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Facultative parasitism and reproductive strategies in *Chroodiscus* (Ascomycota, Ostropales)

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Facultative parasitism in foliicolous species of *Chroodiscus* was investigated using epifluorescence microscopy and the evolution of biological features within members of the genus was studied using a phenotype-based phylogenetic approach. Facultative parasitism occurs in at least five taxa, all on species of *Porina*, and a quantitative approach to this phenomenon was possible in the two most abundant taxa, *C. australiensis* and *C. coccineus*. Both show a high degree of host specificity: *C. australiensis* on *Porina mirabilis* and *C. coccineus* on *P. subepiphylla*. Parasitic specimens are significantly more frequent in *C. australiensis*, and this species also shows a more aggressive behaviour towards its host. Cryptoparasitic specimens, in which host features are macroscopically inapparent, are also most frequent in *C. australiensis*. Facultative vs. obligate parasitism and corresponding photobiont switch are discussed as mechanisms potentially triggering the evolution of new lineages in species with trentepohlioid photobionts. *C. parvisporus* and *C. rubentiicola* are described as new to science. The terminology for the vegetative propagules of *C. mirificus* is discussed.

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Fakultativer Parasitismus von foliicolen *Chroodiscus*-Arten wurde mithilfe der Epifluoreszenzmikroskopie studiert. Die Evolution von biologischen Merkmalen der Gattung wurde in einem phylogenetischen Ansatz, basierend auf Merkmalen der Phänotyps, untersucht. Fakultativer Parasitismus ist bei mindestens 5 Taxa vorhanden, die alle auf Arten der Gattung *Porina* auftreten. Eine quantitative Auswertung war bei den zwei häufigsten Arten möglich: *C. australiensis* and *C. coccineus*. Beide sind hochspezifisch an ihre Wirte gebunden: *C. australiensis* auf *Porina mirabilis* und *C. coccineus* auf *P. subepiphylla*. Parasitismus scheint wesentlich häufiger in *C. australiensis* vorzukommen, und diese Art ist auch deutlich aggressiver gegenüber ihrem Wirt. Kryptoparasitische Aufsammlungen, bei denen Wirtsmerkmale makroskopisch nicht erkennbar sind, sind ebenfalls häufiger bei *C. australiensis* zu beobachten. Fakultativer (vs. obligater) Parasitismus und der damit verbundene Wechsel der Photobionten werden als mögliche Auslöser der Evolution von neuen Sippen, inbesondere bei Arten mit trentepohlioiden Photobionten, diskutiert. *C. parvisporus* and *C. rubentiicola* werden neu beschrieben. Die Terminologie der vegetativen Ausbreitungseinheiten von *C. mirificus* wird diskutiert.

K e y w o r d s : Foliicolous lichens, Ostropales, *Chroodiscus*, lichenicolous, epifluorescence microscopy.

Introduction

Lichenization is one of the most successful lifestyles within Ascomycota, and it substantially contributed to the evolutionary diversity of this phylum (KIRK et al. 2001). Major clades of lichenized Ascomycota are thought to either being polyphyletically derived by independent lichenization events (GARGAS et al. 1995), or forming a paraphyletic entity from which entire orders of non-lichenized fungi, such as the Chaetothyriales, evolved secondarily via delichenization (LUTZONI et al. 2001). Further data are required to validate the contribution of either of these hypotheses in the context of a putative rapid radiation of ascomycetes (BERBEE & TAYLOR 1995, BERBEE et al. 2000), however, secondary loss of lichenization plays an important role within smaller groups of extant lichens.

Two orders, Arthoniales and Ostropales, comprise large groups of non-lichenized, lichenized, and lichenicolous fungi (GILENSTAM 1969; KORF 1973, 1990; SHERWOOD 1977; SHERWOOD-PIKE 1987; LUMBSCH et al. 1997; TEHLER 1990; GRUBE 1998; HENSSEN & LÜCKING 2001), and are crucial to the understanding of lichenization and delichenization events within Ascomycota. Especially genera such as *Arthonia*, *Opegrapha*, and *Gyalideopsis*, which include both lichenized and lichenicolous species (MATZER 1996; LÜCKING 1997; GRUBE & MATZER 1997), can serve as model organisms for the study of secondary delichenization. A particular biological lifestyle is found in *Diploschistes* and *Chroodiscus* in the Thelotremataceae, where the same species can adopt both a lichenized and lichenicolous lifestyle (POELT & DOPPELBAUER 1965; LUMBSCH 1989; KALB & VEZDA 1992; LÜCKING 1992).

While juvenile and facultative parasitism in *Diploschistes* is well studied (POELT & DOPPELBAUER 1965; FRIEDL 1987; LUMBSCH 1989), the lichenicolous lifestyle in *Chroodiscus* has not yet been investigated. Although Thelotremataceae are abundant tropical lichens, *Chroodiscus* is the only genus in the family including regularly foliicolous species. Its biology must be seen in the context of the ephemeral habitat provided by the leaf surface, the phylloplane. Lichens must reproduce before leaves are shed, and correspondingly, their life-cycle is accelerated and only little biomass is invested into the thin, crustose thalli (LÜCKING 2001). As side effect, this prevents them from intercepting too much light, which would be detrimental to leaf functions and jeopardize their substrate (COLEY & KURSAR 1996).

Contrary to other lichens, foliicolous lichens chiefly reproduce aposymbiotically by ascospores and conidia, while genuine soredia and isidia are rare (LÜCKING 2001). Thus, although spatial competition seems not to be pronounced, one would expect strong competition for photobionts between germinating mycobionts. In lichens with chlorococcoid algae, this association is initiated by individual attachment of photobiont cells to mycobiont hyphae or spores, while in species with trentepohlioid photobiont, independently formed algal thalli are entered by the mycobiont (SANDERS 2001, GRUBE & LÜCKING, in prep.). Trentepohlioid photobionts are common among foliicolous lichens, and the latter are highly specific in their photobiont choice (LÜCKING & MATZER 1996; LÜCKING & VEZDA 1998; GRUBE & LÜCKING, in prep.). The question arises whether photobiont com-

petition favors evolution of a lichenicolous, parasitic or parasymbiontic lifestyle, and how this might be related to photobiont specificity.

Chroodiscus provides an excellent opportunity to address these questions. Most species are foliicolous, although corticolous taxa, formerly placed in *Thelotrema*, occur (SANTESSON 1952; KALB 1991; KALB & VEZDA 1992; LÜCKING 1999a; SANTESSON & LÜCKING 1999; KANTVILAS & VEZDA 2000). Excluding the taxonomically isolated *Chroodiscus anomalus* Vezda, the nine foliicolous representatives form a presumedly monophyletic group. All species reproduce via ascospores; only *C. mirificus* additionally forms disc-shaped, vegetative isidioid propagules (SANTESSON 1952). Facultative lichenicolous growth has been reported from *C. australiensis*, *C. coccineus*, and *C. verrucosus* (KALB & VEZDA 1992; LÜCKING 1992, 1999a). In these taxa, the photobiont of the attacked host lichens, exclusively species of *Porina* (Trichotheliales), differs from that of the autonomous lichen, which suggests this lifestyle to be comparable to the juvenile parasitism in *Diploschistes*. To test this assumption, we studied biological relationships in different *Chroodiscus* species, and used epifluorescence as tool to visualize anatomical details of mycobiont-photobiont associations.

Material and Methods

Studied specimens

The following species and specimens were studied (in alphabetical order; total number of specimens given in brackets):

Chroodiscus australiensis VEZDA & LUMBSCH: Costa Rica: LÜCKING 87-374, 87-787a-h, 88-92a-b, 91-3141, 91-3433, 91-4957, 91-4996, 91-5208, 91-5640, 92-1592, 92-4685, 92-4685, 97-738, 97-865, 97-1398, 99-134, 00-234, and s.n. Ecuador: LÜCKING 96-696. French Guyana: LÜCKING 95-1316, 95-1462. Brazil: KALB & KALB s.n. Australia: HENSSEN s.n. (all hb. LÜCKING).

Chroodiscus coccineus (LEIGHT.) MÜLL. ARG.: Costa Rica: LÜCKING 87-38, 87-374, 87-427, 87-787c, 88-92c, 88-516, 91-474, 91-815, 91-854, 91-1662, 91-1761, 91-1926, 91-1927, 91-2511, 91-2567, 91-4997, 91-4998, 92-4157, 92-4685, 92-5265, 97-1567, 00-165, GRUBE XI.99-1(hb. GRUBE), GRUBE XI.99-2 (hb. GRUBE). Cocos Island (Costa Rica): LÜCKING 92-790. Ecuador: LÜCKING 96-86, 96-451, 96-954, 96-1001. Guyana: LÜCKING 96-3558, 96-3807. French Guyana: LÜCKING 95-1337, 95-1356, 95-1460, 95-1545, 95-1546, 95-1577. Brazil: CÁCERES s.n., LÜCKING 96-5032, 96-5035 (all hb. LÜCKING, if not otherwise stated).

Chroodiscus neotropicus KALB & VEZDA: Costa Rica: LÜCKING 91-5189, 92-1437, 92-1591, 97-508, 97-1357. Brazil, LÜCKING 95-206, CÁCERES & LÜCKING 98-491 (all hb. LÜCKING), KALB & PLÖBST s.n. (holotype, hb. KALB; isotype, hb. VEZDA).

Chroodiscus mirificus (KREMP.) R. SANT.: Malaysia: Mohamed s.n. (hb. LÜCKING), VEZDA & CENI s.n. (hb. LÜCKING). Philippines: KALB & SCHRÖGL s.n. (hb. LÜCKING). Papua New Guinea: MABBERLEY s.n. (hb. LÜCKING, GZU).

Chroodiscus parvisporus KALB & LÜCKING: Cocos Island (Costa Rica), LÜCKING 1033. Guyana, LÜCKING 96-3193 (all hb. LÜCKING), SIPMAN (Lichenoth. Latinoam. 3). Malaysia, VEZDA & CENI s.n. (all hb. LÜCKING). Australia, KALB & KALB s.n. (holotype, hb. KALB).

Chroodiscus rubentiicola LÜCKING, GRUBE & KALB: Brazil, KALB & KALB (holotype, hb. KALB).

