

Phylogeny and classification of *Cryptodiscus*, with a taxonomic synopsis of the Swedish species

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The phylogeny, taxonomy and classification of *Cryptodiscus* are examined. The current generic and species delimitations, and the relationship of the genus within the *Ostropomycetidae*, are tested by molecular phylogenetic analyses of the nuclear ITS and LSU rDNA and the mitochondrial SSU rDNA. In our new circumscription *Cryptodiscus* is a monophyletic group of saprotrophic and lichenized fungi characterized by small, urceolate apothecia, mostly hyaline ascomatal walls without any embedded crystals, no clear periphysoids, and with oblong to narrow-cylindrical septate ascospores. *Cryptodiscus* forms a well-supported clade together with *Absonditella* and the remaining *Stictidaceae*. *Paschelkiella* and *Bryophagus* are synonymised with *Cryptodiscus*. Species excluded from *Cryptodiscus* are *Cryptodiscus anguillosporus*, *C. angulosus*, *C. microstomus*, and *C. rhopaloides*. *Cryptodiscus* in Sweden is revised and six species are accepted, of which one is newly described: *C. foveolaris*, *C. gloeocapsa* comb. nov. (\equiv *Bryophagus gloeocapsa*), *C. incolor* sp. nov., *C. pallidus*, *C. pini* comb. nov. (\equiv *Paschelkiella pini*), and the rediscovered species *C. tabularum*. The additional new combinations *Cryptodiscus similis* comb. nov. and *C. minutissimus* comb. nov. are coined for the remaining former *Bryophagus* species. Lectotypes are designated for *Bryophagus gloeocapsa* Arnold, *Odontotrema pini* Romell and *Stictis foveolaris* Rehm.

Key words: *Ascomycota*, discomycetes, lichens, molecular phylogeny, *Ostropomycetidae*

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Introduction

Cryptodiscus (*Stictidaceae*, *Ostropomycetidae*, *Lecanoromycetes*) is a group of small and inconspicuous discomycetes, most of which are saprotrophs on dead wood. This cosmopolitan genus comprises only a few currently accepted species, but these fungi are rarely collected and studied and our knowledge is thus very limited. In the latest monograph of *Cryptodiscus*, Sherwood (1977) accepted six species; *C. pallidus* (type species), *C. foveolaris*, *C. microstomus*, *C. pumilus*, *C. stercicola* and *C. speratus*. The three last ones are temperate and tropical American species that were described as new by Sherwood. She commented only on some of the ca. thirty additional species described at that time and

listed in Saccardo's *Sylloge Fungorum* (Saccardo, 1889; Saccardo and Sydow, 1899, 1902; Saccardo and Trotter, 1913; Saccardo *et al.*, 1928), many of which are only known from fragmentary or lost type material. Additional species are *C. sambuci* (USA; Cash, 1943), *C. tabularum* (Germany; Kirschstein, 1936), *C. rutilus* (Germany), which was originally described as *Calonectria* (Kirschstein, 1939) and recombined by Rossman (1979; 1980), and *C. anguillosporus* (Sweden), which was newly described by Holm and Holm (1981).

Species of *Cryptodiscus* have been described from decaying palm fronds, lycopods and the polypore *Stereum* sp., but most species occur on weathered decorticated wood of various trees. Traditionally *Cryptodiscus* includes saprotrophic species with ascomata immersed

in the substrate, which become erumpent in some taxa. The margin is thin and somewhat indistinctive, the disc deeply urceolate. The asci are 8-spored and cylindrical-clavate, the spores hyaline, one- to pluriseptate, and the paraphyses simple, sometimes forked at the end.

The classification of *Cryptodiscus* and other *Stictidaceae* has varied over time. Minks (1881) and Lettau (1937) were early to suggest a relationship between saprotrophic *Stictidaceae* with the lichenized *Gyalectaceae*. This was mainly due to the superficial resemblance of the ascomata between *Stictis stellata* and some *Gyalectaceae*, but also due to the similar development of the ascomata. Mycologists later assumed that the *Stictidaceae* are related to other ascomycete groups e.g. *Clavicipitales* (Gäumann, 1964; Kreisel, 1969). Korf (1973) and Dennis (1978) included *Cryptodiscus* in the *Dermateaceae* (*Helotiales*) separate from the other *Stictidaceae*. Vězda (1966) suggested that *Stictidaceae* might be more closely related to the lichenized *Thelotremataceae*, agreed on by Gilenstam (1969) and Henssen and Jahns (1974) and later confirmed by molecular phylogenetic results (Winka *et al.*, 1998). In the first molecular phylogenetic study that included *Cryptodiscus*, the single analysed species *C. foveolaris* did not group with other members of *Stictidaceae*, but rather with *Thelotrema* (Wedin *et al.*, 2005). *Stictidaceae* and *Graphidaceae* (including *Thelotremataceae*; Mangold *et al.*, 2008) are currently included in the *Ostropales* in the *Ostropomycetidae* (Lumbsch *et al.*, 2007; Hibbett *et al.*, 2007), but the delimitation of this order is admittedly rather unclear (Tehler and Wedin, 2008).

In the present study, we attempted to include as many Swedish representatives of *Cryptodiscus* as possible and in addition a selection of other *Ostropomycetidae*, into an updated molecular phylogeny. The aim is to analyse the phylogenetic position of *Cryptodiscus* within the *Ostropomycetidae*, to test the current generic concept and delimitation, and to investigate species boundaries. The relationship of saprophytic *Cryptodiscus* species with lichens will be discussed. Our field studies focussing on ostropalean fungi in Sweden revealed an undescribed *Cryptodiscus*

species as well as species that need to be combined into this genus. For this reason the taxonomy and nomenclature of the Swedish species of *Cryptodiscus* are revised, based on both morphological and molecular studies. Information on substrate specificity and ecological preferences of Swedish species is interpreted based on field experience, own collections and herbarium material studied.

Materials and methods

Specimens

We analysed mainly fresh material collected in different areas of Sweden and supplemented own collections with herbarium material from the herbaria K, S, and UPS (abbreviations according to Holmgren and Holmgren, 1998; <http://sweetgum.nybg.org/ih/>). Examined types and specimens used for microscopic studies are listed following the species description. We collected eight species of *Cryptodiscus* in Sweden and sequenced twenty specimens of *Cryptodiscus* and one of *Absconditella lignicola* for this project. Voucher details are given in Table 1. Additional sequences of *Cryptodiscus* and other genera that were used in the phylogenetic analyses were taken from GenBank and are listed in Table 2.

Microscopic studies

For routine identification sections were cut by hand with a razor blade. Sections with the freezing microscope were used for detailed studies of the anatomy. Measurements of spores, asci, hymenium and details of the apothecial wall were done in water. Lugol's solution was used for the detection of amyloid structures. Several sections of each species were stained with cotton blue in lactic acid to enhance the contrast for a better observation of hyphal structures.

DNA extraction, PCR and sequencing

Total DNA was extracted from apothecial tissue with the DNeasy Plant Mini Kit (Qiagen) according to the instructions of the manufacturer. The small subunit of the mitochondrial rDNA (mtSSU) was amplified with the primers mrSSU1 and mrSSU3R (Zoller *et al.*, 1999) and the internal transcribed

Table 1. Voucher specimens sequenced for this study with collections details and accession numbers of the sequences.

Species		Specimen	mtSSU	nuLSU
<i>Absconditella lignicola</i>	EB211	Sweden, Östergötland, Svensson 941 (priv. Herb. Svensson)	FJ904691	FJ904669
<i>Cryptodiscus foveolaris</i>	EB86	Sweden, Södermanland, Baloch SW072 (S)	FJ904692	FJ904670
<i>C. foveolaris</i>	EB88	Sweden, Lule Lappmark, Gilenstam 2719 (UPS)	FJ904693	FJ904671
<i>C. foveolaris</i>	EB147	Sweden, Lule Lappmark, Gilenstam 2776 (UPS)	FJ904694	FJ904672
<i>C. foveolaris</i>	EB155	Sweden, Skåne, Baloch SW168 (S)	FJ904695	FJ904673
<i>C. gloeocapsa</i>	EB93	Sweden, Jämtland, Tibell 23543 (UPS)	FJ904696	FJ904674
<i>C. incolor</i>	EB164	Sweden, Skåne, Baloch & Arup SW138 (S)	FJ904697	FJ904675
<i>C. microstomus</i>	EB185	Sweden, Lycksele Lappmark, Gilenstam 2784a (UPS)	FJ904698	FJ904676
<i>C. pallidus</i>	EB40	Sweden, Lycksele Lappmark, Gilenstam 2694 (UPS)	FJ904699	FJ904677
<i>C. pallidus</i>	EB60	Sweden, Skåne, Læssøe SW012 (S)	FJ904700	FJ904678
<i>C. pallidus</i>	EB152	Sweden, Lycksele Lappmark, Gilenstam 2475 (UPS)	FJ904701	FJ904679
<i>C. pallidus</i>	EB173	Sweden, Östergötland, Baloch SW174 (S)	FJ904702	FJ904680
<i>C. pini</i>	EB76	Sweden, Småland, Westberg SW137 (S)	FJ904703	FJ904681
<i>C. pini</i>	EB82	Sweden, Östergötland, Baloch SW069 (S)	FJ904704	FJ904682
<i>C. pini</i>	EB178	Sweden, Uppland, Wedin & Baloch 26VII07 (S)	FJ904705	FJ904683
<i>C. pini</i>	EB181	Sweden, Skåne, Baloch & Arup SW175 (S)	FJ904706	FJ904684
<i>C. rhopaloides</i>	EB100	Denmark, Jylland, Læssøe 12881 (S)	FJ904707	FJ904685
<i>C. tabularum</i>	EB62	Sweden, Lycksele Lappmark, Gilenstam 2759 (UPS)	FJ904708	FJ904686
<i>C. tabularum</i>	EB77	Sweden, Småland, Westberg SW136a (S)	FJ904709	FJ904687
<i>C. tabularum</i>	EB87	Sweden, Uppland, Baloch SW073 (S)	FJ904710	FJ904688
<i>C. tabularum</i>	EB169	Sweden, Bohuslän, Westberg SW132 (S)	FJ904711	FJ904689
<i>C. tabularum</i>	CO205	Sweden, Gilenstam 2641a (UPS)	FJ904712	FJ904690

