate, without or with low to medium lipid content. Paraphyses often sparse, filiform, not exceeding the asci, †0.8–2.5 µm wide.

In Fig. 10, the morphological diversity of the genus is shown, demonstrated by four selected species. In total, eight species have been described in the genus and we accepted seven of them: *V. diversipila*, *V. gaylussaciae*, *V. japonica*, *V. pini*, *V. ulicicola*, *V. uliginosa*, and *V. venturioides*. Baral (1993) noted the divergent morphology of *V. heterotricha*, which has, according to a re-examination of the holotype (Baral *in prep.*), 4–6-celled, deep red-brown, entirely smooth spiny hairs and equally long, 4–7-celled, entirely smooth, apically hyaline and helicoid, basally straight and ochre-brown hairs. According to Spooner (1987: 589) and Raitviir (2004), *V. heterotricha* could be a member of an undescribed genus in *Dermateaceae* in the broad sense of that time.

The species of *Venturiocistella* are reported as saprobes on plant debris, and many seem to be host-specific (Baral 1993, Raitviir 2004). Most species of the genus are known from a limited number of collections or only from the types, and their actual distribution (Table 2) remains unknown, though all available records are limited to the temperate regions of the Northern Hemisphere (Baral 1993, Raitviir 2004). Very probably, due to the extremely tiny apothecia, they remain simply overlooked (Galán & Raitviir 1994). Of the seven accepted species of the genus, five are foliicolous and three are restricted to decaying leaves of *Ericaceae*. The few observations available indicate that they may be found mainly on