Chroodiscus submuralis LÜCKING: Costa Rica, LÜCKING 91-1437, 91-3560 (isotype), 91-3695, 92-2537 (all hb. LÜCKING)

Chroodiscus verrucosus R. SANT. & LÜCKING: Guinea: LISOWSKI s.n. Ivory Coast: SANTESSON 10452 (isotype). Ghana: JENIK s.n. Democratic Republic of Congo: LISOWSKI s.n., Tanzania: PÓCS 8426/R, BORHIDI & PÓCS 8455. Kenya: SANTESSON 21879 (all hb. LÜCKING).

Light microscopy

Light and epifluorescence microscopy were carried out using a Zeiss Axioskop compound microscope. The dyes used include Calcofluor White and Cotton Blue, all as 1% aqueous solution. Because transversal sections of thalli are of limited use to observe hyphal patterns, we observed most structural details in surface view. Thalli were either detached directly with a forceps or embedded in a film of nail-varnish prior to detachment (GRUBE 2001). To visualize the hyphae, we applied Calcofluor White (1% aqueous solution) in combination with an epifluorescence optics. The dye was applied for 5 min. After staining with Calcofluor White, rinse with 5% KOH helped to reduce the background fluorescence and resulted in a swelling of the tissue. Furthermore, the algal cell walls appeared bright yellowish green afterwards, whereas the fungal walls fluoresced bright blue. This color difference made it easier to observe minute details of both symbionts.

Phylogenetic analysis

In order to reconstruct the phylogeny of foliicolous species of *Chroodiscus*, we performed a phenotype-based cladistic analysis using 23 morphological, anatomical, chemical and distributional characters (Appendix 1). Eight foliicolous species were included in the analysis (Appendix 2), excluding *C. anomalus* and *C. africanus*, for which we did not have access to material to check the exact photobiont type. The corticolous *C. alborosellus* (NYL.) KALB was designated as outgroup taxon.

Shortest trees were searched according to maximum parsimony, by means of PAUP*4.0b8 (SWOFFORD 2000), using heuristic search based on random stepwise addition with 100 replicates and subtree-pruning-regrafting (SPR) as branch swapping algorithm. Jacknife analysis was performed with 1000 replicates and 85 % resampling (20 characters) for each replicate, with JAC emulation in effect. To test whether alternative phylogenies are in significant conflict with the most parsimonious solution, permutation tests were made on predefined monophyly constraints by means of ingroup taxa permutation via heuristic search on 1000 replicates.

Results

The species

Chroodiscus africanus R. SANT. & LÜCKING

Thallus smooth to uneven, autonomous (only known from the type); isidia absent; photobiont not identified; apothecia 0.15-0.25 mm diam., disc lacking anthraquinones, grey, K- or K+ yellowish; ascospores (6-)8 per ascus, 1-septate, 8-10 x 2-2.5 µm.

Chroodiscus parvisporus KALB & LÜCKING spec. nova. (Fig. 1A)

Sicut a *Chroodiscus mirificus* sed thallo irregulariter verrucoso isidiis nullis ascosporis 3-septatis minoribusque differt. Typus: Australia. Queensland: Surroundings of Daintree village, Daintree river, 20 m, IX. 1992, KALB & KALB s.n. (holotypus, hb. KALB).

Thallus uneven to irregularly verrucose, autonomous; isidia absent; photobiont a species of *Trentepohlia*, with elongate cells in wide open, irregular nets; apothecia 0.2-0.6 mm diam., disc lacking anthraquinones, grey, K– or K+ yellowish; ascospores 6-8 per ascus, (1-)3-septate, 6-10 x 2-3.5 µm.

Chroodiscus parvisporus is intermediate between *C. mirificus* and *C. verrucosus*. All presently known collections produce abundant apothecia but lack isidia, while *C. mirificus* mostly reproduces via isidia. If apothecia are present in the latter, the ascospores are often degenerate and if mature, differ from those of *C. parvisporus* by their larger size and occassional presence of longitudinal septa. *C. verrucosus* has a distinctly verrucose thallus and a *Phycopeltis* photobiont, and its ascospores are slightly larger than those of *C. parvisporus*. Their distribution is also different: while *C. verrucosus* is restricted to tropical Africa, *C. parvisporus* is known from Indomalaysia, Australia, and the Neotropics (collections previously misidentified as *C. verrucosus*). Among the foliicolous *Chroodiscus* species, *C. parvisporus* seems to be the one most closely related to corticolous representatives of the genus.

Chroodiscus mirificus (KREMP.) R. SANT. (Fig. 1B-D)

Thallus smooth to uneven, autonomous; disc-shaped isidia present; photobiont a species of *Trentepohlia*, with elongate cells in wide open, irregular nets; apothecia 0.3-0.8 mm diam., disc lacking anthraquinones, grey, K– or K+ yellowish; ascospores 2-6(-8) per ascus, often degenerate, (1-)3-5-septate and with 0-1 longitudinal septa per segment, (8-)12-15 x 3-5 µm.

Chroodiscus neotropicus KALB & VEZDA (Fig. 1E)

Thallus coarsely verrucose, autonomous or lichenicolous on *Porina* (*P. pseudoapplanata* LÜCKING & CÁCERES); isidia absent; photobiont a species of *Phycopeltis*, with

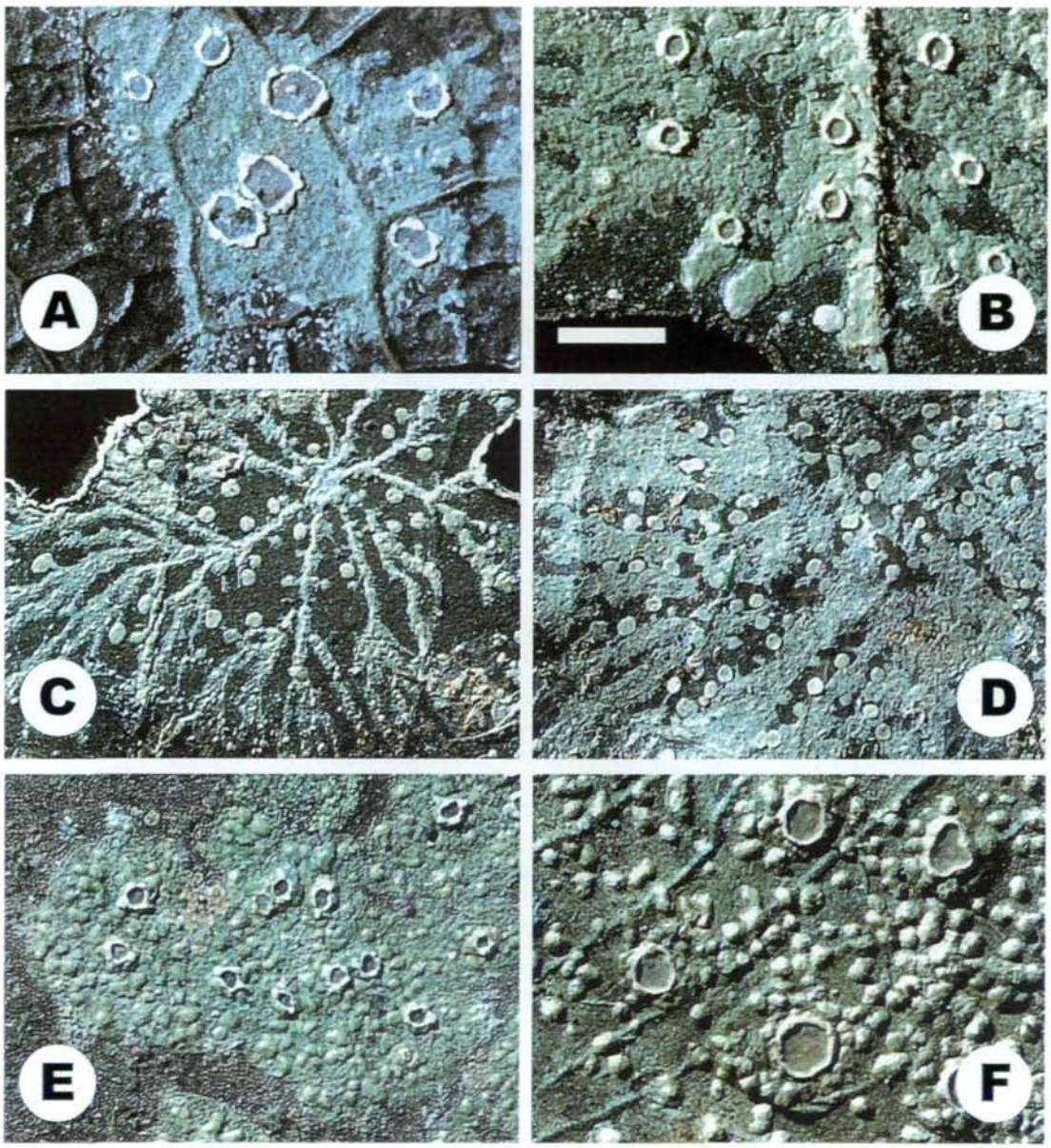

Fig. 1: Habit of *Chroodiscus* species. (**A**) *C. parvisporus*, thallus with apothecia (holotype). (**B-D**) *C. mirificus*. (**B**) Thallus with apothecia and one isidium (Papua New Guinea, MABBERLEY s.n.). (**C**) Young laciniate thallus with numerous isidia (Papua New Guinea, MABBERLEY s.n.). (**D**) Older thallus with numerous isidia (Malaysia, MOHAMED s.n.). (**E**) *C. neotropicus*, verrucose thallus with apothecia (Costa Rica, LÜCKING 91-1591). (**F**) *C. verrucosus*, verrucose thallus with apothecia (Democratic Republic of Congo, LISOWSKI 40326). Scale = 1 mm.