spacer (ITS) and parts of the nuclear large subunit rDNA (nuLSU) were amplified using the primers ITS1F (Gardes and Bruns, 1993) and LR3 (Vilgalys and Hester, 1990). Biotech Ready-To-GoPCR Beads (Amersham Pharmacia) were used for PCR. The conditions for the thermocycling were 94 °C (3 min), six cycles of 94°C (45 s), 56–51°C (45 s), 72°C (1 min 30 s), 35 cycles of 94°C (30 s), 48°C (30 s), 72°C (1 min), and a final extension of 72°C (5 min). PCR products were cleaned using Qiaquick spin columns (Qiagen). Both complementary strands were sequenced with the ABI BigDye Terminator Kit (Applied Biosystems). For sequencing of the ITS/nuLSU fragment the primer ITS4 (White *et al.*, 1990) and LR0R (Rehner and Samuels, 1994) were used in addition to the PCR primers, in case of the mtSSU fragment the same primers as for the PCR were applied. The sequencing products were cleaned with the DyeEx 96 Kit (Qiagen) and were run on an ABI3100 automated sequencer. The raw data were assembled and

edited using the STADEN Package (<http://www.mrc-lmb.cam.ac.uk/pubseq>).

Alignment and Data analysis

The nucleotide sequences were aligned with the multiple sequence alignment option in the program Clustal W (Thompson *et al.*, 1994). We assembled two different data sets, one to optimally investigate the systematic position of the different *Cryptodiscus* species within the *Ostropomycetidae* and another one to analyse the genetic variation and relation of the *Cryptodiscus* species s.str. The first dataset comprises sequences of *Cryptodiscus* species and representatives of all major lineages of *Ostropomycetidae* that were available in GenBank. Four species of *Lecanoromycetidae* were used as outgroup taxa. In the second dataset we included members of *Cryptodiscus* s.str. represented by several specimens per taxa (except *C. incolor*), *Absconditella* species as closest relatives to *Cryptodiscus* and three species of *Stictis* and *Schizoxylon* as outgroup

Table 2. Additional sequences taken from GenBank to include in the phylogenetic analyses.

Species	mtSSU	nuLSU
<i>Absconditella sphagnorum</i>	AY300872	AY300824
<i>Absconditella</i> sp.	AY300873	AY300825
<i>Aspicilia caesiocinerea</i>	DQ986892	DQ986778
<i>Baeomyces placophyllus</i>	AY584695	AF356658
<i>Calenia monospora</i>	AY341365	AY341351
<i>Cladonia rangiferina</i>	AY300881	AY300832
<i>Coenogonium pineti</i>	AY300884	AY300834
<i>C. lepreurii</i>	AY584698	AF465442
<i>Conotrema urceolatum</i>	AY661676	AY661686
<i>Cryptodiscus foveolaris</i>	AY661673	AY661683
<i>C. gloeocapsa</i>	AY300880	AF465440
<i>Diploschistes scruposus</i>	AY584692	AF279389
<i>Echinoplaca epiphylla</i>	AY648891	AY341354
<i>Fissurina marginata</i>	AY648902	AY640012
<i>Glyphis cicatricosa</i>	AY648903	AY640025
<i>Graphis scripta</i>	AY853322	AY853370
<i>Gyalecta jenensis</i>	AY340493	AF465450
<i>G. ulmi</i>	AY300888	AF465463
<i>Gyalidea hyalinescens</i>	DQ972996	DQ973046
<i>Lecanora polytropa</i>	DQ986807	DQ986792
<i>Ochrolechia tartarea</i>	AY300899	AY300848
<i>Odontotrema</i> sp. 1	AY661674	AY661684
<i>Odontotrema</i> sp. 2	AY661675	AY661685
<i>Pertusaria amara</i>	AY300900	AF274101
<i>Phlyctis argena</i>	DQ986880	DQ986771
<i>Phyllobaeis erythrella</i>	DQ986888	DQ986780
<i>P. imbricata</i>	DQ986895	DQ986781
<i>Physcia aipolia</i>	DQ912290	DQ782904
<i>Placopsis perrugosa</i>	AY584716	AF356660
<i>Pyxine soredata</i>	DQ972984	DQ973036
<i>Sagiolechia rhexoblephara</i>	AY853341	AY853391
<i>Schizoxylon albescens</i>	AY661680	AY661689
<i>Stictis populorum</i>	AY527363	AY527334
<i>Stictis radiata</i>	AY300914	AY300864
<i>Thelotrema lepadinum</i>	AY300916	AY300866
<i>Trapelia placodioides</i>	AF431962	AF274103
<i>Trapeliopsis granulosa</i>	AF381567	AF274119

taxa. Separate and combined analyses of mtSSU and nuLSU (first dataset) or ITS-nuLSU (second dataset) sequences were performed using Bayesian inference as well as a maximum parsimony approach. Maximum parsimony analyses were performed using PAUP* 4.0b10 (Swofford 2004). Gaps were treated as missing data. For each run a heuristic search with 1000 random-addition sequence replicates was applied using tree bisection-reconnection (TBR) branch-swapping, with MulTrees on and the steepest descent option not in effect. Bootstrap supports were estimated with 1000 replicates and 10 random sequence additions per bootstrap replicate with the same search parameters as above.

Bayesian Metropolis coupled Markov chain Monte Carlo (B/MCMCMC) analyses were performed in the program MrBayes Version 3.1.2 (Huelsenbeck and Ronquist, 2001, Ronquist and Huelsenbeck, 2003). Each analysis was performed using two independent runs with five chains running for 2000000 generations. Trees were sampled every 100th generation. After 2000000 generations the average standard deviation of the split frequencies between the simultaneous runs was below 0.005 and the log-likelihood had reached stationarity. 25% of the sampled trees were discharged as burnin. The frequencies of topologies in the resulting tree sample represent the posterior probability of the branching patterns (Huelsenbeck and Bollback, 2001). The general time reversible model (GTR) using a gamma shaped distribution and proportion of invariant sites was suggested as the best DNA substitution model for each gene (mtSSU and nuLSU or ITS-nuLSU) for both datasets. This was evaluated with the help of the program MrModeltest (Nylander, 2004), which is a reduced version of Modeltest (Posada and Crandall, 1998).

Results and discussion

DNA sequences and alignments

The first alignment with representatives of *Ostropomycetidae* resulted in a matrix of 2456 nucleotide positions (mtSSU 1009/nuLSU 1447), of which 1128 indel and ambiguous aligned positions were excluded. Of the 1328 included characters (mtSSU 640/nuLSU 688) were 609 parsimony informative (mtSSU 315/nuLSU 294). The second alignment includes 20 sequences of *Cryptodiscus*, three *Absconditella* species and three other *Stictidaceae* as outgroup taxa. The alignment has 2394 (mtSSU 1240/ITS-nuLSU 1154) nucleotide position, of which 762 indel and ambiguously aligned positions were excluded prior analysis. The included 1632 nucleotide positions (mtSSU 688/ITS-nuLSU 944) comprise 436 parsimony informative characters (mtSSU 215/ITS-nuLSU 221).

Separate analyses of two gene regions result in tree topologies that are concordant in strongly supported branches (>70% bootstrap (bs), >95% posterior probability (pp)). The mtSSU rDNA analysis, however, provides a far

