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Gregorella, a new genus to accommodate *Moelleropsis humida* and a molecular phylogeny of *Arctomiaceae*

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Abstract: The phylogenetic position of the European crustose pioneer lichen *Moelleropsis* (*Biatora*) *humida* (Kullhem) Coppins & P. M. Jørg. is studied using partial sequences of the mitochondrial SSU and nuclear LSU rDNA of 64 ascomycetes, including sequences of all known species of *Arctomiaceae*. The analysis places *M. humida* in the *Arctomiaceae* with strong support as sister to the Tasmanian genus *Wawea*. The genus *Arctomia* is monophyletic and sister-group to the *Wawea*+*Moelleropsis humida* clade. The new genus *Gregorella* is described to accommodate *Moelleropsis humida* and the new combination *Gregorella humida* (Kullhem) Lumbsch is proposed. The ontogeny of the ascomata of *Gregorella humida* is similar to that of other *Arctomiaceae*, in that the generative tissue is formed on a thallus outgrowth. The *Arctomiaceae* did not cluster with the bulk of cyanobacterial lichens in the *Lecanorales* suborder *Peltigerineae* (or *Peltigerales*), but is part of Ostropomycetidae. The closest relative of *Arctomiaceae* could not be identified, since the relationships of major clades within Ostropomycetidae lacked support.

Key words: *Arctomiaceae*, ascoma ontogeny, cyanophilous lichens, molecular phylogeny

Introduction

The phylogeny of lichenized ascomycetes that form symbiotic relationships with cyanobacteria as the primary photobiont has recently been the focus of several studies (Eriksson & Strand 1995; Miądlikowska & Lutzoni 2000; Schultz *et al.* 2001; Ekman & Jørgensen 2002; Lohtander *et al.* 2002; Thomas *et al.* 2002; Miądlikowska *et al.* 2003; Wiklund & Wedin 2003; Schultz & Büdel 2003; Miądlikowska & Lutzoni 2004; Wedin & Wiklund 2004). Ascomycetes in different clades, such as *Agyriales* (Lumbsch *et al.* 2001; Schmitt *et al.* 2003), *Pertusariales* (Lumbsch *et al.* 2001*a*; Schmitt *et al.* 2001) or different subclasses of *Lecanorales* (e.g. Stenroos & de Priest 1998; Wiklund & Wedin 2003; Miądlikowska & Lutzoni 2004), form symbiotic associations with cyanobacteria and green algae in a tripartite symbiosis. However, ascomycetes forming bipartite symbiotic relationships with cyanobacteria occur only in few clades. With the exception of the *Lichinales*, which have been classified as a separate subclass, Lichinomycetidae (Lutzoni *et al.* 2004; Reeb *et al.* 2004), most of these fungi are closely related. Consequently, the bulk of cyanobacterial lichens, except Lichinomycetidae, was placed in the suborder *Peltigerineae* of the *Lecanorales* (Wiklund & Wedin 2003; Wedin & Wiklund 2004), accepted at ordinal level by Miądlikowska & Lutzoni (2004).

However, the phylogenetic relationships of a small family of cyanobacterial lichens, the *Arctomiaceae*, remains poorly understood. This family occurs in polar and alpine regions of the northern and southern Hemispheres and includes four species that are classified in two genera: *Arctomia* Th. Fr. and the monotypic *Wawea* Henssen & Kantvilas (Henssen 1969; Henssen & Kantvilas 1985; Jørgensen 2003). The *Arctomiaceae* is characterized by the external development of the ascomata, which

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TABLE 1. *Species and specimens used in the current study. Newly obtained sequences are in bold face*