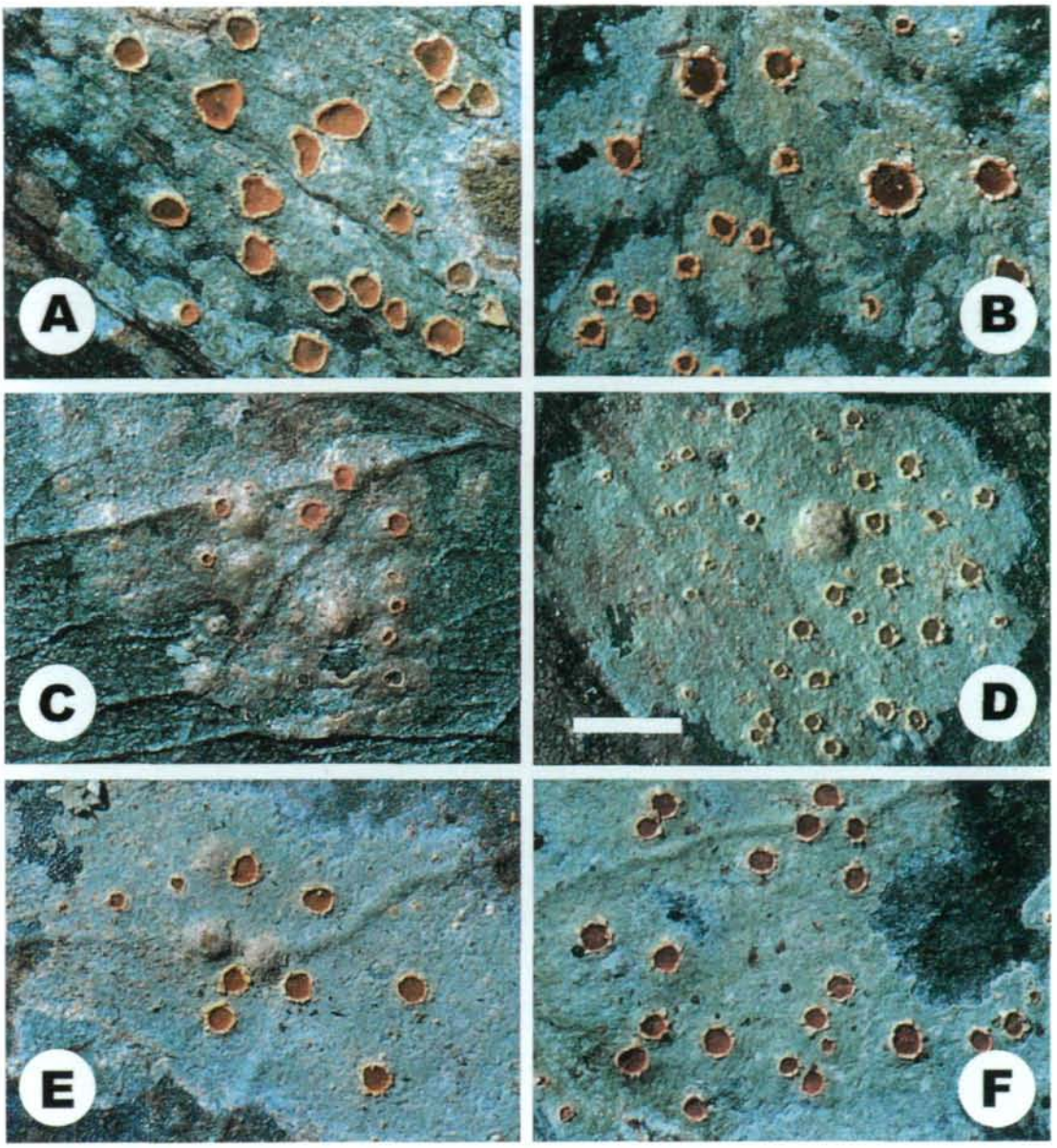

Fig. 2: Habit of *Chroodiscus* species. (**A-F**) *C. australiensis*. (**A-B**) Autonomous thalli with large apothecia (A: Costa Rica, LÜCKING 97-1398; B: Costa Rica, LÜCKING 00-234). (**C**) Young parasitic specimen on sound thallus of *Porina mirabilis* (Costa Rica, Lücking 97-738). (**D**) Parasitic specimen on partly necrotic thallus of *P. mirabilis* (Australia, HENSSEN s.n.). (**E**) Parasitic specimen on dead thallus of *P. mirabilis* (Ecuador, LÜCKING 96-696). (**F**) Cryptoparasitic specimen (Costa Rica, LÜCKING 99-134). Scale = 1 mm.

rectangular cells in closed, radiate rows; apothecia 0.15-0.25 mm diam., disc lacking anthraquinones, grey, K– or K+ yellowish; ascospores (6-)8 per ascus, 1-septate, 6-10 x 2-2.5 µm.

Chroodiscus verrucosus R. SANT. & LÜCKING (Fig. 1F)

Thallus coarsely verrucose, autonomous or lichenicolous on *Porina* (species not identified); isidia absent; photobiont a species of *Phycopeltis*, with rectangular cells in closed, radiate rows; apothecia 0.2-0.5 mm diam., disc lacking anthraquinones, grey, K– or K+ yellowish; ascospores 6-8 per ascus, 3-septate, 10-13 x 3-4 µm.

Chroodiscus australiensis VEZDA & LUMBSCH *(Fig. 2A-F)*

Thallus smooth, autonomous or lichenicolous on Porina (P. mirabilis Lücking & Vezda, rarely P. lucida R. Sant.); isidia absent; photobiont a species of Trentepohlia, with rectangular to rounded cells in open, parallel rows or irregular plates; apothecia 0.2-0.5 mm diam., disc with anthraquinones, bright orange red, K+ purple; ascospores (6-)8 per ascus, 1-septate, 7-10 x 2-2.5 µm.

Chroodiscus coccineus (LEIGHT.) MÜLL. ARG. (Fig. 3A-E)

Thallus coarsely verrucose, autonomous or lichenicolous on *Porina* (*P. subepiphylla* LÜCKING & VEZDA, rarely *P. epiphylla* (FÉE) FÉE); isidia absent; photobiont a species of *Phycopeltis*, with rectangular cells in closed, radiate rows; apothecia 0.2-0.6(-1.3) mm diam., disc with anthraquinones, bright orange red, K+ purple; ascospores 6-8 per ascus, (1-)3(-4)-septate, 8-12 x 2.5-4 µm.

Chroodiscus submuralis LÜCKING (Fig. 3F)

Thallus coarsely verrucose, autonomous or lichenicolous on *Porina* (species not identified); isidia absent; photobiont a species of *Phycopeltis*, with rectangular cells in closed, radiate rows; apothecia 0.2-0.5 mm diam., disc with anthraquinones, bright orange red, K+ purple; ascospores 6-8 per ascus, 3-5-septate and with 0-2 longitudinal septa per segment, 12-16 x 3.5-5 µm.

Chroodiscus rubentiicola LÜCKING, GRUBE & KALB spec. nova (Fig. 4)

Sicut a *Chroodiscus coccineus* sed thallo in *Porina rubentior* lichenicola et ascosporis 3-5-septatis differt. Typus: Brazil. Amazonas: Rio Preto near confluence with Amazonas, 80 km E of Manaus, 40 m, VIII. 1993, Kalb & Kalb s.n. (holotypus, hb. Kalb).

Thallus smooth, lichenicolous on *Porina* (*P. rubentior* (STIRT.) MÜLL. ARG.); isidia absent; photobiont a species of *Phycopeltis*, with rectangular cells in closed, radiate rows; apothecia 0.1-0.2 mm diam., disc with anthraquinones, bright orange red, K+ purple; ascospores 4-8 per ascus, 3-5-septate, 12-16 x 2.5-3 µm.

This new species differs from the other three taxa with anthraquinones by its lichenicolous growth on *Porina rubentior*, its smooth thallus lacking any crystalline verrucae, its very small apothecia, and its 3-5-septate, comparatively narrow ascospores. The

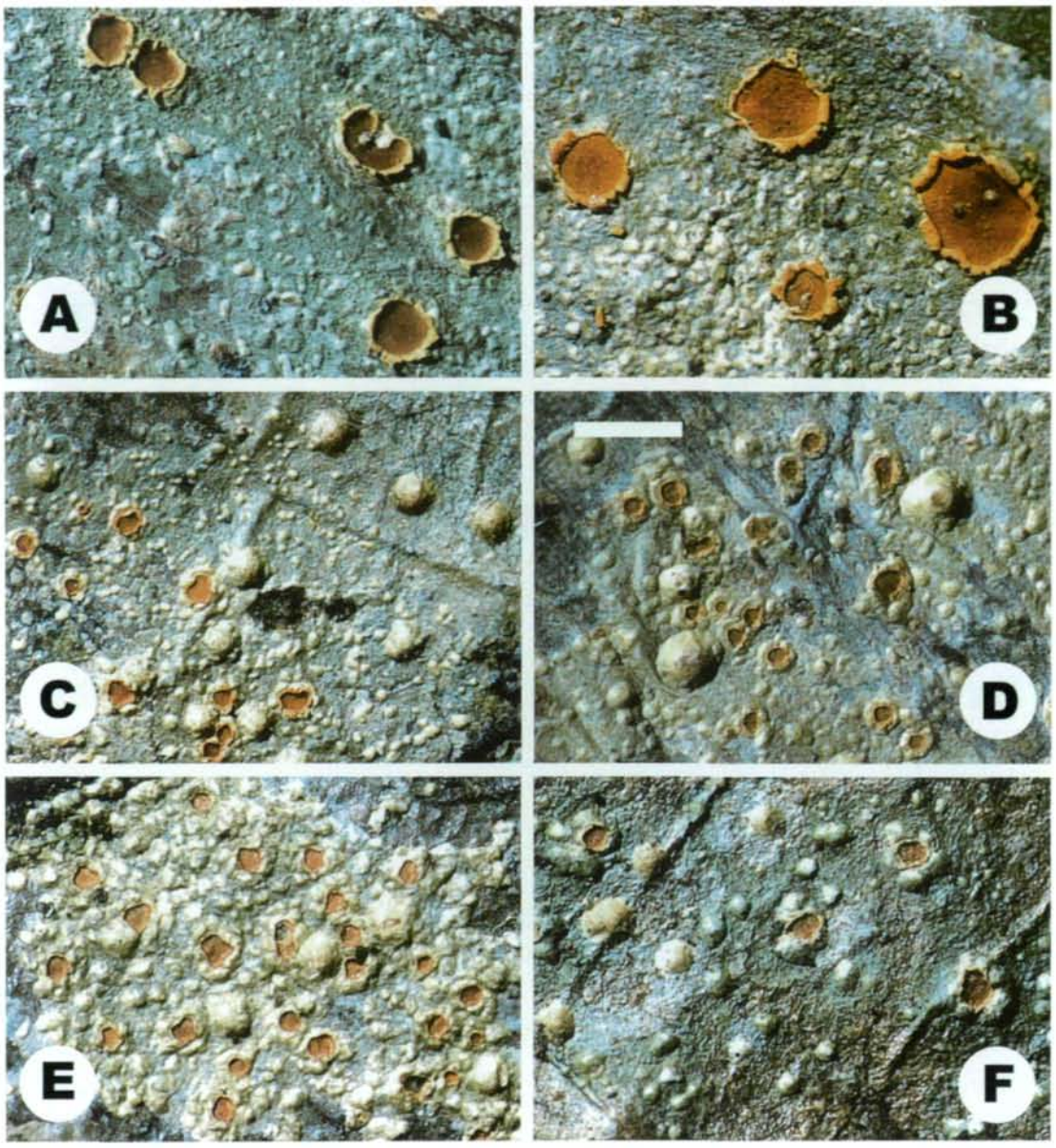

Fig. 3: Habit of *Chroodiscus* species. (**A-E**) *C. coccineus*. (**A-B**) Autonomous thalli with large apothecia (A: Ecuador, LÜCKING s.n.; B: Ecuador, LÜCKING 96-86). (**C**) Parasitic specimen on partly uninfected thallus of *Porina subepiphylla* (Costa Rica, LÜCKING 92-4157). (D) Parasitic specimen on sound thallus of *P. subepiphylla* (Costa Rica, SIPMAN s.n.). (**E**) Parasitic specimen on dead thallus of *P. subepiphylla* (Costa Rica, LÜCKING 92-4157). (**F**) *C. submuralis*, parasitic specimen on dead thallus of *Porina* sp. (isotype). Scale = 1 mm.