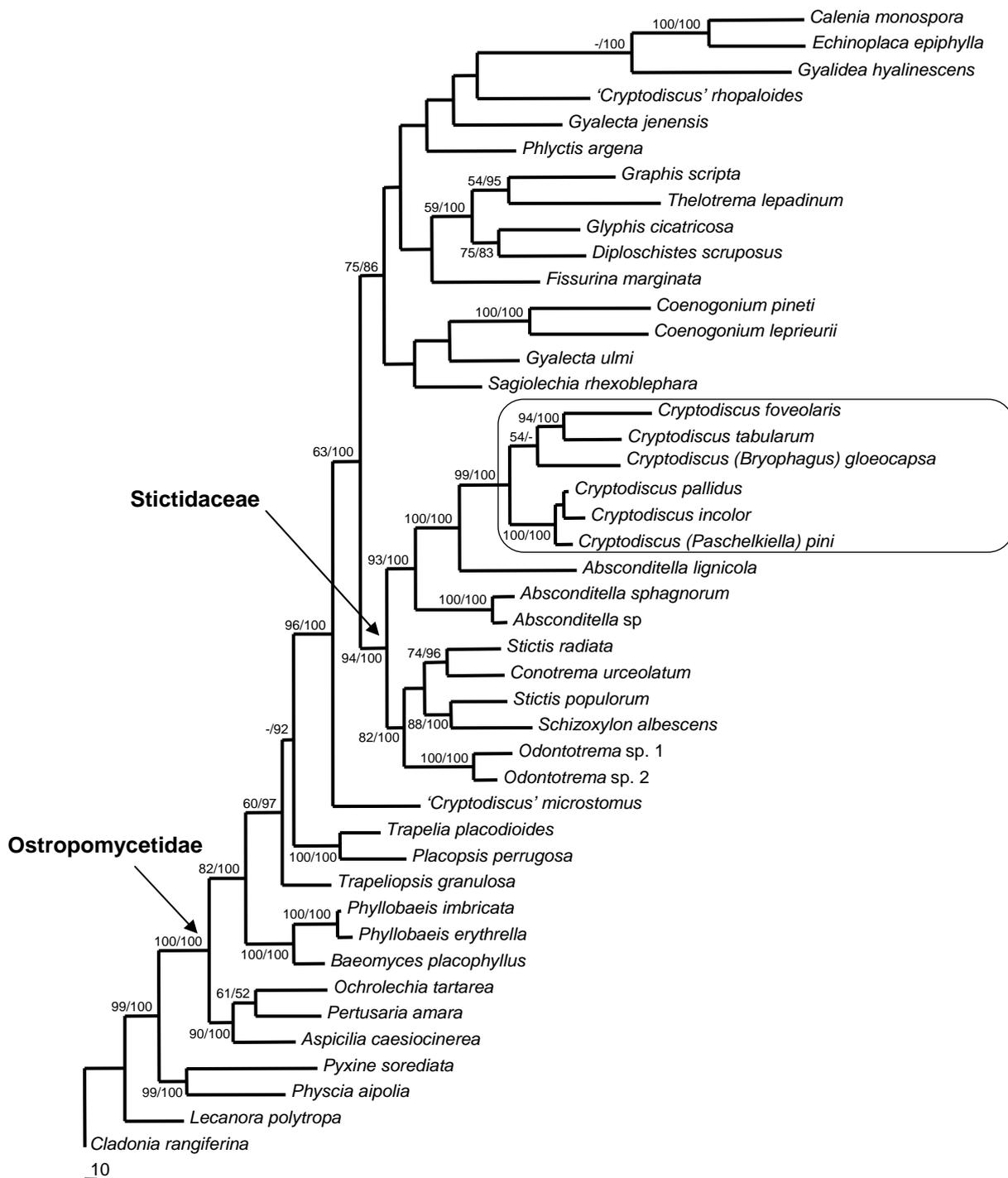


Fig. 1. *Cryptodiscus* within *Ostropomycetidae*. One of 3 most parsimonious trees inferred from mitochondrial SSU and nuclear LSU rDNA sequence data. Bootstrap supports and posterior probabilities (bs/pp) are indicated next to the node.

better resolution than the nuLSU rDNA analysis which to some extent was unresolved. We will thus only discuss the combined analyses (mtSSU + nuLSU) below and comment on the few differences there are. Although the separate gene trees are congruent, the maximum parsimony and the Bayesian analyses differ in terms of the position of *Bryophagus gloeocapsa*. In the maximum parsimony analysis *B. gloeocapsa* is sister to

Cryptodiscus foveolaris and *C. tabularum*. This is only supported by the mtSSU data (bs=78), but not the nuLSU, which resulted in a 74% bootstrap support in the combined analysis (Fig. 2a). In the Bayesian tree *B. gloeocapsa* groups with *C. pallidus* and *Paschelkiella pini*, however with low support in the single gene analyses (mtSSU: pp=88, nuLSU: pp=86, combined: pp=99) (Fig. 2b).

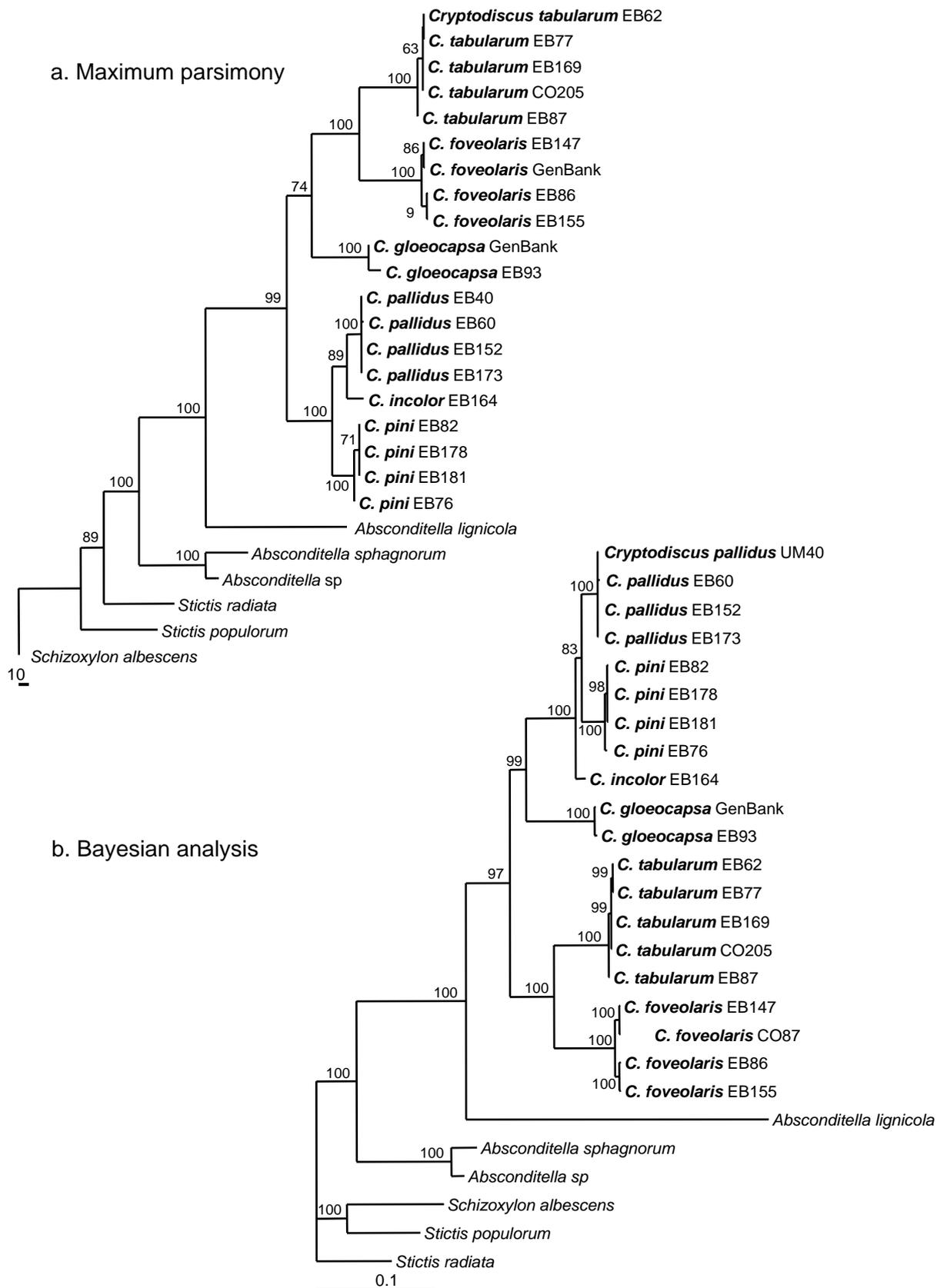


Fig. 2. Phylogeny of *Cryptodiscus sensu stricto*. **a.** Most parsimonious trees inferred from a combined analysis of mitochondrial SSU and nuclear ITS-LSU rDNA sequence data. Bootstrap supports above 50% are indicated next to the node. **b.** 50% Majority-rule consensus tree of 421000 trees from a B/MCMC tree sampling procedure analysing the same dataset as in a. Posterior probabilities are indicated next to the node.

Cryptodiscus* within *Ostropomycetidae

Cryptodiscus s.str. forms a monophyletic clade with strong support (bs=99, pp=100), including the genera *Paschelkiella* and *Bryophagus*, which are nested within *Cryptodiscus*. *Absconditella* is supported as paraphyletic with *Absconditella lignicola* as the sister taxon of *Cryptodiscus* (bs=100, pp=100). *Absconditella sphagnum*, the type of *Absconditella*, forms the sister group to *Cryptodiscus* and *A. lignicola* (bs=93, pp=100) together with an unidentified but closely related *Absconditella*. Vězda and Pisút (1984) provided detailed studies on the development of the asci in *A. lignicola* and concluded that no characters contradict the classification of *Absconditella* in the *Stictidaceae*. Sherwood (1977) suggested that *Absconditella* is morphologically and anatomically very close to *Cryptodiscus*, which was also mentioned by Spribille *et al.* (2009). Nevertheless we hesitate to include *Absconditella* in *Cryptodiscus* as there are slight differences in appearance of the ascomata and in thickness and structure of the ascomatal wall in some species of *Absconditella*. The phylogenetic distance of *A. sphagnum* to *Cryptodiscus* s.str. is already quite substantial. Additionally, the position of the remaining *Absconditella* species seems to be rather unpredictable. Before taxonomic decisions can be made, a larger number of *Absconditella* species need to be analysed together with a comprehensive comparative study of *Absconditella* and *Cryptodiscus*.