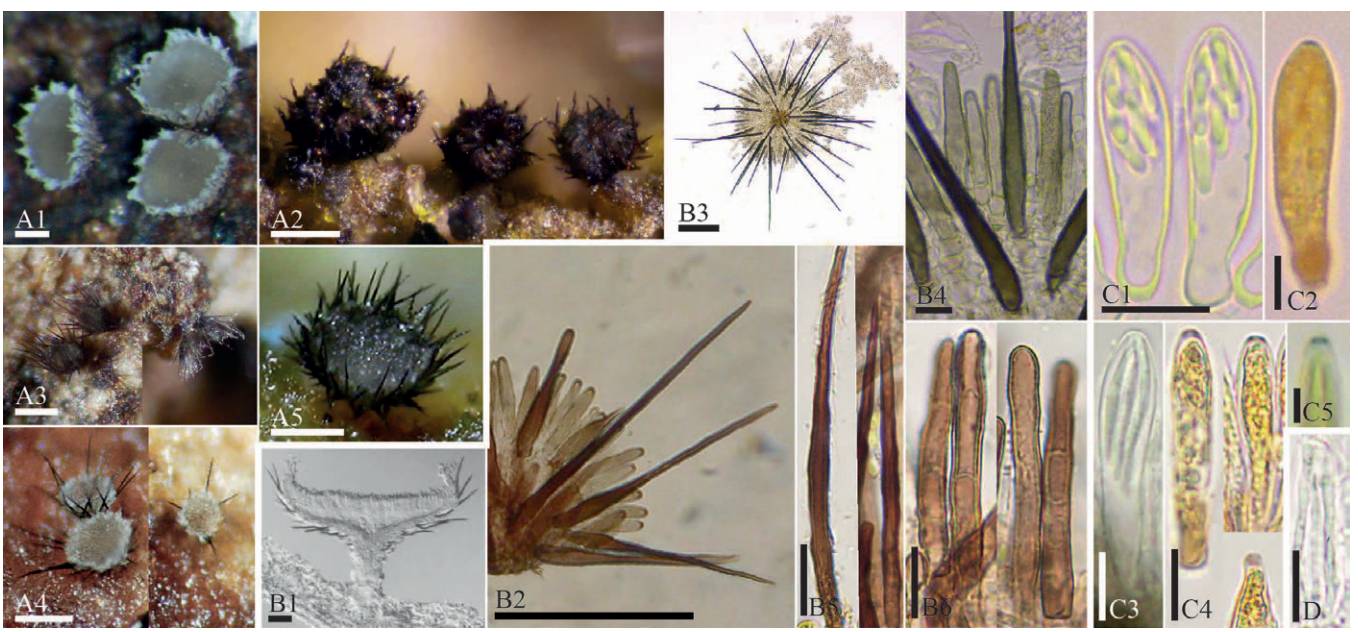

Fig. 10. Detailed morphology of the genus *Venturiocistella*. **A.** Fresh and dry apothecia. **B.** B1. Median section of apothecium; B2. Squash mount showing spiny and cylindrical hairs (in polyvinyl alcohol); B3. View of lower side of apothecium; B4–6. Spiny and cylindrical hairs. **C.** C1–5. Living and dead asci showing arrangement of spores, hemiamyloid (C4–5, C5 KOH-pretreated) and euamyloid (C2) apex. **D.** Living paraphyses. Collections: *V. japonica* = A1, B1 (TNS-F-18030). *V. diversipila* = A3 (SBRH264); A4 (J.H. Petersen, JHP-99.475); B2 (HB3586b); B3, B4, C1, C2 (ES 14.10.2017). *V. pini* = A5 (G. Marson, 7.XII.2007). *V. ulicicola* = A2, B5, B6, C4, D (ERD-6422); C3, C5 (HB7648a). Scale bars: A1–A5, B3 = 100 µm; B1, B2 = 50 µm; B4–6, C1–4, D = 10 µm; C2, C5 = 5 µm.

last year's unskeletonised leaves (Baral 1993). *Venturiocistella venturioides* is known on leaves of *Vaccinium uliginosum* growing in raised bogs in Northern Europe and the Alps (Nannfeldt 1936, Eriksson 1970, Remler 1979, Baral 1993). *Venturiocistella uliginosa* has also been reported on *Va. uliginosum* leaves from Europe (Norway, Switzerland) and South Siberia (Baral 1993, Raitviir 2004). *Venturiocistella gaylussaciae* is known only from the type collection on leaves of *Gaylussacia dumosa* and *G. resinosa* in eastern North America (Ellis & Everhart 1888, Dennis 1963, Baral 1993). *Venturiocistella diversipila* has been reported on fallen leaves of a variety of deciduous hardwoods (*Quercus*, *Populus*, *Betula*) across Europe (the UK, Germany, and Spain) (Graddon 1977, Baral 1993, Galán & Raitviir 1994). Galán & Raitviir (1994) supposed that *V. diversipila* may be a widely distributed species on a wide variety of fallen leaves in late autumn. *Venturiocistella japonica*, another foliicolous species, was described on decaying leaves of *Cercidiphyllum japonicum* from northern Honshu, Japan (Hosoya & Harada 1999). An unidentified or undescribed foliicolous *Venturiocistella* sp. was reported from leaves of *Acer pseudosieboldianum* in Korea (Han *et al.* 2014). The two remaining species are corticolous. *Venturiocistella pini* has been found on bark and resin of several species of *Pinus* (*P. nigra*, *P. sylvestris*, *P. mugo*, *P. radiata*) and is not uncommon in Europe, being reported from Austria, France, Lithuania, Luxembourg, Netherlands and the UK (Höhnel 1907, Graddon 1980, Baral 1993, Schultheis *et al.* 2001, Ayel & Van Vooren 2005, Kutorga & al. 2012). According to Baral (1993), *V. pini* is often observed on resinous secretions in and around the wound on pine branches and trunks in association with other ascomycetes (*e.g. Zythia resinae*, *Ciliolarina laricina*, *Claussenomyces kirschsteinianus*). The only known collection of *V. ulicicola* originates from the charred bark of *Ulex europaeus* in the UK (Graddon 1980, Baral 1993).

Dennis (1963) and later Baral (1993) noted the similarity between *Venturiocistella* and *Fuscolachnum* (Dennis as *Dayscyphus*, *i.e. D. misellus*) by explaining that *Fuscolachnum* differs in lacking the spiny hairs (as 'setae'), the latter author also in a partial granulation of excipular cells (those giving rise to the hairs). Currently there are no molecular data available for the type species (*V. venturioides*). Our phylogenetic analyses (Fig. 2) indicate that species identified as *Fuscolachnum* (members of the *F. misellum* aggregate), fall within the *Venturiocistella* clade, which is discussed in detail in section 8 (Notes on *Fuscolachnum*). We could not verify the presumed monophyly of *Venturiocistella* because of the paucity of sequences; molecular data are only available for *V. japonica* and an unidentified *Venturiocistella* sp. Therefore, we refrain from proposing any combinations of *Fuscolachnum* spp. in *Venturiocistella* until more information is available.