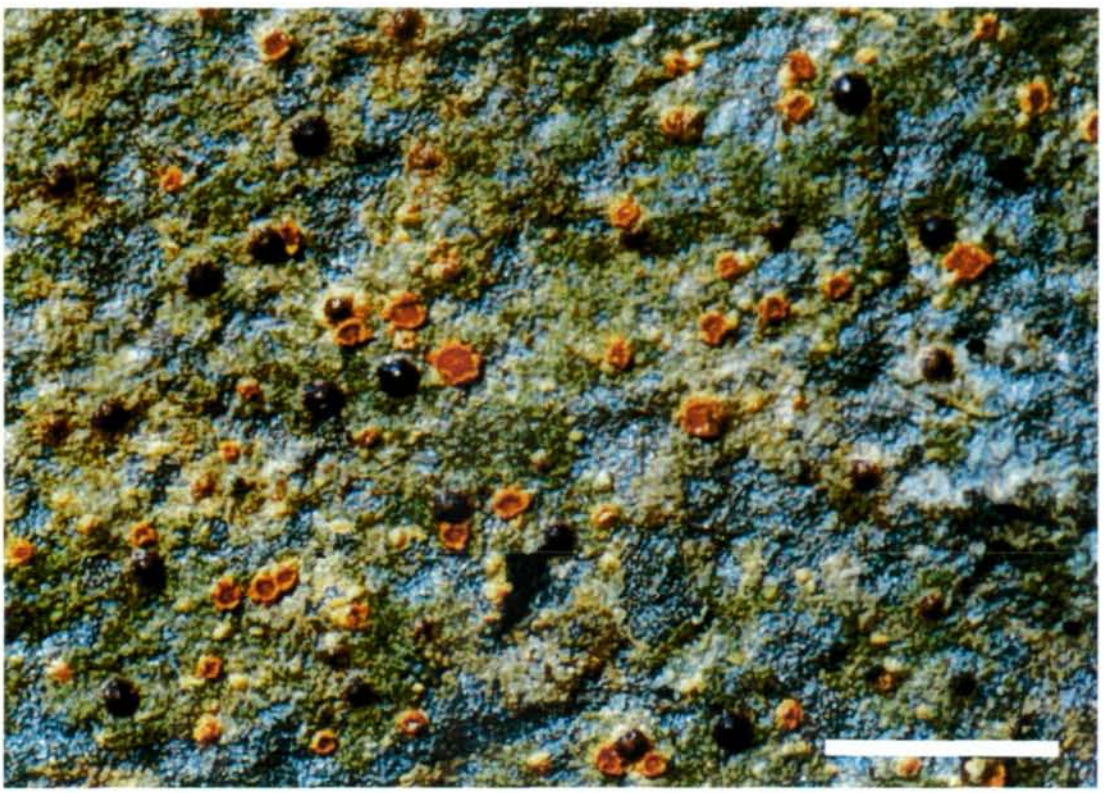

Fig. 4: Habit of *Chroodiscus* species. *C. rubentiicola*, parasitic specimen on *Porina rubentior* (holotype). Scale = 1 mm.

ascospores are similar to those of a probably undescribed taxon from tropical Africa (KALB & VEZDA 1992: 200, fig. 3.5s-t), but the latter differs by the absence of anthraquinones.

Phylogenetic analysis

Three groups are distinguished in the analysis. In one of three most parsimonious trees (Fig. 5A), the two species lacking anthraquinones and with *Trentepohlia* photobionts, *Chroodiscus parvisporus* and *C. mirificus* (*C. mirificus* group, G1) are situated on monophyletic clade close to the base. The four taxa with anthraquinones, *C. australiensis*, *C. rubentiicola*, *C. coccineus*, and *C. submuralis* (*C. coccineus* group, G2) form a paraphyletic grade, with *C. australiensis* closest to the base of the tree. This grade features two nested subgroups: the three species with *Phycopeltis* photobiont (*C. rubentiicola* subgroup), and the two species with distinct crystalline verrucae (*C. submuralis* subgroup). The remaining two species, lacking anthraquinones and with verrucose thallus and *Phycopeltis* phycobiont, viz. *C. neotropicus* and *C. verrucosus* (*C. verrucosus* group,

G3) appear as monophyletic sister clade to *C. coccineus*. This topology is rather well supported by the majority rule and the jackknife consensus (Fig. 5B–C).

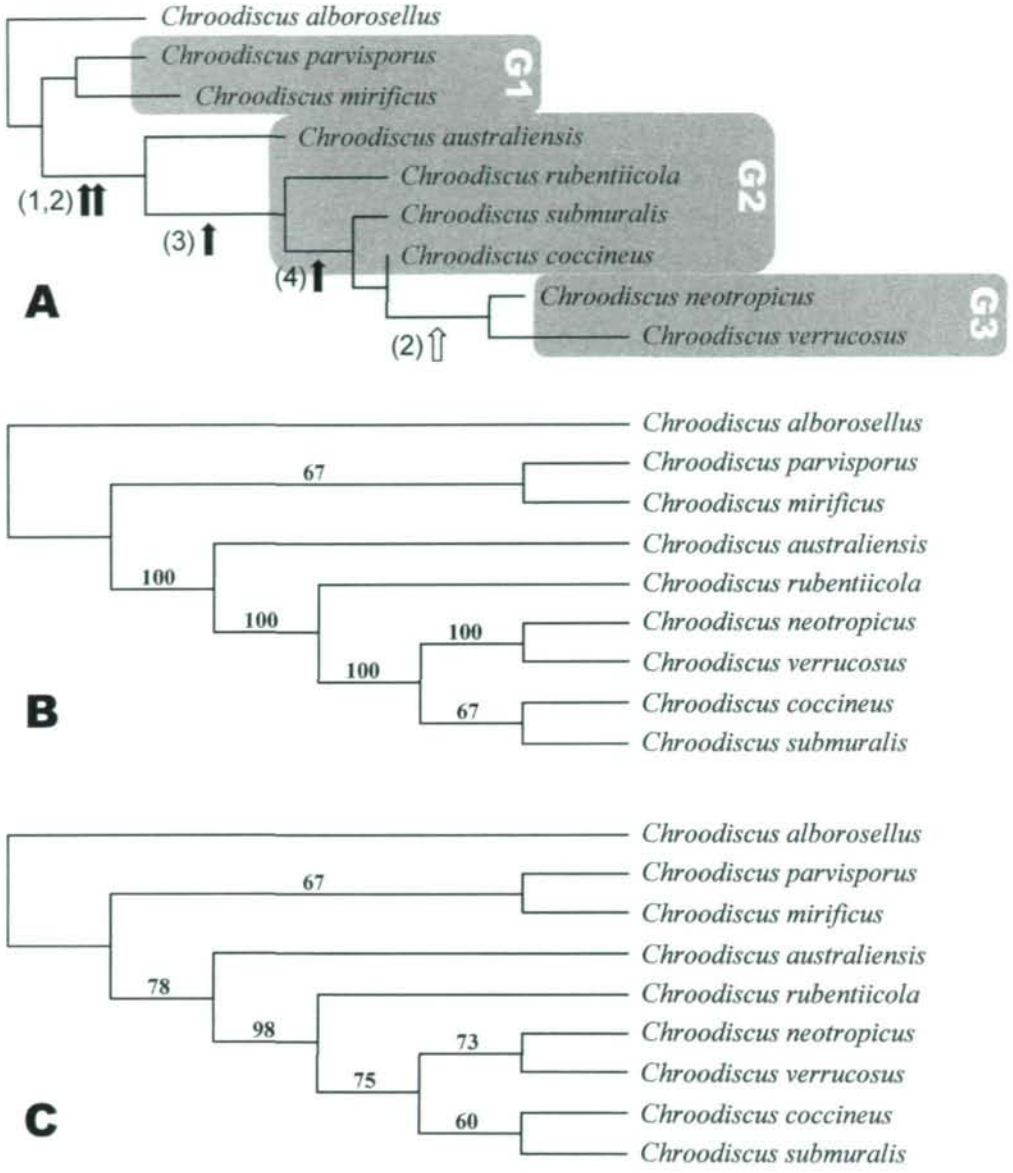

Fig. 5: Phylogenetic analysis of *Chroodiscus* species. (A) One of three most parsimonious trees (length = 37 steps; CI = 0.649, RI = 0.618, HI = 0.351), the three major groups and synapomorphies and reversals highlighted; 1 = lichenicolous growth habit, 2 = anthraquinones, 3 = *Phycopeltis*, 4 = distinct verrucae. (B) Majority rule consensus of three most parsimonious trees, the group frequencies indicated. (C) Jackknife consensus of 1000 replicates (15 % deletion, JAC emulation in effect), the jackknife values indicated.