The lichenized fungus *Bryophagus gloeocapsa*, the type species of *Bryophagus*, is nested within *Cryptodiscus*, and as a result, *Bryophagus* should be treated as a synonym to *Cryptodiscus*. Morphology and general appearance support the relationship. Like *Cryptodiscus*, *Bryophagus* has yellowish, ochraceous to orange coloured ascomata with deeply concave discs (Fig. 3b), and hyaline ascomatal walls without clear periphysoids. The development of the ascomata follows the typical ostropalean ontogeny and young ascomata are at the beginning closed and spherical, with punctiform openings that widen with maturation. *Bryophagus* species mainly differ from saprotrophic *Cryptodiscus* species in that they are lichenized and grow on different substrates like mosses, soil and

hepatics. It is clearly a common phenomenon in *Stictidaceae* that closely related taxa vary in lifestyle; in *Stictis*, even the same species may be either weakly lichenized or saprotrophic (Wedin *et al.*, 2004; 2006). Although *B. gloeocapsa* was the only *Bryophagus* species for that we could obtain fresh material, the morphological characters of the other species currently classified in this genus are fully consistent with a reclassification within *Cryptodiscus*. We thus coin the relevant combinations below.

Paschelkiella is a monotypic genus that is nested within *Cryptodiscus* in our analysis (Fig. 1). *Paschelkiella pini* was originally described as *Odontotrema pini*. The erumpent ascomata with dark brown margins (Fig. 3e) look superficially very much like an *Odontotrema*. The non-carbonated wall of the apothecia convinced Sherwood-Pike (1987), however, that this species could not be congeneric with *Odontotrema*. She thus described the new genus *Paschelkiella*, and noted that it had an intermediate position between *Odontotrema* and *Cryptodiscus*. As *P. pini* is nested within *Cryptodiscus* in our analyses and the anatomic details of this species are consistent with other *Cryptodiscus* species, we suggest transferring it to this genus below.

As can be seen in Fig. 1, *Cryptodiscus* forms a monophyletic group together with *Absconditella*, two yet undescribed *Odontotrema* (s. lat.) species and *Stictidaceae* s.str. We propose that this whole clade is treated as the family *Stictidaceae*.

'*Cryptodiscus*' *rhopaloides* does not group with *Cryptodiscus*. Based on morphological and anatomical observations already Dennis (1981) stated that *C. rhopaloides* "is not a good *Cryptodiscus*, but has affinities rather with *Melittosporiella* and may eventually be transferred to *Karstenia*". The ascomatal wall and the conspicuous periphysoids, a character not found in *Cryptodiscus* s. str., as well as the close resemblance with *Karstenia idaei* convinced Baral (<http://wwkk.mikologia.pl/files/fos1errata.doc>) to agree with Dennis (1981). At present we do not assign this taxon to a genus since further studies are needed. It is certain that '*C.*' *rhopaloides* is within the monophyletic clade comprising *Graphidales*, *Gyalectales*, *Stictidaceae*, and *Trichotheliales*,

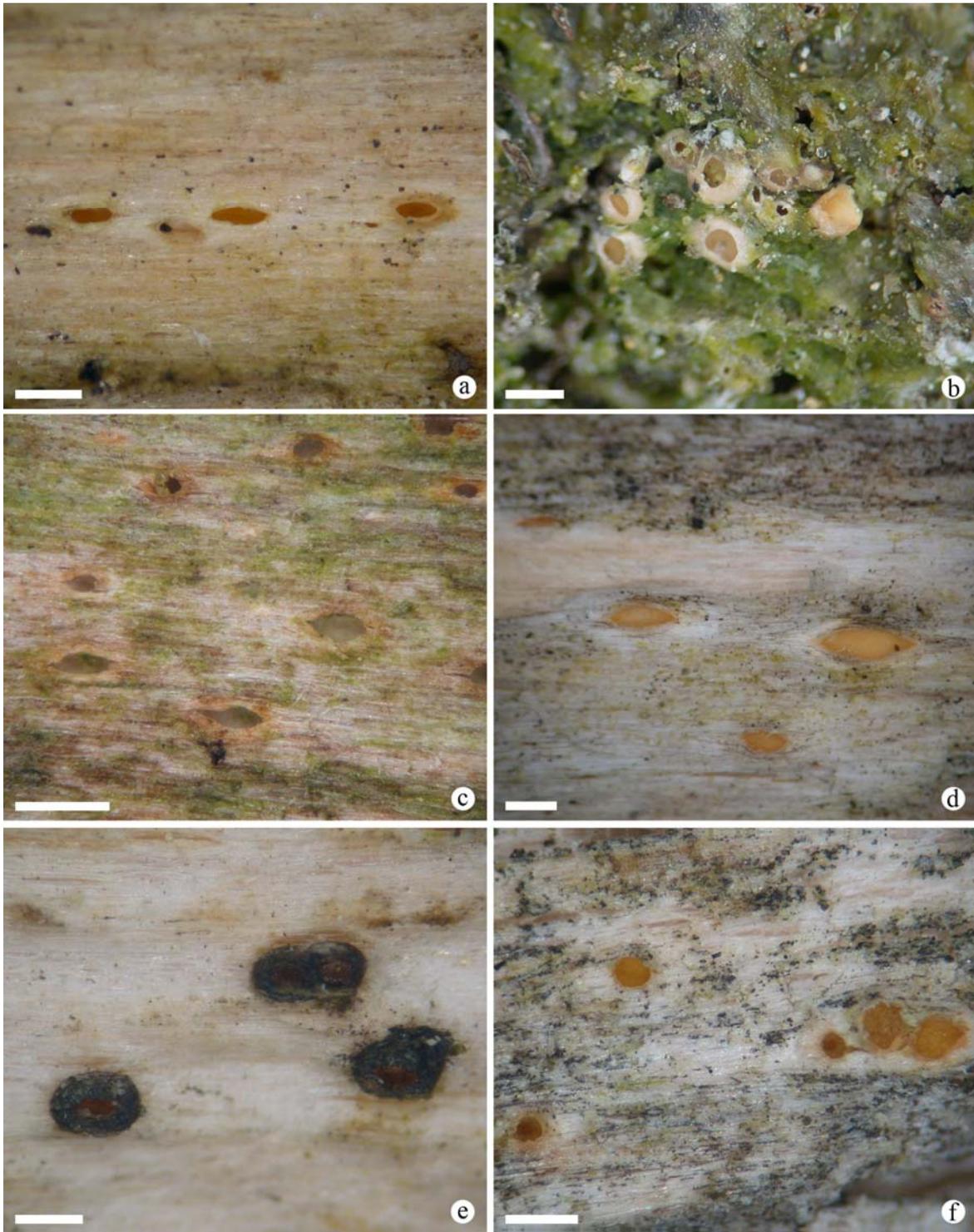


Fig. 3. Habit of the six *Cryptodiscus* species in Sweden. **a.** *C. foveolaris* (Baloch SW126, S), **b.** *C. gloeocapsa* (Tibell 23543, UPS), **c.** *C. incolor* (Baloch & Arup SW138, S), **d.** *C. pallidus* (Gilenstam 2475, UPS), **e.** *C. pini* (Westberg SW199, S), **f.** *C. tabularum* (Gilenstam 2641a, UPS).

but like a number of other taxa it cannot be assigned to any of these orders. We had no fresh material of a *Karstenia* available to include in our sampling, but ‘*Cryptodiscus*’ *rhopaloides* might be closely related to or congeneric with *Karstenia*.

Our results also suggest the exclusion of *C. microstomus* as it did not group near

Cryptodiscus or the *Stictidaceae*. Unlike ‘*C.*’ *rhopaloides*, *C. microstomus* was accepted in *Cryptodiscus* by Sherwood (1977). She noted in her description that the type and only examined specimen “may be slightly immature”. We were able to collect this species several times in Sweden. Younger apothecia of our specimens are identical to the type of

C. microstomus. When maturing, the overall appearance of the ascomata changes and the ascomatal wall becomes much darker, but microscopical characters leave no doubt that our Swedish specimens are conspecific with the type of *C. microstomus*. *Cryptodiscus microstomus* belongs to the subclass *Ostropomycetidae* and as shown in our results is the sister taxon of the monophyletic *Graphidales-Gyalectales-Stictidaceae-Trichotheliales* clade (Fig. 1). Presumably it is outside of this clade and its closest relatives still need to be found.

Cryptodiscus sensu stricto

In the second dataset we included a larger number of samples of the collected species that ended up in *Cryptodiscus* s. str. Here, the relationship and the delimitation of the species within *Cryptodiscus* s. str. were investigated. We have been able to identify six morphologically well-circumscribed phylogenetic species within *Cryptodiscus* s. str., which are further fully congruent between the mtSSU and ITS-nuLSU rDNA datasets (phylogenetic species recognition; Taylor *et al.*, 2000, Grube and Kroken, 2000). The separate analyses of mtSSU and ITS-nuLSU rDNA are not shown here; the resulting trees of the combined analyses are presented in Fig. 2.

The included species form two highly supported clades. One clade includes *C. pallidus*, *C. pini*, and the sole specimen of *C. incolor*, and in the other clade *C. tabularum* and *C. foveolaris* form a group (bs=100, pp=100). Although *C. gloeocapsa* is highly supported within *Cryptodiscus*, its relationship with other *Cryptodiscus* species is unclear (see above and Fig. 2). Interestingly, the two species with one-septate spores (*C. pini* and *C. foveolaris*) do not group together, but both are more closely related to species with multi-septate spores. *Cryptodiscus tabularum* superficially similar to *C. pallidus* with which it has been confused (see note under *C. tabularum*), is clearly a distinct species and not even sister to *C. pallidus*.

Comments on ecology and distribution of Swedish species

Except one lichenized species, all the Swedish *Cryptodiscus* species are saprotrophs on wood. In general the species grow on

weathered decorticated wood that often is moist but still firm. *Cryptodiscus pallidus* seems to prefer wood of deciduous trees and has mostly been found on *Populus* and *Salix*, but it has also been collected on *Fagus*, *Rosa*, and once on well weathered wood of *Juniperus*. Like other species it can occur on decorticated branches still attached to the tree, or on logs lying on the ground. *Cryptodiscus foveolaris* is the least host specific species. It grows on a large variety of different trees, both deciduous trees and conifers. We assume that *C. foveolaris* is less demanding concerning the moistness of the substrate and/or the quality of the wood, compared to *C. pallidus*, which would explain the wider host diversity. Both species were frequently collected on dead wood in forests, but their occurrence in one locality is usually rather scattered.