Key to accepted species of *Venturiocistella* based on sexual morphs:

1. Asci arising from simple septa, hairs pale brownish 20–70 × 5–6.5 µm, setae smooth in upper part, 45–85 × 5–6.5 µm, asci 40–60 × 6–8 µm, ascospores 12–17.5 × 2–3 µm, on leaves of *Ericaceae* in Europe and Asia ..... *V. uliginosa*
1'. Asci arising from croziers 2

2. Hairs 5–7 µm wide, asci 17–22 × 4.5–6 µm, ascospores 5–9 × 1.5–2.4 µm, on deciduous leaves in Europe ..... *V. diversipila*
2'. Hairs up to 3–5 µm wide 3

3. Ascospores 1–3 septate, fusoid, 15–22 × 1.5–2 µm, on bark of *Ulex* in Europe ..... *V. ulicicola*
3. Ascospores aseptate, cylindric-clavate-fusoid-ellipsoid, 6–18 × 1.5–2.7 µm, on leaves, bark or cones in the northern hemisphere 4

4. Average ascus length less than 10 µm 5
4'. Average ascus length greater than 10 µm 6

5. Apothecia up to 0.15 mm diam, hairs 35 × 3.5–5 µm, setae 80–250 × 4–7 µm, on fallen leaves of *Ericaceae* in Europe ..... *V. venturioides*
5'. Apothecia 0.25–0.4 mm diam, hairs 50 × 4 µm, setae 80–115 × 4–7 µm, on fallen leaves of *Cercidiphyllaceae* in Japan ..... *V. japonica*

6. Average ascus width less than 30 µm, ascospores cylindric-clavate, 7–13 × 1.5–2.1 µm, on fallen leaves of *Ericaceae* ..... *V. gaylussaciae*
6'. Average ascus width greater than 30 µm, ascospores fusoid, 9–18 × 1.5–2.7 µm, on bark and cones of *Pinaceae* ..... *V. pini*

Notes on *Gamarada*: This monotypic genus was recently erected by Midgley *et al.* (2018), though the type species, *G. debralockiae*, had been studied and reported by authors for more than two decades earlier, mostly as "*Woollsia* mycorrhizal taxon VI." The morphology of the genus provides few characters since the one species only forms a slow-growing sterile mycelium, sometimes with exudates, in culture. No sexual morph is known.

Gamarada debralockiae is well known as an extremely widely distributed ericoid mycorrhizal fungus in Australia, forming associations with species in multiple genera of *Ericaceae*. Midgley *et al.* (2018) identified several other groups of sequences as putative species of *Gamarada* based on a greater than 97 % similarity in ITS sequences compared with those for *G. debralockiae*; these relationships were not recovered with support in their phylogenetic analyses, however. *Gamarada* "sp. 2" and "sp. 3" also appear to be associated with the roots of *Ericaceae* in Australia, with the latter having also been detected in Malaysia and Japan. Two sequences from Japanese records included in *Gamarada* were not assigned to a putative species, one being similarly isolated in association with *Ericaceae*, the other in association with roots of *Fagaceae*.

Phylogenetically, *Gamarada* is sister to *Glutinomyces*, another genus of root associated fungi for which no sporulating morphs are known. Further phylogenetic work is warranted to probe the boundary between these two genera.

Table 2. Ecology and distribution of *Hyphodiscaceae*. Sex = sexual morph, Asex = asexual morph; Ang = angiosperm, Gym = gymnosperm, Pte = pteridophytes, Her = herbaceous plants, Bry = bryophytes, Fun = fungi; W = wood and bark, S = stems, L = leaves, R = roots, D = debris; NA = North America, Eu = Europe, As = Asia, Af = Africa, SA = South America, O = Oceania, An = Antarctica.