Assuming the foliicolous growth as a synapomorphy for the whole entity, the phylogenetic analysis suggests the following characters as group synapomorphies (Fig. 5A): (1) facultatively lichenicolous growth (*Chroodiscus coccineus* and *C. verrucosus* group); (2) presence of anthraquinones (*C. coccineus* group, with reversal in the *C. verrucosus* group); (3) presence of *Phycopeltis* photobiont (*C. rubentiicola* subgroup plus *C. verrucosus* group); presence of distinct crystalline verrucae (*C. submuralis* subgroup plus *C. verrucosus* group). The interpretation of lack of anthraquinones in *C. neotropicus* and *C. verrucosus* is well supported by the distribution of two functionally independent characters, viz. phycobiont and crystalline verrucae. An alternative topography assuming a monophyletic *C. coccineus* group vs. a para- or monophyletic *C. mirificus* plus *C. verrucosus* group, i.e. a single gain of anthraquinones without reversal, would require two reversals in other characters (*Phycopeltis* to *Trentepohlia*, loss of crystalline verrucae) and produce significantly longer trees (TPT permutation test: $p = 0.52$ and $p = 0.64$, respectively).

Lifestyles

The facultative lichenicolous lifestyle was found in four species during our study, viz. *C. australiensis*, *C. submuralis*, *C. coccineus*, and *C. neotropicus*, and is also reported for *C. verrucosus*. *C. rubentiicola* is only known from the lichenicolous type material. The assumption that autonomous and lichenicolous populations are conspecific is supported by the identity of thallus and apothecial features in all four species investigated; particularly, the crystalline verrucae characterizing autonomous thalli of *C. coccineus* and *C. submuralis*, as well as *C. neotropicus* and *C. verrucosus*, are easily observed in lichenicolous specimens (Fig. 3 C-F). The alternative hypothesis that the lichenicolous populations are independent taxa would imply a high level of homoplasy regarding evolution of the lichenicolous growth habit.

We identified four different states of thallus development: (1) lichenized and autonomous, (2) lichenicolous and parasitic, (3) lichenicolous and cryptoparasitic, and (4) mixed. Autonomous thalli contain a single photobiont type proper of the species and feature all typical thallus characters, such as a cartilaginous cortex in *Chroodiscus australiensis* causing a smooth, slightly nitidous surface (Fig. 2A-B), and crystalline verrucae in *C. coccineus*, *C. neotropicus*, and *C. verrucosus* (Fig. 1A-B, 3A-B). All specimens referable to *C. parvsporus* and *C. mirificus*, as well as most individuals of *C. neotropicus* and *C. verrucosus* studied are autonomous. Autonomous thalli are also most frequent in *C. coccineus*, while they only account for slightly more than one forth of all investigated individuals in *C. australiensis* (Fig. 6).

Parasitic forms are easily recognized by the presence of *Chroodiscus* apothecia on the fertile (with perithecia) host thallus (Fig. 2C-E, 3C-F). Advanced stages of thalli parasitized by *C. australiensis* usually have a matt, farinose surface (Fig. 2E), while those attacked by *C. coccineus* become white. In all cases, host perithecia and ascospores become necrotic, a phenomenon much more pronounced in hosts of *C. australiensis* compared to those of *C. coccineus* (Fig. 7). Death of the host eventually also causes death of the parasitic *Chroodiscus*.

Cryptoparasitic thalli have been found in *C. australiensis* and *C. coccineus*; macroscopically, they resemble autonomous thalli in featuring only apothecia of *Chroodiscus*, but microscopical examination demonstrates the presence of primordial or residual, strongly necrotic host perithecia, easily detected by the differential K reaction (orange red in perithecia of *Porina* vs. purple in apothecia of *Chroodiscus*). Cryptoparasitic thalli are very rare in *C. coccineus*, but the most common stage in *C. australiensis* (Fig. 6); in this species, they can often be identified by their matt, farinose surface. Cryptoparasitic thalli presumedly represent forms in which the host is attacked in an early stage, suppressing the formation of mature perithecia.

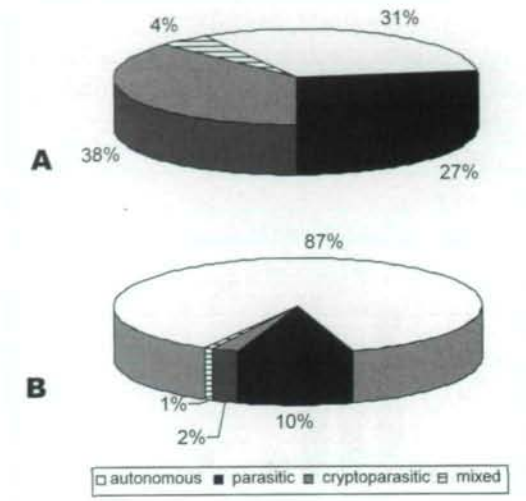

Fig. 6: Proportion of life style types, (**A**) *Chroodiscus australiensis* (n = 67). (**B**) *C. coccineus* (n = 161). Autonomous = lichenized with proper phycobiont, parasitic = apothecia growing on host thallus and host thallus macroscopically recognizable by presence of perithecia, cryptoparasitic = apothecia growing on host thallus but host thallus only microscopically recognizable by presence of perithecial remnants, mixed = parasitic parts contiguous with autonomous parts lichenized with proper phycobiont.

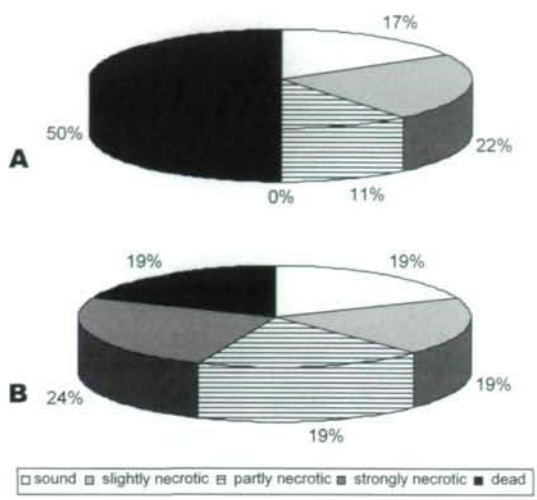

Fig. 7: Proportion of necrotic thallus parts (decolorated perithecia, degenerated hymenia) in host lichens attacked by parasitic *Chroodiscus* species. (**A**) *C. australiensis* (n = 18). (**B**) *C. coccineus* (n = 16). Sound = host thallus intact and producing sound ascospores, slightly necrotic = host thallus damaged up to 30%, partly necrotic = host thallus damaged up to 30%, strongly nec-rotic = host thallus damaged up to 90%, dead = host thallus damaged to 100%.

In both *Chroodiscus australiensis* and *C. coccineus*, apothecial size in parasitic and cryptoparasitic thalli is significantly smaller compared to autonomous thalli (Fig. 8). Assuming that apothecial size is a function of time, this might reflect the ability of autonomous thalli to grow for a longer period, while growth of parasitic forms is restricted by the eventual death of their hosts. However, apothecial size differences have also been found in mixed populations of *C. coccineus* containing both autonomous and parasitic individuals and which presumedly originate from a single dispersal event (Fig. 9). This

suggests that in parasitic forms of *Chroodiscus*, interactions with the host mycobiont (*Porina*) delay the development of apothecia.

Mixed thalli are forms where a single, contiguous individuum of *Chroodiscus* is partly autonomous and partly growing parasitically on a *Porina* host. They can be recognized by the presence of different photobionts in the two thallus parts, and the absence of any necrotic deformations in the autonomous part. Such mixed thalli have only been found in a single collection of *Chroodiscus australiensis* (three thalli) and two collections of *C. coccineus* (Fig. 6).

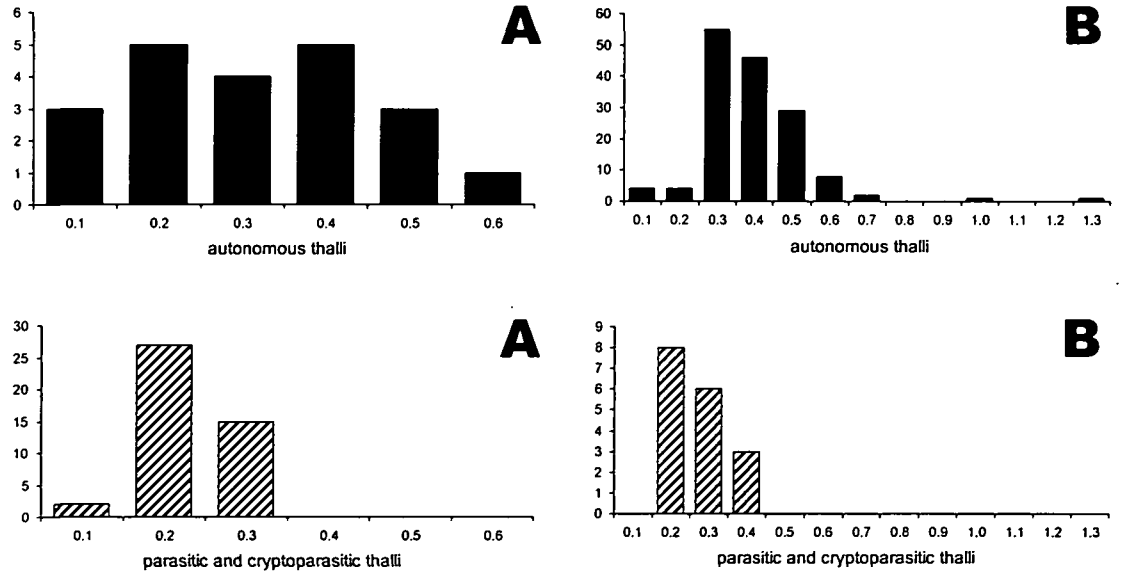

Fig. 8: Differences in apothecial sizes in autonomous vs. parasitic and cryptoparasitic specimens of *Chroodiscus* species. (**A**) *C. australiensis* (n = 64). (**B**) *C. coccineus* (n = 157). Kruskal-Wallis ANOVA for comparison of apothecial size differences between autonomous and parasitic / cryptoparasitic specimens: H = 5.9, p = 0.015 for *C. australiensis* (differences significant); H = 17.4, p < 0.001 for *C. coccineus* (differences highly significant).