In Sweden *C. tabularum* and *C. pini* have only been collected on pine wood. Both species are relatively frequent in more mature pine forests, and in the central and southern parts of Sweden they were often found at the same localities. In suitable habitats they can be even abundant. *Cryptodiscus pini* is known from Scandinavia, Scotland, and western North America, where it was collected on cultivated *Libocedrus* (Sherwood-Pike, 1987). *Cryptodiscus tabularum* has been collected in Scotland, Sweden and southern Germany. The type specimen grew on a board of a shed composed of weathered conifer wood, (presumably spruce or larch but not pine wood), all other specimen were collected on *Pinus sylvestris*. Unlike *C. tabularum*, *C. pini* has not been documented from northern Sweden and it is possible that its distribution does not extend as far north as *C. tabularum* does. Finally, the sole specimen of *C. incolor* was collected on a wet log of a deciduous tree in southern Sweden.

In general, all *Cryptodiscus* species are inconspicuous and have been collected only by a few mycologists. *Cryptodiscus tabularum*, although it is certainly widespread and relatively common in Sweden, has for instance not been deposited in the herbaria of Lund (LD) and Uppsala (UPS). In Stockholm (S) two specimens of *C. tabularum* have been found among the rich *C. pallidus* collections. We estimate that it is highly probable that new species of this genus could be discovered in

other climate zones and different parts of the world.

Key to the species of *Cryptodiscus* s. str. in Sweden

1. Growing as a lichen on dead mosses or soil.....
.....*C. gloeocapsa* (= *Bryophagus gloeocapsa*)
1. Growing as a saprobe on decorticated wood..... 2
2. Ascospores 1-septate..... 3
2. Ascospores 3-septate, or more 4
3. Ascomata pale, deeply immersed; disc ochraceous to yellowish-orange; on wood of both conifers and deciduous trees..... *C. foveolaris*
3. Ascomata dark brown, becoming +/- erumpent when mature; disc pale brownish without orange tinge; on pine wood..... *C. pini* (= *Paschelkiella pini*)
4. Ascomata ca 0.1-0.2 mm diam; disc pale flesh coloured, almost hyaline *C. incolor*
4. Ascomata ca 0.2-0.5 (-0.8) mm diam; disc ochraceous to yellowish-orange 5
5. Ascomata ellipsoid, seemingly splitting the substrate lengthwise; disc pale ochraceous; spores 3-septate and usually with constrictions at septa; usually on wood of deciduous trees..... *C. pallidus*
5. Ascomata roundish, not splitting the substrate; disc usually distinctly yellowish-orange; spores 3 (-7) septate, constrictions at septa only if spores have more than 3 septa; on pine wood *C. tabularum*

Taxonomy of the Swedish *Cryptodiscus* s. str.

Cryptodiscus Corda (1838)

Type species: *Cryptodiscus pallidus* (Pers.) Corda (1838; lectotype designated by Rehm, 1888)

= *Bryophagus* Arnold (1862)

Type: *Bryophagus gloeocapsa* Arnold (1862)

= *Gloeolecta* Lettau (1937)

Type: *Secoliga bryophaga* Arnold (1864;

= *Bryophagus gloeocapsa* Arnold, 1862)

= *Paschelkiella* Sherwood (1987)

Type: *Paschelkiella pini* (Romell) Sherwood (1987)

Mycelium either saprotrophic and immersed in dead, decorticated wood, or lichenized with a very thin gelatinous thallus; in lichenized species photobiont *Gloeocystis*-like; *apothecia* round to ellipsoid, closed and immersed in substrate in early stages of development, *apothecia* eventually open by a round pore that widens to \pm size of fruiting body, mostly persistently immersed in substrate, rarely erumpent in mature state; *disc* hyaline, ochraceous, yellowish, pale orange or dark brownish, concave and immersed in substrate;

margin hyaline or brownish, entire, no proper periphysoids, sometimes short-celled hyphae without clear direction can be observed on inner side of excipulum, mostly no differentiation into layers; *subhymenium* thin and small celled; *hymenium* concave, I+ reddish-brown to I- and KOH/I+ blue (Lugol); *asci* cylindrical to somewhat clavate, 8-spored; *ascus* wall usually KOH/I+ faintly blue (Lugol); *tholus* present, no apical structures visible in KOH/I; *ascospores* hyaline, ovate to narrowly ellipsoid, transversely 1–7 (–9) -septate; *paraphyses* numerous, filiform, simple, sometimes slightly forked in upper part, apices often enlarged, sometimes knoblike; *conidiomata* only observed in lichenized taxa, pycnidia pyriform, immersed, conidia short-cylindrical.

Cryptodiscus can be distinguished from other ostropalean genera in that the species develop no distinct periphysoids, have more or less hyaline ascomatal walls except in *C. pini* without any embedded crystals, and have comparatively short and few-celled ascospores.

Cryptodiscus foveolaris (Rehm) Rehm (1888)

Basionym: *Stictis foveolaris* Rehm (1881)

Type: Rehm Ascom. 121; **Germany**, Sugenheim in Franken (Bavaria), on *Quercus* (**S lectotype designated here**)

= *Stictis fagicola* Phil. (1887)

Type: Britain, W. Phillips *Elvellacei* *Britanici* 200, isotype (K) (Figs 3a, 5a)

Apothecia round to ellipsoid, 0.2–0.3 mm diam, substrate often split slightly lengthwise by *ascomata*, scattered to crowded; *disc* pale ochraceous to orange coloured; *margin* hyaline to pale ochraceous, ca 25–50 μm thick, strongly interwoven hyphae, no differentiation into layers (similar to *C. tabularum*, see Fig. 4d); *hymenium* 50–80 μm , I- and KOH/I+ blue; *asci* 50–65 \times 4–5 μm ; *ascospores* one-septate, 6–9 \times 2.5–3 μm , oblong; *paraphyses* 1 μm broad, enlarged to knoblike apex.

Substrate: on decorticated wood of deciduous trees (*Betula* sp., *Corylus avellana*, *Populus tremula*, *Quercus* sp., *Salix caprea*) and conifers (*Picea abies*, *Pinus sylvestris*).

Known distribution: Europe and North America; in Sweden it has been found in the provinces Lule Lappmark, Lycksele Lappmark, Dalarna, Uppland, Södermanland, Östergötland and Skåne. It can be frequent, but always scattered at its localities.

Notes: This species is similar in gross morphology to *C. pallidus*, but the consistently 1-septate spores make it easy to identify. Our molecular studies confirm that it is a well-circumscribed species (Fig. 2).

Specimens examined: **Germany:** lectotype (S); **Sweden:** Lule Lappmark: Jokkmokk par., Randijaur, Njallaluokta, *Gilenstam 2776* (UPS); Lycksele Lappmark: Lycksele par., Furuvik, *Gilenstam 2653* (UPS); Dalarna: St. Kopparberg par., close to St. Östborn, near the river Sundbornsån, 26.III.1979, K. & L. *Holm 1552c* (UPS-F124553); Uppland: Sollentuna par., Järvafältet, 29.III.2007, *Baloch SW128* (S); Dalby par., Viggebylund, 23.IV.1980, K. & L. *Holm 2031e* (UPS-F124555); Dalby par. ENE of Jerusalem, 20.I.1978, K. & L. *Holm 1215a* (UPS-F124565); Södermanland: Tyresö par., Tyresta National Park, 30.X.2006, *Baloch & Wedin SW072*, (S); Östergötland: Kolmården, Marmorbruket, 23.X.2006, *Baloch SW170*, (S); Skåne: Norra Mellby par., Maglö, 19.VI.2007, *Baloch & Arup SW166* (S); Åhus par., Northern Åhus, 'Östra Sandar', 20.VI.2007, *Baloch & Arup SW168* (S);

***Cryptodiscus gloeocapsa* (Arnold) Baloch, Gilenstam & Wedin comb. nov.**

Basionym: *Bryophagus gloeocapsa* Arnold (1862) Flora 45: 58.

Type: **Germany**, Nordrhein-Westfalen: auf feuchten Erdwällen, bei Münster, *Nitschke* (Arnold, Lich. exs. no. 214, **S lectotype designated here**, UPS, isolectotype; Rabenhorst, Lich. eur. exs. no. 608 (S), Zw. exs. 428 (not seen), isolectotypes)

≡ *Secoliga bryophaga* Arnold (1864) (Figs. 3b, 4a, 5b)

Lichenized thallus crustose, not stratified, becoming gelatinous when wet; *photobiont* *Gloeocystis*-like, globose or elongate, in colonies; *apothecia* roundish, 0.2–0.5 mm in diameter, open with narrow pore, first immersed becoming erumpent at later stage, mostly scattered, sometimes crowded; *disc* pale yellow-brown to orange-red; *margin* hyaline, 25–70 µm in upper part; *hymenium* 50–60 µm high, I- yellow brown, KOH/I+ faint blue; *asci* 40–60 × 4–6 µm; *ascospores* 3–4-septate, 20–30 × 1.5–2 µm, cylindrical-fusiform, often tapering at one end; *paraphyses* about 0.8 µm thick, no apical thickening; *conidiomata* immersed pyriform pycnidia, conidia shortly cylindrical.