Accepted species	Sex	Asex	Host							Host part					Distribution						
			Ang	Gym	Pte	Her	Bry	Fun	Soil	W	S	L	R	D	NA	Eu	As	Af	SA	O	An
Hyphodiscus auricolor	✓	×		■						■							■				
H. brachyconius	×	✓	■							■						■					
H. brevicollaris	×	✓						■								■					
H. cajaniensis	✓	✓																			
H. delitescens	✓	?					■								■	■	■				
H. hyaloscyphoides	✓	✓	■							■							■				
H. hymeniophilus	✓	✓						■							■	■	■	■			
H. incrustatus	✓	×						■							■	■					
H. luxurians	×	✓								■						■					
H. otanii	✓	✓	■	■						■							■				
H. pinastri	✓	×		■						■								■			
H. smaragdinus	✓	×	■							■						■					
H. theiodeus	✓	×						■							■	■	■				
H. ucrainicus	✓	×						■								■	■				
Hyphopeziza pygmaea	✓	×	■									■				■	■				
Scolecolachnum pteridii	✓	?			■							■							■		
Fuscolachnum boreale	✓	×		■						■		■			■	■					
F. hainesii	✓	×			■							■				■	■				
F. inopinatum	✓	×			■							■			■	■					
F. labradoricum	✓	×	■									■			■						
F. misellum	✓	×	■									■			■	■					
F. necator	✓	×					■									■					
F. pteridis	✓	×			■						■				■	■	■				
Venturiocistella diversipila	✓	×	■									■				■					
V. gaylussaciae	✓	×	■									■			■						
V. japonica	✓	×	■									■					■				
V. pini	✓	×		■						■						■					
V. ulicicola	✓	×	■							■						■					
V. uliginosa	✓	×	■									■				■					
V. venturioides	✓	×	■									■				■					
Microscypha arenula	✓	×			■						■	■				■	■				
M. cejpii	✓	×	■									■				■					
M. enrhizus	✓	×	■									■				■					
M. fuscoparaphysata	✓	×	■									■					■				
M. septospora	✓	×								■							■				
Gamarada debralockiae	×	×	■										■							■	
Glutinomyces brunneus	×	×	■										■				■				
G. inflatus	×	×	■										■				■				
G. takaragaikensis	×	×	■										■				■				
G. vulgaris	×	×	■										■				■				
Soosiella minima	×	×							■							■					

Notes on *Glutinomyces*: Selected publications chronologically arranged are Crous *et al.* (2017), Nakamura *et al.* (2018), Nakamura *et al.* (2019a), and Nakamura *et al.* (2019b). The genus was first described by Nakamura in Crous *et al.* (2017) for *Glutinomyces brunneus*. Nakamura *et al.* (2018) added three additional species. The species only form a slow-growing sterile mycelium with sticky exudates in culture, sometimes with "chlamydospore-like" structures. Of the four species in the genus, only *G. brunneus* is morphologically distinguishable from the others in that it is not white in culture. The other three species (*G. inflatus*, *G. takaragaikensis*, and *G. vulgaris*) can only be distinguished by molecular methods. Interestingly, though sporulating forms of these species have not

been encountered, there is evidence that the sterile mycelia of *G. brunneus* are able to interact parasexually and transfer genetic material (Nakamura *et al.* 2019a).

Species of *Glutinomyces* have been isolated in Japan from surface sterilised roots of *Quercus* spp. and (with the exception of *G. takaragaikensis*) *Castanopsis cuspidata*. Their specific ecology is not known, but they were likely present as endophytes. More recently, sequences from tree litter in the Netherlands (Veen *et al.* 2021), lichen-containing reindeer food samples in Norway (Meyer 2019), grape skins (Sun *et al.* 2021) and fermenting soy sauce (Kuang *et al.* 2022) in China, and root tips in Michigan (Pellitier & Zak 2021), Malaysia (Segnitz 2019), and Indonesia (Mujahidah *et al.* 2018) have been identified as belonging to the genus *Glutinomyces*; unfortunately, the evidence provided in these sources is not sufficient to verify their identifications.