Host and photobiont specificity

Hosts were identified to species level in all parasitic samples of *Chroodiscus australiensis* and *C. coccineus* and the single parasitic collections of *C. rubentiicola* and *C. neotropicus*. In the latter two, the host species are *Porina rubentior* and *P. pseudoapplanata*, respectively. In *Chroodiscus australiensis*, all but one of the attacked hosts represent *Porina mirabilis*, whereas in *C. coccineus*, all but one are *P. subepiphylla* (Fig. 10), which indicates a strong degree of host specificity. The hosts of the latter two species belong to the *Porina epiphylla* group (*Porina* sensu HARRIS 1995), while *P. rubentior* and *P. pseudoapplanata* are representatives of the *P. rufula* group (*Segestria*

Fig. 9: Mixed population of autonomous and parasitic specimens of *Chroodiscus coccineus* probably originating from a single dispersal event and with different apothecial sizes.

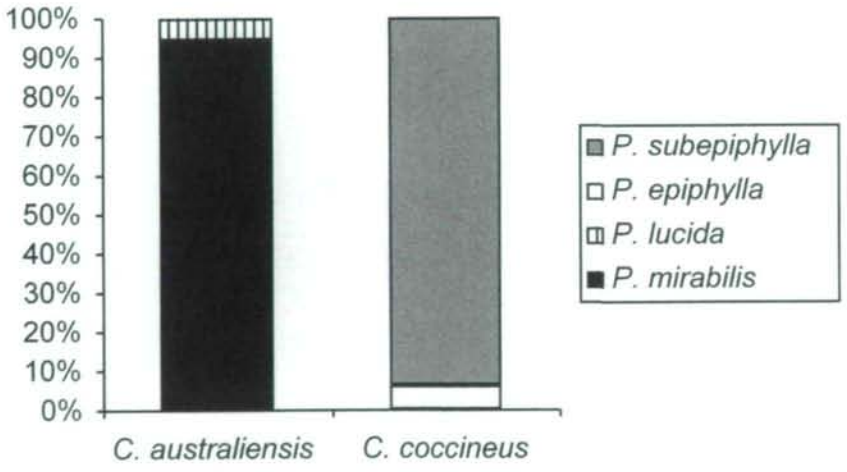

Fig. 10: Proportion of host lichens attacked by parasitic *Chroodiscus australiensis* (n = 18) and *C. coccineus* (n = 16).

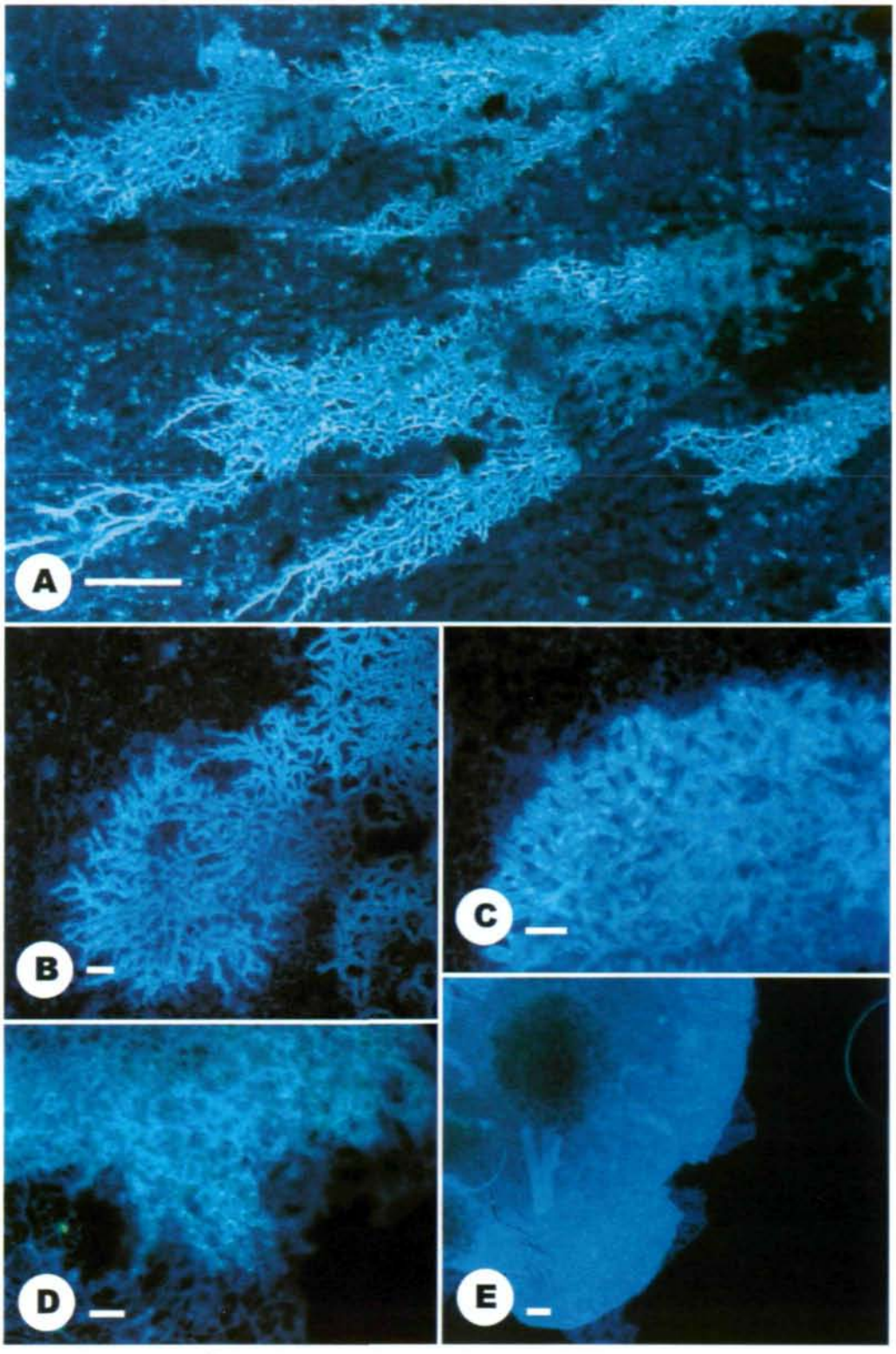

Fig. 11: Epifluorescence images. (A-C) *Chroodiscus mirificus* (New Guinea, 21. July 1972, leg. D.J. MABBERLEY, GZU): (A) Part of thallus, scale = 200 µm. (B) Young isidioid structure, scale = 20 µm. (C) Part of mature isioidoid structure, scale = 20 µm. (D) *C. australiensis* (Costa Rica, LÜCKING 91-352), part of thallus with photobiont, scale = 20 µm. (E) *C. coccineus* (Costa Rica, GRUBE XI.1999-1), part of thallus with photobiont, scale = 20 µm.

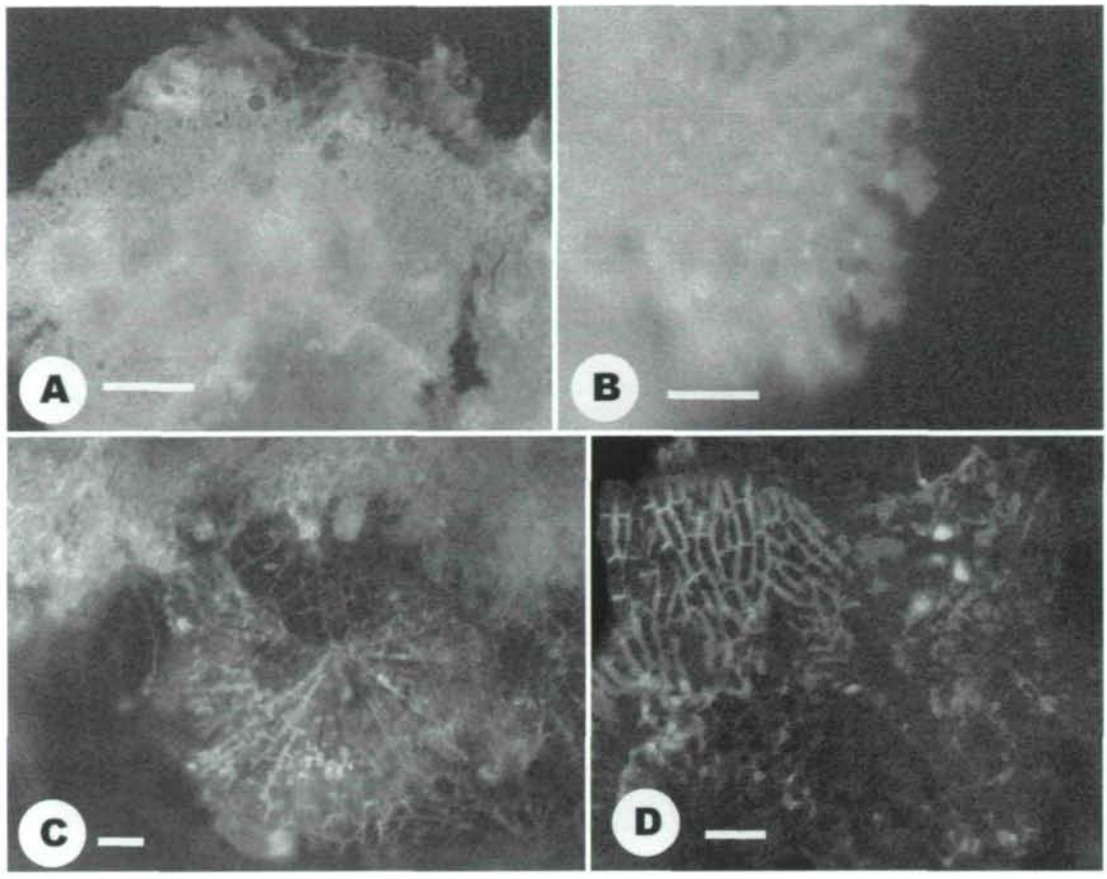

Fig. 12: Epifluorescence images. Photobiont in the parasitic form of *Chroodiscus coccineus* (Costa Rica, GRUBE XI.1999-2). (A) Overview, scale = 100 µm; (B) Detail, scale = 20 µm. (C, D) Mixed photobionts in *C. coccineus* (Costa Rica, LÜCKING 91-815). scales = 20 µm.

sensu HARRIS 1995). However, *P. pseudoapplanata* has been characterized as transitional between both groups, being in fact a close relative of *P. mirabilis*, the host of *Chroodiscus australiensis* (LÜCKING & CÁCERES 1999).