Substrate: on bryophytes and algal mats, especially on recently disturbed soil, on shaded road-cuttings and banks as well as mineralized, acid soil associated with mine activity in past.

Known distribution: frequent and widespread, in Europe from northern Scandinavia to the Alps and Carpathians, Madeira, Azores.

The species has been recorded from all Swedish provinces (see also Santesson *et al.* 2004).

Note: *Bryophagus gloeocapsa* was collected by Nitschke and published as a *nomen nudum* in 1861 (Exs. Rabenhorst, Flecht. eur. no. 608, 1861). The name was later validated by Arnold (1862), see also Hawksworth *et al.* (1980). Arnold (1862) cites the exsiccates Arnold, Lich. exs. no. 214 and Rabenhorst Lich. eur. exs. no. 608 as original material, collected by Nitschke in Germany, Westfalen by Münster. Vězda (1966) overlooked the original publication and treated *Secoliga bryophaga* Arnold (1864) as the oldest name for this species. Here, Arnold referred to a paper earlier the same year in Flora (Zwack, 1864), but this paper only cites a new locality for *Bryophagus gloeocapsa*. The Körber exsiccate included by Arnold (1864) in the protologue of *Secoliga bryophaga* was not included in the protologue of *Bryophagus* in 1862 and accordingly the lectotype designated by Vězda (1966) is erroneous. We here designate a lectotype from the material actually cited in the protologue.

Specimens examined: **Germany:** lectotype (S); isolectotype (UPS); Rabenhorst, Lich. eur. exs. no. 608 (S, syntype); **Sweden:** Lule Lappmark: Åtnaråvve, 21.VII.2004, *Hermansson 13983a*, (UPS-L147599); Jämtland: Undersåker par., NW of Ottsjö, 12.VII.2004, *Tibell 23543* (UPS-L150940);

Additional extra-european *Bryophagus* species:

Two further '*Bryophagus*' species are known and they also fit well in *Cryptodiscus*.

***Cryptodiscus similis* (Vězda) Baloch comb. nov.**

Basionym: *Gloeoelecta similis* Vězda (1966) Folia Geobot. Phytotax. Bohemoslov. 1: 171.

Type: **Jamaica**, on mosses, *Cummings* [NY, holotype (not seen); FH, LE (not seen), O, isotypes]

≡ *Bryophagus similis* (Vězda) Kalb (1984)

The species is very similar to *C. gloeocapsa*. The apothecia are 0.3–0.5 mm diam and often found in clusters. The disc is flesh-coloured to yellowish-brown with a pale greyish to brownish margin. The ascospores are 1–3 septate and 12–15 × 2.5–3 µm. The species grows on dead mosses and has been found in tropical and subtropical America (Vězda, 1966).

Specimens examined: **Brasil:** Sao Paulo, Parelheiros, on mosses, 25.V.1980, *Kalb* (UPS-L021529); **Jamaica:** isotype (O)

***Cryptodiscus minutissimus* (Vězda) Baloch comb. nov.**

Basionym: *Gloeoelecta minutissima* Vězda (1973) Folia Geobot. Phytotax. Bohemoslov. 8: 312.

Type: **New-Guinea**, Bismark Ranges: Mount

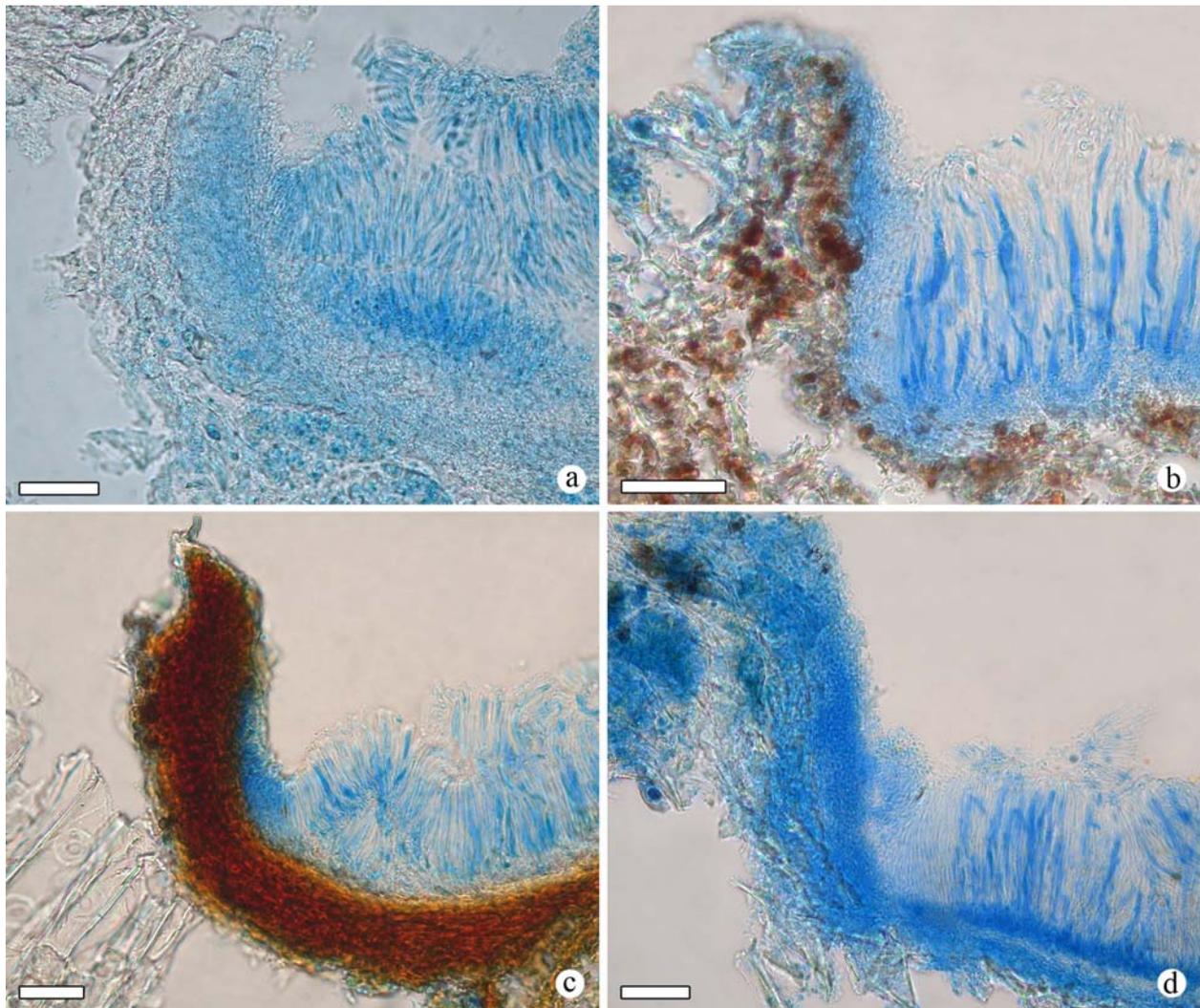


Fig. 4. Ascomatal wall structure in *Cryptodiscus*; the sections are coloured with cotton blue. **a.** *C. gloeocapsa* (Tibell 23543, UPS), note the rather thick margin; the symbiotic algae are visible below the ascoma; **b.** *C. incolor* (Baloch & Arup SW138, S); **c.** *C. pini* (Westberg SW199, S), note the dark coloured ascomatal wall also below the subhymenium and on the inner side of the wall hyaline small celled hyphae; **d.** *C. tabularum* (Gilenstam 2641a, UPS).

Wilhelm, 26.VI.1968, *Weber & McVean* (COLO L48422b, holotype)

≡ *Bryophagus minutissimus* (Vězda) D. Hawksw. (1984)

This species has a reduced to invisible thallus. The apothecia are minute with c. 0.06–0.13 mm diam. The disc is pale yellowish and the margin hyaline. The bacilliform ascospores are 3-septate and 8–13 × 1 μm. The species was found on hepatics in New-Guinea and in Tasmania (Vězda, 1973; Kantvilas, 2002).

Specimen examined: **New-Guinea:** holotype (COLO)

***Cryptodiscus incolor* Baloch spec. nov.**

Type: **Sweden**, Skåne, Hällarp par., close to Stenskildstorp, on decorticated lying log, 19.VI.2007, Baloch & Arup SW138 (S, holotype; K, isotype)

(Figs 3c, 4b, 5c)

Mycobank: 513323.

Etymology: Named for its colourless apothecia that distinguishes this taxon from the other lignicolous *Cryptodiscus* species, which have ochraceous, orange or brownish ascomata.

Species haec ab *Cryptodisco pallido* differt ascomatibus minoribus incoloribus. Ascosporae cylindricae nonnihil clavatae, 3–5-septatae et 18–20 × 3.5–5 μm.