Notes on *Soosiella*: This monotypic genus was erected by Hujslová *et al.* (2014) for *Soosiella minima*. The single species forms a very slow-growing sterile mycelium in culture. The authors note that on potato carrot agar, colonies are "yeast-like". Based on their descriptions for the other taxa in the same paper, this seems to be a macroscopic observation of the colonies rather than an indication of the presence of a single-celled yeast morph.

The only reports of *Soosiella minima* have been those in the original description (Hujslová *et al.* 2014). All isolates were derived from samples of highly acidic soil in Czech Republic. Subsequent growth tests in culture suggest that *S. minima* is fairly acidotolerant and halophilic but the species does not exhibit a preference for acidic growing environments. The species is one of a small number of fungal species detected growing in highly acidic soils (Hujslová & Gryndler 2019). Its ecology is unclear.

Phylogenetic analyses place *Soosiella* sister to *Hyphopeziza*. Further work is needed to clarify the boundaries between these monotypic genera.

CONCLUSIONS AND FUTURE DIRECTIONS

The circumscription and boundaries of *Hyphodiscaceae sensu* Ekanayaka *et al.* (2019) are clarified and refined through this work, but our examination has revealed numerous taxonomic issues in the family remaining to be resolved. *Microscypha* and *Fuscolachnum* are polyphyletic, as are *Hyphodiscus hymeniophilus* and *Fuscolachnum misellum*; the boundaries between *Fuscolachnum s. str.* and *Scolecolachnum* are not well resolved; and the genera *Fuscolachnum*, *Microscypha* and *Venturiocistella* contain morphologically strongly divergent species or groups of species whose relationship to the rest of the genus has not been tested with molecular methods, and in some cases even modern morphological methods. An overarching issue in the family that contributes to these problems is the lack of molecular data for many species in genera erected based on morphological features only. *Microscypha* and *Venturiocistella* in particular are poorly sampled, with only one species of the accepted species in each genus sequenced. Another broad issue is one of geographic sampling: all material examined in this study was Eurasian in origin, and most identified representative sequences for the family are as well (*S. pteridii* is from South America, and *G. debralockiae* is from Oceania). There is some evidence that diversity should be higher in other parts of the world; for instance, ITS sequencing from specimens from New Zealand native forests (images in https://biotanz.landcareresearch.co.nz/scientific-names/bd4e773c-c76a-4065-a439-7a3e0d53bef1) suggest at least 10 species within the family, with some possibly representing novel genera. Species in *Hyphodiscaceae*, as is true of many in *Leotiomycetes*, are easily overlooked and do not easily lend themselves to molecular methods since ascomata are found on unusual substrates, are small and can be produced sparsely. These last two features in turn further limit the possibilities of generating sequences from historical types of species collected only once.

Possible solutions are available for most of these issues. Targeted collecting efforts should be undertaken in undersampled areas of the globe, such as the Southern Hemisphere and North America, with an emphasis on unusual substrates (such as bryophytes and fungi). Such collections of members of this family can be used to generate sequence data and reliable morphological data, preferably from living specimens. Efforts should also be made to recollect, examine alive, and sequence already described species by visiting type localities; this is particularly crucial in the case of generic types, in order to allow a clear and appropriate application of generic names. Freshly obtained material should be cultured providing both additional characters and larger quantities of material for molecular study. This could also provide links to as-yet-unidentified asexual morphs. Types which have not been examined using modern techniques for discomycetes should also be re-examined to test past taxonomic hypotheses.

In addition to more easily attainable goals, there are some critical but more difficult needs. It is crucial to develop molecular techniques to reliably generate sequence data from scant historical types. Recollection of even relatively common fungi is often highly unpredictable, and so recollecting material of rare taxa from unusual localities may be near impossible. It is also important to provide formal names for existing specimens that appear to represent undescribed species.

In addition to helping clarify the taxonomic issues in *Hyphodiscaceae*, the generation of reliably identified sequence data will help ecologists who are working more and more with e-DNA derived from wood or other plant tissues and need identified voucher sequences for barcode comparisons. There is also evidently a great number of unidentified, extant sequences belonging in this family, which sequences from reliable sources should help to identify. With cooperation and a good amount of work, it should be possible to clarify and flesh out this poorly known family in the future.

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DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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