We detected four different photobiont morphotypes in the investigated foliicolous species of *Chroodiscus* and their hosts. Type I is composed of pale yellowish green, either elongate cells forming irregular nets with large interspaces or rounded cells arranged in closed, irregular plates (Fig. 11A). Their shape may be somehow modified in vegetative propagules of the lichen (Fig. 11B, C). Type II features bright green, either rectangular cells forming open, parallel rows or rounded cells arranged in closed, irregular plates (Fig. 11D). Type III is composed of pale yellowish green, rectangular cells in closed, radiate rows (Fig. 11E). Finally, type IV forms angular-rounded cells with partly wavy outline, arranged in closed, irregular plates (Fig. 12A, B). Types I and II are supposed to represent *Trentepohlia*, while types III and IV belong to *Phycopeltis*.

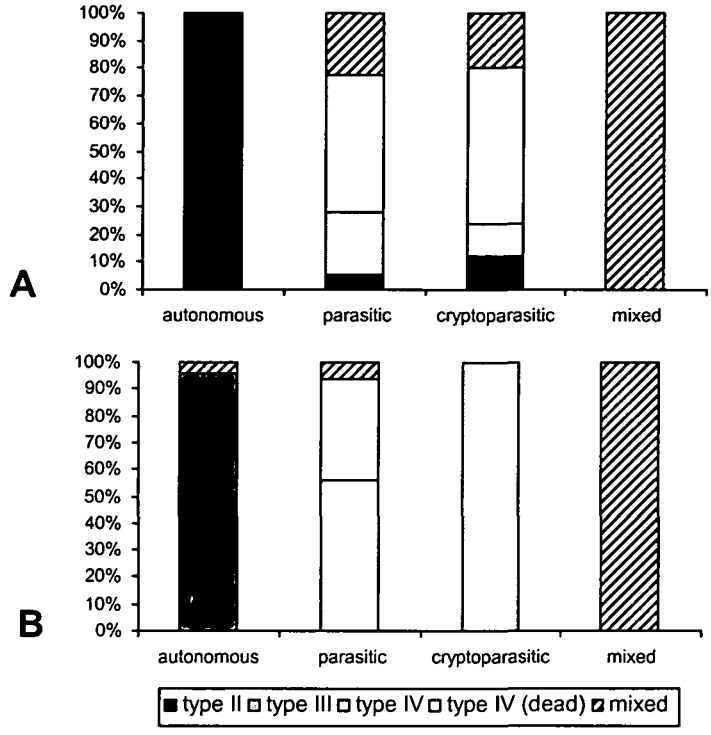

Fig. 13: Proportion of different algal types present in thalli depending on life style types in *Chroodiscus* species. (A) *C. australiensis* (n = 67). (B) *C. coccineus* (n = 161). Autonomous = lichenized with proper phycobiont, parasitic = apothecia growing on host thallus and host thallus macroscopically recognizable by presence of perithecia, cryptoparasitic = apothecia growing on host thallus but host thallus only microscopically recognizable by presence of perithecial remnants, mixed = partly parasitic and partly lichenized with proper phycobiont (contiguous). Type II = *Trentepohlia* with rectangular cells in open, parallel rows, type III = *Phycopeltis* with rectangular cells in closed, radiate rows, type IV = *Phycopeltis* with angular-rounded cells in closed, non-radiate plates (dead = decolorate contents).

Type I is typically found in autonomous thalli of *Chroodiscus parvisporus* and *C. mirificus*. The rounded cells, which are present near apothecia and in the latter species also in the isidia, appear to be functional modifications of the same algal species and individual. The same phenomenon is found in *C. australiensis* (type II) which features elongate cells in the thallus and rounded cells around the apothecial margins. Although type II resembles the cell structure of a *Phycopeltis* alga, the cellular plasticity supports its placement in *Trentepohlia*, for which such plasticity is characteristic. Type III is the photobiont of *Chroodiscus coccineus*, *C. submuralis*, *C. neotropicus*, and *C. verrucosus*; it is also found in the hosts of *C. rubentiicola* and *C. neotropicus*, viz. *Porina rubentior* and *P. pseudoapplanata*. On the contrary, hosts of *C. australiensis* and *C. coccineus*, all belonging to the *Porina epiphylla* aggregate, feature a photobiont of type IV.

Accordingly, autonomous thalli of *Chroodiscus australiensis* and *C. coccineus*, i.e. those which lack any signs of host structures, feature photobionts of type II and IV, respec-

tively (Fig. 13). Some individuals of presumed autonomous thalli in *C. coccineus* contained a photobiont of type IV. These are probably cryptoparasitic but might also indicate acquisition of a free host photobiont before it was lichenized. Thalli parasitized by *Chroodiscus australiensis* mostly feature the type IV photobiont characteristic of the host, *Porina mirabilis*, in the majority of these cases with dead cells, as indicated by colourless cell contents. In about one forth of the thalli, a second photobiont of type II was found, usually developed around the margins of the parasitic apothecia. The situation was quite similar in cryptoparasitic forms of this species (Fig. 13). *C. coccineus* differs in that type IV photobionts in hosts of parasitic forms are more frequently healthy, and in that both parasitic and cryptoparasitic forms show much less incidents of mixed photobionts. In both species, the few detected mixed forms contain type II and type III photobionts in the autonomous parts, respectively, while the parasitized parts feature type IV photobionts or a mixture (Fig. 13).

Discussion

Our observations suggest that most foliicolous representatives of *Chroodiscus* (Thelotremataceae) are facultative parasites on foliicolous lichens of the genus *Porina*, with a high specificity for their host species. Facultative parasitism is well known among lichenized fungi and occurs in the Thelotremataceae in the genus *Diploschistes*, e. g. in *D. bisporus*, *D. caesioplumbeus*, and *D. euganeus* (LUMBSCH 1989). Beside that, *D. muscorum* is a juvenile parasite (POELT & DOPPELBAUER 1965; FRIEDL 1987): the ascospores first germinate on the appropriate host thallus (*Cladonia* spp., rarely *Sterocaulon* spp. according to LUMBSCH 1989) and form a juvenile thallus by steeling the host photobiont. Later during development, a switch towards the proper photobiont of the *Diploschistes* species takes place, and the mature thallus is formed (FRIEDL 1987).

Although parasitic samples with mixed photobionts of *Chroodiscus* have been found, truly mixed thalli which indicate successful autonomous growth from a primarily parasitic juvenile stage are extremely rare and seem to be the result of chance encounters rather than part of the normal life cycle of the species. In fact, in most cases the initially parasitic forms retain their parasitic behaviour until maturity and until they eventually die after killing their host lichens. These species must therefore be considered facultative parasites, i.e. the ascospores are capable of associating either with the proper photobiont to form an autonomous thallus, or with a host photobiont to produce a parasitic thallus, in both cases developing mature apothecia and ascospores.

The biological advantage of such behaviour is apparent: since the hosts are abundant foliicolous lichens (LÜCKING 1999b, c) and probably even more abundant than the free-living proper photobionts of *Chroodiscus*, the chance of a germinating ascospore to encounter a photobiont and produce apothecia and ascospores again is greatly increased. Thus, facultative parasitism ensures frequent reproduction, either via autonomous or parasitic thalli. Facultatively parasitic forms might then be regarded as an intermediate generation in the life history, in case the proper photobiont is not contacted upon ascospore germination. In some way, this strategy recalls phycosymbiodemes involving

cyanobacterial and green algal morphs, where cyanobacterial *Dendriscocoulon* morphs are found under conditions which are too invariantly humid for green algal morphs (JAMES & HENSSEN 1976). However, the underlying biological reasons for the formation of such morphs are certainly different, dependent on the habitat conditions and not involving parasitism.

We have unsuccessfully attempted to determine the involved *Phycopeltis* species using the monograph by THOMPSON & WUJEK (1997). This is partly due to the fact that sexual structures of the algae necessary for their determination seem to be supressed in the lichenized stage. It is also likely that the lichen photobionts represent previously unrecognized species. For this reason, and because no recent data exist on *Trentepohlia* species, we named the morphologically distinguishable photobionts informally as different types. The rarity of parasitic and cryptoparasitic specimens featuring mixed photobionts, and the absence of any morphological connections between such mixed photobionts when they are present, confirms the hypothesis that these algal types represent taxonomically different entities and not modifications induced by the mycobiont. Otherwise, one would expect that parasitic *Chroodiscus* species would just take over the host photobiont and modify it accordingly to form its own thallus, which apparently does not happen in most of the cases.

This raises the questions, however, why the common parasitic forms, *C. australiensis* and *C. coccineus*, do not parasitize host lichens with the same photobiont as present in their autonomous thalli, and why they parasitize lichenized instead of free-living photobionts. The latter might be due to the high competition for photobionts among foliicolous lichens, possibly resulting in early lichenization of practically all available juvenile stages of free photobionts. This is especially true for the type IV *Phycopeltis* photobiont: very joung, non-lichenized stages of this photobiont may be observed on exposed glass slides (SANDERS 2001), but it is apparently unknown as non-lichenized in later stages (THOMPSON & WUJEK 1997; GRUBE & LÜCKING, unpublished observations). Competition for this photobiont might be extremely high, since it is found in most species of the *Porina epiphylla* group, which dominate the appearance of foliicolous lichen communities in the rainforest understory where the species of *Chroodiscus* are found (LÜCKING 1999b, c).

The fact that *Chroodiscus australiensis* and *C. coccineus* enter into competition for exactly this and not another photobiont might have an evolutionary explanation and is not necessarily related to the photobiont itself. One of the 'difficulties' for a lichenicolous fungus or lichen to infest on the hosts photobiont are defense mechanisms of the host mycobiont. Therefore, adaptations against host mycobiont defense mechanisms might be more sophisticated than those required to colonize the host photobiont. Once adapted to a host mycobiont, a switch toward another host lichen, which would feature a more appropriate photobiont might then be difficult. This is confirmed by the high specificity observed in parasitic *Chroodiscus* species, which even surpasses that of many lichenicolous fungi on the same group of host lichens (MATZER 1996).