Apothecia round to ellipsoid, 0.1–0.2 mm diam, permanently immersed, but opening to surface by a pore, no obvious lengthwise splitting of substrate; *margin* colourless to pale brownish-ochraceous, 10–14 μm, no differentiation into layers, smooth transition to substrate; *disc* rather colourless to pale brownish, concave; *hymenium* 70–90 μm thick, I-, KOH/I+ blue; *asci* 40–60 × 6–7 μm, I-; *ascospores* 3–5-septate, 18–20 × 3.5–5 μm, cylindrical-clavate with rounded ends;

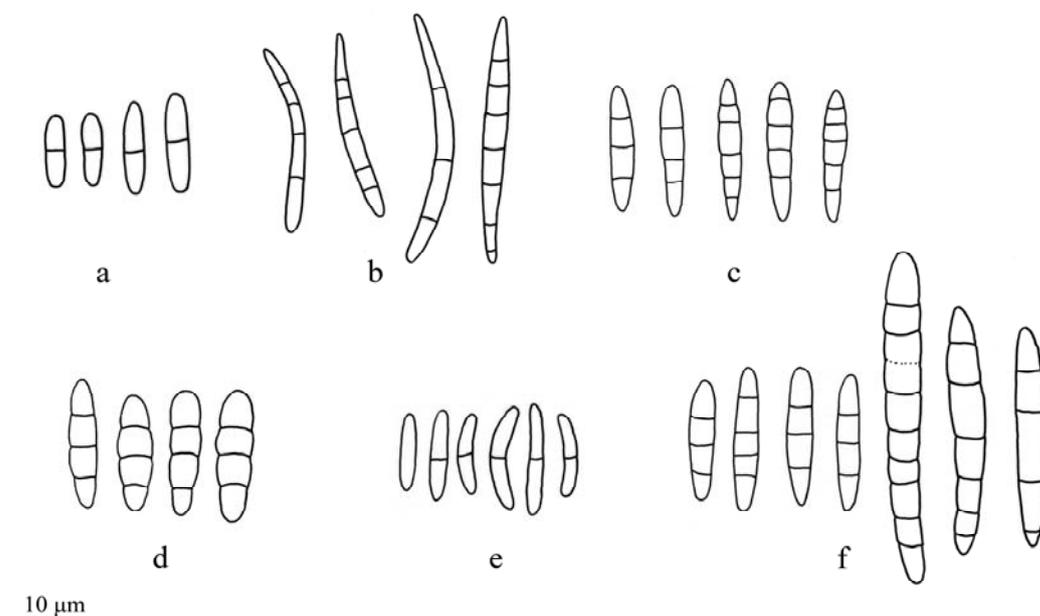


Fig. 5. Ascospores of *Cryptodiscus*. **a.** *C. foveolaris* (Baloch SW128, S), **b.** *C. gloeocapsa* (Vězda exs. 1086 and Vězda 403 both S), **c.** *C. incolor* (Baloch & Arup SW138, S), **d.** *C. pallidus* (Gilenstam 2694, UPS), **e.** *C. pini* (Baloch SW172, S), **f.** *C. tabularum* (Wedin 8271 and Westberg SW132 both S), note the variation in size between the short 3-septate spores commonly observed in specimen and the rarely collected mature state with 5–8-septate spores with constrictions at the septa.

paraphyses 1.0 µm wide, hardly enlarged at apices.

Substrate: on decorticated, decaying wood of a deciduous tree.

Known distribution: only known from the type locality in Skåne, southern Sweden, most probably overlooked.

Note: This species is characterized by very small and colorless ascomata that grow densely but never clustered. All other wood-dwelling *Cryptodiscus* species have slightly bigger ascomata that are either ochraceous-orangish or brownish. The ascospores of *C. incolor* are up to 5-septate and slightly clavate.

Specimen examined: **Sweden:** type (S, K)

Cryptodiscus pallidus (Pers.) Corda (1838)

Basionym: *Stictis pallida* Pers. (1800)

Type: Herb. Persoon 910.264-843, locality unknown, neotype designated by Sherwood 1977: 90 (L) = *Peziza* (*Stictis*) *punctiformis* Pers. (1801)

Type: Herb. Persoon 910.264-846, locality unknown, labelled as *Stictis punctiformis* (L, not seen, fide Sherwood)

= *Stictis patellea* Cooke (1878)

Type: USA, New York, *Gerard* 212 (K, holotype) (Figs 3d, 5d)

Apothecia ellipsoid, 0.3–0.8 × 0.2–0.4 mm diam, with an average length/width ration of 2.0, permanently immersed in substrate,

appears to split wooden substrate lengthwise; *disc* pale ochraceous; *margin* hyaline to pale ochraceous, 20–60 µm thick, of thin walled interwoven hyphae; *hymenium* 45–80 µm, I+ reddish-brown, KOH/I+ blue; *asci* 40–65 × 5–6 (–8) µm; *ascospores* 3-septate, 12–16 × 3.5–5 µm, when mature clearly constricted at septa, cylindrical to slightly fusiform; *paraphyses* ca 1 µm thick with knoblike apices;

Substrate: on soft decorticated wood of deciduous trees and shrubs (*Alnus glutinosa*, *Fagus sylvatica*, *Populus tremula*, *Rosa* sp., *Salix cinerea*), in one case also on *Juniperus communis*.

Known distribution: known from Europe, North America and Canary Islands. In Sweden it is reported from many provinces and can probably be found in appropriate habitats all over the country.

Notes: *Cryptodiscus pallidus* is the type species of *Cryptodiscus*. It is similar to *C. tabularum*, which is often found with 3-septate spores, but is characterized by larger, ellipsoid ascomata that slightly split the woody substrate lengthwise during growth. The spores of *C. pallidus* are somewhat thicker than those of *C. tabularum*, have always only three septa and often pronounced constrictions at the septa.

It usually grows on decorticated wood of broad-leaved trees and has never been recorded on pine. A specimen collected in Norway, however, was found on wood of juniper.

We examined the type specimen of *Stictis patellea*, a taxon synonymised with *C. pallidus* (Sherwood, 1977). The rounded apothecia resemble those of *C. tabularum*. The ascomatal walls of *Stictis patellea* are clearly darker compared to *C. tabularum*, and, when mature, major parts of the ascomata are emergent above the substrate level. The substrate of the type specimen is wood of a broad-leaved tree. On the other hand the ascomata of *C. tabularum* stay deeply immersed in the substrate, which is pine wood. Because of these differences, we conclude that *C. tabularum* is not conspecific with *S. patellea*. It is possible that *S. patellea* is a separate North American *Cryptodiscus* species, but until further collections are available for study we consider it as a synonym of *C. pallidus*.

Specimens examined: **Europe**: neotype (L); **Finland**: Tavastia Australis, Tammela par. Mustiala, 27.X.1869, *Karsten* (UPS-F124574); **Norway**: Sør-Trøndelag: Oppdal, N of the lake Gjevilvatnet, 23.VIII.1973, *K. & L. Holm 94c*, (UPS-F124554); **Sweden**: Lycksele lappmark: Lycksele par., Bocksliden, *Gilenstam 2694* (UPS); Gästrikland: Gävle, Tolfforsskogen, 6.VI.1953, *Nannfeldt 12707* (UPS-F124573), Uppland: Sollentuna par., Järnafältet, 27.III.2007, *Baloch SW127* (S); Dalby par., Jerusalem, 24.XI.1986, *K. & L. Holm 4346b* (UPS-F124566); Östergötland: St. Anna par., Norra Finnö, between Gäddvik and Ämtevik, 5.V.2007, *Baloch & Wedin SW174* (S); Gryt par., Gamla Gryt, Alnäset, 22.IV.1946, *Nannfeldt 8287* (UPS-F124568); Småland: Femsjö par., Hägnen, 9.VII.1929, *Nannfeldt 2322* (UPS-F124571); Skåne: Höör par., close to the cottage Stenskildstorp, 19.VI.2007, *Arup & Baloch SW139* (S); Konga par., Söderåsen national park, 3.VI.2006, *Læssøe SW0126* (S); **USA**: holotype of *Stictis patellea* (K).

***Cryptodiscus pini* (Romell) Baloch, Gilenstam & Wedin comb. nov.**

Basionym: *Odontotrema pini* Romell (1895) Bot. Notiser 1895: 75.

Type: Romell, Fungi exs. praes. scand. 200: In ligno nudo ramulorum humi jacentium Pini silvestris ad Drottingholm prope Stockholm, 18.V. 1890 (**S lectotype, designated here, K isolectotype**); Romell, Fungi exs. praes. scand. 200: Hallaböke in paroecia Femsjö (Småland) 7.IX.1890

≡ *Paschelkiella pini* (Romell) Sherwood (1987)

= *Ocellaria phialopsis* Rehm (1912)

Type: **Germany**, Oberfranken, Mainecker-Forst bei Weissman, ex Herb. Rehm, 23.X.1908 (S)

(Figs 3e, 4c, 5e)

Apothecia roundish, 0.3–0.6 µm diam, margin becomes erumpent when mature, only hymenium stays shallowly immersed; *disc*: brownish, concave; *margin* in two layers: outer margin dark reddish brown, also in basal margin, up to 60 µm, inner layer hyaline with small cells about 2 µm diam; *hymenium* 60–80 µm; I- and KOH/I+ faintly blue; *asci*: 40–60 × 6–7 µm, diffusely faintly I+ blue; *ascospores* 1-septate, 9–13 (-15) × 1.5–2 µm, narrowly oblong; *paraphyses*: 1.0 µm diam, hardly enlarged at apices;

Substrate: on conifer wood, in Sweden only on decorticated branches of *Pinus sylvestris*, in USA known from *Libocedrus*, mostly on dead branches still attached to the tree;

Known distribution: Scandinavia, Scotland, and western North America; in Sweden the species was collected in the provinces Jämtland, Hälsingland, Uppland, Bohuslän, Östergötland, Småland, and Skåne.

Notes: *Cryptodiscus pini* was first described in *Odontotrema* by Romell (1895). Romell recognized its affiliation to ostropalean fungi, but was misdirected by its dark appearance superficially similar to the genus *Odontotrema*. Höhnelt (1917) suggested that it was wrongly classified in this genus. Sherwood-Pike (1987) established the new genus *Paschelkiella* for it within the *Odontotremataceae*. In all its characters *C. pini* fits well within *Cryptodiscus*, apart from the comparatively erumpent and dark ascomatal margin. It has a fleshy, non-carbonized margin with a non-dentate opening, no hymenial iodine reaction without pre-treatment with KOH and asci with a distinct thickened tholus.

Specimens examined: **Great Britain**: Scotland: Rothiemurchus Forest, Easternness, 1.V.1980, *Sherwood & Coppins* (K(M)156612); Wester Ross, between Torredon and Allegin, 14.VI.1983, *Clark* (K(M)48177); **Sweden**: Jämtland: Ragunda par., along Indalsälven, Edesmoarna, 7.VI.2007, *Westberg SW199* (S); Hälsingland: Bjuråker par., close to road between Skålsvedja and Friggesund, 13.VIII.2006, *Westberg SW173* (S); Uppland: Rehm, Ascomyceten 1283, Skokloster par., *Starbaeck* (K); lecto- and isolectotype (S, K); Tierp par., Båtfors naturreservat, W of Mehedeby, 26.VII.2007, *Wedin & Baloch* (S); Bohuslän: Högås par., Havsten, close to camp-ground, 24.XII.2006, *M. & E. Westberg SW131* (S); Östergötland: Rönö, S of Vånga, 24.X.2006, *Baloch SW069* and *SW172*, (both S); Småland: Kråksmåla par., south end of lake Boasjö, 23.VI.2006, *Westberg SW137* (S); Femsjö, 7.IX.1890, *M.*

& *L. Romell* (K, S); Skåne: Åhus par., northern Åhus, 'Östra Sandar', 20.VI.2007, *Baloch & Arup SW167* (S) and *SW177* (LD); Åhus par., southern part of Åhus, Äspet, Kronoskogen, 20.VI.2007, *Baloch & Arup SW178* (S) and *SW179* (LD);

Cryptodiscus tabularum Kirschst. (1936)

Type: **Germany**, Bayern, Bayerischer Wald, Bayerisch Häusl near Eisenstein, on weathered board of a shed, conifer wood, 1935, *Kirschstein* (holotype, B).

(Figs 3f, 4d, 5f)

Apothecia roundish, ca 0.2–0.4 (–0.5) mm in diam, more or less circular with a length/width ratio of 1.2, persistently immersed in substrate; *disc* usually stronger coloured than *C. pallidus*, ochraceous to orange; *margin* 40–80 µm thick; *hymenium* (45–) 50–70 (–80) µm, I+ reddish-brown, KOH/I+ blue; *asci* 40–60 × 6–8 µm; *ascospores* mostly found slightly immature, then 3-septate, and 12–18 × 2.4–4 µm, occasionally with bigger and more septate spores, then 5–7 septa and 18–25 × 3.2–4.4 µm; constrictions at septa only occur in spores with more than 3 septa, cylindrical to slightly fusiform; *paraphyses* enlarged apex, sometimes branched.

Substrate: on decorticated, weathered wood of *Pinus sylvestris*; on fallen logs and branches as well as on branches still attached to the tree, often quite abundant in old growth pine forests.

Known distribution: Northern and Central Europe, collections from Germany, Sweden and Scotland; in Sweden widespread and probably occurring in all provinces (recorded for: Pite Lappmark, Lycksele Lappmark, Härjedalen, Södermanland, Bohuslän, Östergötland, and Småland).

Notes: The first and only report of this species in the literature is its description by Kirschstein (1936). Interestingly enough this species turned out to be not rare in Swedish pine forests. Still *C. tabularum* was rarely collected and then usually determined as *C. pallidus*. Sherwood investigated a specimen collected in Scotland (K) and concluded on a handwritten note that, although this specimen has more narrow and 3–5-septate spores, "it is doubtfully worthy of specific rank and might best be considered a variety of *C. pallidus*" (M.A. Sherwood, 25.II.1980). Our phylo-

genetic analyses clearly show that *C. pallidus* and *C. tabularum* are separate species (Fig. 2). *Cryptodiscus tabularum* differs from *C. pallidus* in substrate preference, ascospore characters, and shape and colour of the apothecia. It never looks as if the ascomata split the substrate lengthwise. *Cryptodiscus tabularum* is mostly found with 3-septate spores, two specimens however, one from Sweden (Bohuslän SW132, S) and one from Great Britain (Scotland, K) have been found with larger and more septate spores. This may be the mature state of the ascospores. Our DNA sequence analyses do not indicate any genetic heterogeneity. The especially large and more than 7-septate spores of the specimen from Bohuslän, Sweden (Fig. 5f) could also be an abnormality.

Specimens examined: **Germany**: holotype (B); **Great Britain**: Scotland: Wester Ross, Kinlochewe, Coille na Glas-leitire, 20.VIII.1963, *Dennis* (K(M)159144); **Sweden**: Pite Lappmark: Arjeplog par., Jäkkvik, 23.VIII.2006, *Baloch SW017* (S); Lycksele Lappmark: Lycksele par., Furuvik, Prästhölm, *Gilensham 2759* (UPS); Härjedalen: Tännäs par., N of Vivalen, 5.VI.2007, *Westberg SW198* (S); Södermanland: holotype (S); Bohuslän: Högås par., Havsten, S tip of Havstensudden, *Westberg SW132* (S); Östergötland: Kolmården, Marmorbruket, 23.X.2006, *Baloch SW171* (S); St. Anna par., Island Svensmarö, 5.V.2007, *Baloch & Westberg SW183* (S); Småland: Kråksmåla par., lake Boasjö, 23.VI.2006, *Westberg SW136a* (S);

Species excluded from *Cryptodiscus*

'*Cryptodiscus anguillosporus* L. Holm & K. Holm (1981)

Type: **Sweden**, Uppland, Dalby par. Hammarskog, on *Lycopodium complanatum*, 29. VI.1980, *K. & L. Holm 1893a* (holotype examined, UPS)

We have not seen any recent material of this species and could not include it in our phylogenetic analyses. Judging from the morphology, this does not appear to be a true *Cryptodiscus*. The spores are vermiform (20–28 × 1 µm), apparently non-septate, and the margin of the ascomata has short periphysoid hyphae. The vermiform spores and the periphysoids are atypical for *Cryptodiscus* species but common in other *Stictidaceae*. Holm and Holm (1981) also mention another undescribed '*Cryptodiscus*' which grows on *Lycopodium alpinum*.

'Cryptodiscus' angulosus P. Karst. (1885)

Type: **Finland**, close to Jakobstad and Wasa, on dry twig of *Salix caprea*, 1862, *Karsten* (holotype, S)

The species is not a *Cryptodiscus* and differs from the genus in many morphological and anatomical characters. The pruinose ascomata are large, 1.5 mm, diam with a blue-green-grayish tinge, and the disc is flat, not urceolate. The ascomata are initially immersed and closed, but the disc is finally exposed. The margin adheres to the ruptured host tissue which is split into irregular lobes. Unlike in *Cryptodiscus*, a periphysoid layer is well developed and the structure of the wall differs. We cannot suggest a new classification at present, but this taxon does not appear to belong in the *Ostropomycetidae*.

Specimens examined: **Finland**: holotype (S); **Sweden**: Västerbotten: Umeå, Brännland, 24.XI.1968, *Eriksson* (UME);

'Cryptodiscus' microstomus (Berk.) Sacc. (1889)

Basionym: *Stictis microstoma* Berk. (1836)

Type: **Great Britain**, no collection data, holotype (K), according to Sherwood (1977)

This species is not a *Cryptodiscus*, but it is a typical *Ostropomycetidae*. In a young stage the ascomata resemble *Cryptodiscus*. They are small in size and, at an early stage the walls of the ascomata are pale brown. This is the stage of the holotype. Upon maturation the ascomatal wall becomes darker changing to dark-brown or blackish. In habit, mature specimens thus resemble *Odontotrema*. The round opening of the apothecium is small and the thin dark wall covers most of the barely urceolate disc. *'Cryptodiscus' microstomus* is known from wood of *Juniperus communis*, *Pinus sylvestris*, *Populus tremula* and *Salix caprea*.

Specimens examined: **Great Britain**: holotype (K); **Sweden**: Pite Lappmark: Arjeplog par., Stor-Graddis, 22.VIII.2006, *Baloch SW021* (S); Lycksele Lappmark: Lycksele par., Lycksbäcken, *Gilenstam 2784a* (S); Västerbotten: Robertsfors kommun, Överklinten, 27.V.2007, *Gilenstam 2780* (UPS); Tavelsjö par., 1 km E Varmvattnet village, 8.V.2008, *Wedin & Gilenstam 8255* and *8258* (both S); Södermanland: Nacka, at lake Källstorpssjön, 10.III.2007, *Baloch SW115* (S);

'Cryptodiscus' rhopaloides Sacc. (1881)

Type: **Italy**, Padova Ital. bor., in sarmentis corticatis *Vitis viniferae*, *Bizzozero* (PAD)

'Cryptodiscus' rhopaloides is different from *Cryptodiscus*. The disc is pruinose and

flat, but immersed. The covering layer splits into triangular teeth and the margin of the ascomata adheres tightly to the ruptured substrate. The wall is clearly pseudoparenchymatous with a fringe of bacillary cells towards the hymenium forming short but distinct periphysoids. It appears to be related to the genus *Karstenia* and the lichen species *Ramonia interjecta*, with which it shares several characteristics such as the similar ascospore dimensions, i.e. clavate, 7–9-septate, 29–43 × 4–5 µm, and general appearance.

Specimens examined: **Denmark**: Jylland, Grenå, 9.XII.2006, *Læssøe*, (S); **Great Britain**: England, Huntingdonshire, Woodwalton Fen NNR, 11.IX.2004, *Parslow* (K(M)125627); **Italy**: no collection data (PAD, with annotations by Saccardo).

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