The phylogenetic analysis suggests the parasitic behaviour in *Chroodiscus* to be synapomorphic, which means that it appeared once in a hypothetical ancestral taxon and was

inherited to all descendants. Although such an ancestral taxon is unknown, two alternative scenarios could be postulated: (1) its photobiont and that of the parasitized host lichen(s) were of a single, common type, and facultatively parasitic behavior was induced by strong photobiont competition, or (2) facultatively parasitic growth was favored by the fact that the ancestral taxon could, for some reason, overcome the defense mechanisms of a certain host lichen and took advantage of its photobiont, which was not necessarily the same as that of the autonomous lichen. The latter hypothesis is improbable, however, since the rather aggressive behaviour of *C. australiensis* and *C. coccineus*, both eventually killing their hosts, indicates strong detrimental interactions between the involved mycobionts.

Another reason for evolving a facultatively parasitic behaviour might be that the proper photobiont becomes rare or unavailable. In fact, the type II *Trentepohlia* photobiont of *Chroodiscus australiensis* has so far not been found in other foliicolous lichens, and its specific identity remains unclear. Parasitic forms are much more common in this taxon than in *C. coccineus* or other species of the genus, and the aggressive behaviour is much more pronounced. If this assumption holds true, photobiont switch associated with parasitic behaviour would be logical. In this case, *C. australiensis* could be regarded as the evolutionary prototype for facultatively parasitic growth, and indeed, the phylogenetic analysis places this taxon as sister to a clade including all other facultatively parasitic species. The subsequent switch to the type V *Phycopeltis* photobiont in this clade could be seen as an alternative result of rareness of the original photobiont. *C. coccineus* would then have inherited the facultatively parasitic growth on species of the *Porina epiphylla* group while at the same time itself having acquired a different photobiont. This would make facultatively parasitic growth less important for this and other derived species, and such behavior is indeed much less common compared to *C. australiensis.*

The increased agressivity of parasitic forms of *Chroodiscus*, eventually resulting in the death of host photo- and mycobionts, is interesting from another perspective, as similar phenomena are known from other fungi in connection with host switching. *Trichophyton* species, which occur asymptomatically in the fur of mammals, can cause serious infections when accidentially transmitted to humans (Yvonne GRÄSER, pers. comm. 2001). Accordingly, when the comensalic association with original symbionts in autonomous lichens is surpassed by a change to another photobiont, this would cause physiological stress. Particularly in trentepohlioid photobionts, with their thalline growth, stress is likely to be associated with differences in morphological characters of the photobiont, including varying growth rates. This would explain why algal switch associated with facultative parasitism in *Chroodiscus* results in enhanced agressivity.

It could be argued whether the initially aggressive association with a particular new host photobiont could eventually evolve into a more balanced form not involving parasitic behaviour but associating early with non-lichenized initials of this photobiont. Requiring efficient dispersal of fungal diaspores, selection pressure towards such non-parasitic associations would putatively create new, genetically differenciated phylogenetic lineages within lichenized species. Possible examples for such evolutionary events might be found in foliicolous *Arthonia*, *Opegrapha*, and *Porina* species, where closely related taxa often differ in their photobiont type (LÜCKING 1995, 1996; LÜCKING & MATZER 1996).

Alternatively, the parasitic behaviour could be maintained in the evolution, including situations where the lichenized and the parasitic forms may have existed together until the former disappeared while the latter has adapted to the host thallus. The close phenotypic relationships of lichenicolous and lichenized *Arthoniales* species on leaves may be reminiscent of this development. For example, the lichenized *Arthonia orbygniae* (H.B.P. UPADHYAY) MATZER is closely related to some non-lichenized, lichenicolous species (MATZER 1996). While *A. orbygniae* has a rare, lobate *Phycopeltis* photobiont, the lichenicolous *A. intermedia* Matzer, *A. pseudopegraphina* Matzer, and *A. santessonii* Matzer attack hosts with at least two further, different photobiont types. These species also differ from *A. orbygniae* by microscopic ascomatal characters (MATZER 1996; GRUBE & MATZER 1997).

If similar is true in *Chroodiscus*, it could be argued whether or not the parasitic forms represent separate species compared to the autonomous forms. This might be the case in *C. rubentiicola*, which is so far only known from a lichenicolous collection, with its autonomous counterpart being unknown. In the other species, however, the presence of separate species is inapparent, since it would imply that the lichenicolous growth habit evolved independently in at least five taxa and not as a synapomorphy as indicated in our phylogenetic analysis. Moreover, it would require that the lichenicolous forms retained all phenotypical characters typical of autonomous forms. Such an assumption is also contradicted by the, although rare, occurrence of forms with mixed photobionts and with transitions from parasitic to autonomous thalli. Cryptoparasitic thalli are particularly critical and may lead to misinterpretations. If host perithecial primordia are absent, such forms might not be properly recognized as a parasitic, but erroneously be regarded as a different lichen species with a different photobiont.

The vegetative diaspores exclusive to *Chroodiscus mirificus* are usually called isidia, although according to the dictionary of fungi (KIRK et al. 2001), this term is restricted to 'photobiont-containing protuberances of the cortex in lichens'. In *C. mirificus*, the propagules more exactly represent thallus patches with modified morphology, thus thallus fragments are dispersed and the term isidium cannot applied in its strict sense here. New terms were already used for some vegetative, algal-containing propagules (SCUTARI 1990), and particularly in corticolous Thelotremataceae, further new, yet unnamed types may occur (KOMPOSCH, pers. comm.). On the other hand, we hesitate to introduce new terms for such propagules, at least until their diversity is better interpreted and different types are unambiguously discerned by their homology criteria. Disc-shaped vegetative diaspores of various kinds are widespread among foliicolous lichens and might represent ecorticate thallus outgrowths, modified thallus parts, or even strongly derived conidiomata (LÜCKING 2001), and naming them differently would result in a unfortunate inflation of termini. We suggest to name any individual, autapomorphic types that do not fit the exact definition of isidia, as 'isidioid propagules'.

The absence of such isidioid propagules in all other species of *Chroodiscus* raises the question whether isidioid structures evolved after the branching of the *C. mirificus* clade or are lost in the other taxa. The latter seems highly improbable since the frequent occurrence of such structures in several unrelated lineages of foliicolous lichens suggest strong selective pressure towards their evolution and continuous formation. It also seems that

their formation is not triggered by the photobiont type, since *C. parvisporus* has the same type of photobiont, but all known collections lack propagules, while these are present in most samples of *C. mirificus* (otherwise distinguished by its smoother thallus and slightly different ascospores). The complete absence of parasitic behaviour in *Chroodiscus mirificus* might be connected to the abundant vegetative reproduction of this species via isidioid structures. This is a logical alternative to prevent from photobiont competition, but naturally goes along with the formation of widespread, genetically uniform clones. Thus the genetic structure of populations in this species is potentially different from the other species. This, as a genetic restriction, may also limit adaptation to new photobionts and evolution in general. As a matter of fact, in most foliicolous lichens with isidioid outgrowths, these are restricted to few or single species within a genus (e.g. *Pocsia*, *Phylloblastia*, *Porina*, *Echinoplaca*, *Coenogonium*, *Bacidina*), although the structure itself is ecologically successful, indicating that further radiation was prevented by reduced sexual reproduction.

Conclusions

Foliicolous species of *Chroodiscus* have evolved two different types of life histories as possible reaction to high photobiont competition. *C. mirificus* reproduces both sexually via ascospores and vegetatively via isidioid propagules. The latter strategy is more frequent and makes the species independent of photobionts accessibility, which corresponds to the decreased development of mature ascospores within individual apothecia. This suggests that present-day populations represent genetically uniform clones with reduced evolutionary potential, which might explain that there is only a single species with isidia. Most of the other species reproduce only sexually via ascospores which, however, are capable of facultatively associating with a proper photobiont to form an autonomous thallus or parasitizing a host lichen with an alternative photobiont. In both cases, reproduction is ensured by the formation of apothecia, while direct formation of an autonomous thallus from an initial parasitic stage is rare. This facultative parasitism thus differs from the juvenile parasitism found in other species of the family (*Diploschistes muscorum*), although it might have the same evolutionary triggering mechanism. Continuous sexual reproduction, associated with alternating photobionts, maintained a high evolutionary potential, which explains the apparent radiation of species with that lifestyle. Eventually, it led to speciation combined with an obligately parasitic lifestyle, as suggested by *C. rubentiicola*, and might be considered as a model for the evolution of secondarily delichenized, lichenicolous lineages in other groups of Ascomycota, such as Arthoniales.

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Appendix. 1: Characters for the phylogenetic analysis.

01 Corticolous growth habit: [0] present — [1] absent.
02 Foliicolous growth habit: [0] absent — [1] present.
03 *Trentepohlia* photobiont: [0] present — [1] absent.
04 *Trentepohlia* type I photobiont: [0] absent — [1] present.
05 *Trentepohlia* type II photobiont: [0] absent — [1] present.
06 *Phycopeltis* (type III) photobiont: [0] absent — [1] present.
07 Smooth thallus: [0] present — [1] absent.
08 Uneven thallus: [0] absent — [1] present.
09 Distinctly verrucose thallus: [0] absent — [1] present.
10 Isidia: [0] absent — [1] present.
11 Anthraquinones: [0] absent — [1] present.
12 One transversal septum: [0] absent — [1] present.
13 Three transversal septa: [0] absent — [1] present.
14 Five transversal septa: [0] absent — [1] present.
15 Seven transversal septa: [0] absent — [1] present.
16 Longitudinal septa: [0] absent — [1] present.
17 Lichenized lifestyle: [0] present — [1] absent.
18 Lichenicolous lifestyle: [0] absent — [1] present.
19 *Phycopeltis* type IV photobiont in host: [0] absent — [1] present.
20 *Phycopeltis* type III photobiont in host: [0] absent — [1] present.
21 Neotropics: [0] absent — [1] present.
22 African Paleotropics: [0] absent — [1] present.
23 Eastern Paleotropics: [0] absent — [1] present.

Appendix. 2: Species included in the phylogenetic analysis and binary character matrix.

Chroodiscus alborosellus	00000010000111100000111
Chroodiscus parvisporus	11010011100110000000101
Chroodiscus mirificus	11010011010111010000001
Chroodiscus neotropicus	11100100100100000101100
Chroodiscus verrucosus	1110010010011000 01--010
Chroodiscus australiensis	11001011001100000110111
Chroodiscus coccineus	11100100101110000110100
Chroodiscus submuralis	11100100101111010110100
Chroodiscus rubentiicola	11100110001111001101100

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