Species	Order (after Eriksson *et al*. 2004)	Collection	Genbank accession no.	
			nuLSU	mtSSU
Absconditella sphagnorum Vězda & Poelt	*Ostropales*	—	AY300825	AY300873
Adelolecia pilatii (Hepp) Hertel & Hafellner	*Lecanorales*	—	AY300826	AY300874
Agonimia sp.	*Verrucariales*	—	AY300827	AY300875
Agonimia tristicula (Nyl.) Zahlbr.	*Verrucariales*	—	AY300828	AY300876
Arctomia delicatula Th. Fr.	*Lecanorales*	—	AY853307	AY853355
A. interfixa (Nyl.) Vain.	*Lecanorales*	USA, Washington, Olympic Peninsula, *Thomson* 15456 (WIS)	DQ007345	DQ007348
A. teretiuscula P.M. Jørg	*Lecanorales*	China, Sichuan, (GZU—holotype)	DQ007346	DQ007349
Bacidia rosella (Pers.) De Not.	*Lecanorales*	—	AY300829	AY300877
Calicium viride Pers.	*Lecanorales*	—	AF356670	AY143402
Caloplaca flavorubescens (Huds.) J.R. Laundon	*Lecanorales*	—	AY300831	AY143403
Capronia mansonii (Schol-Schwarz) E. Müll.	*Chaetothyriales*	—	AY004338	AF346422
Ceramothyrium carniolicum (Rehm) Petr.	*Chaetothyriales*	—	AY004339	AF346423
Chromatochlamys muscorum (Fr.) H. Mayrhofer & Poelt	Family of uncertain position	—	AY60773	AY607743
Coccotrema cucurbitula (Mont.) Müll. Arg.	*Pertusariales*	—	AF274092	AF329161
C. maritimum Brodo	*Pertusariales*	—	AF329164	AF329163
Conotrema populorum Gilenstam	*Ostropales*	—	AY300833	AY300882
Dermatocarpon luridum (With.) J.R. Laundon	*Verrucariales*	—	AY607732	AY607744
Diploschistes muscorum (Scop.) R. Sant.	*Ostropales*	—	AY300836	AY300886
D. thunbergianus (Ach.) Lumbsch & Vězda	*Ostropales*	—	AF274095	AF431955
Hymenelia lacustris (With.) M. Choisy	*Lecanorales*	—	AY853323	AY853371
Lecania cyrtella (Ach.) Th. Fr.	*Lecanorales*	—	AY300840	AY300891
Lecanora intumescens (Rebent.) Rabenh.	*Lecanorales*	—	AY300841	AY300892
Lecidella meiococca (Nyl.) Leuckert & Hertel	*Lecanorales*	—	AY300842	AY300893
Lobaria pulmonaria (L.) Hoffm.	*Lecanorales*	—	AY340548	AY340503
L. retigera (Bory) Trevis	*Lecanorales*	—	AY340550	AY340505
Moelleropsis humida (Kullh.) Coppins & P.M. Jørg.		—	AY853329	AY853378
Neobelonia sp.	*Ostropales*	—	AY300830	AY300879
Nephroma bellum (Spreng.) Tuck.	*Lecanorales*	—	AY300844	AY300895
Norrlinia peltigericola (Nyl.) Theiss. & Syd.	*Verrucariales*	—	AY300845	AY300896
Ochrolechia androgyna (Hoffm.) Arnold	*Pertusariales*	—	AY300846	AY300897
O. tartarea (L.) A. Massal.	*Pertusariales*	—	AY300848	AY300899
Orceolina kerguelensis (Tuck.) Hertel	*Agyriales*	—	AF274116	AF381561

TABLE 1. *Continued*

Species	Order (after Eriksson *et al*. 2004)	Collection	Genbank accession no.	
			nuLSU	mtSSU
Peltigera aphthosa (L.) Willd.	*Lecanorales*		AF286759	AY340515
P. praetextata (Flörke ex Sommerf.) Vain.	*Lecanorales*		AF286814	AY124167
Pertusaria albescens (Huds.) M. Choisy & Werner	*Pertusariales*	—	AF329176	AF329175
P. amara (Ach.) Nyl.	*Pertusariales*	—	AF274101	AY300900
P. erythrella Müll. Arg.	*Pertusariales*	—	AF274100	AF431958
P. leioplaca DC.	*Pertusariales*	—	AY300852	AY300903
P. pertusa (Weigel) Tuck.	*Pertusariales*	—	AF279300	AF381565
P. rupicola var. *coralloidea* (Anzi) Croz.	*Pertusariales*	—	AY300853	AY300904
P. subventosa Malme	*Pertusariales*	—	AY300854	AY300905
P. tejocotensis de Lesd.	*Pertusariales*	—	AF279301	AF381566
Physcia aipolia (Ehrh. ex Humb.) Fürnr.	*Lecanorales*	—	AY300857	AY143406
Placopsis bicolor (Tuck.) de Lesd.	*Agyriales*	—	AY212834	AY212857
P. gelida (L.) Linds.	*Agyriales*	—	AY212836	AY212859
Protothelenella corrosa (Körb.) H. Mayrhofer & Poelt	Family of uncertain position	—	AY607734	AY607746
P. sphinctrinoidella (Nyl.) H. Mayrhofer & Poelt	Family of uncertain position	—	AY607735	AY607747
Pyrenula laevigata (Pers.) Arnold	*Pyrenulales*	—	AY607736	AY568029
P. nitida (Weigel) Ach.	*Pyrenulales*	—	AY607737	AY568030
Scoliciosporum umbrinum (Ach.) Arnold	*Lecanorales*	—	AY300861	AY300911
Sticta fuliginosa (Dicks.) Ach.	*Lecanorales*		AY340573	AY340530
Stictis radiata (L.) Pers.	*Ostropales*	—	AY300864	AY300914
Strigula stigmatella (Ach.) R.C. Harris	Family of uncertain position	—	AY607738	AY607748
Thelenella antarctica (I.M. Lamb) O.E. Erikss.	Family of uncertain position	—	AY607739	AY607749
Thelotrema lepadinum (Ach.) Ach.	*Ostropales*	—	AY300866	AY300916
T. suecicum (H. Magn.) P. James	*Ostropales*	—	AY300867	AY300917
Thrombium epigaeum (Pers.) Wallr.	Family of uncertain position	—	AY607740	AY607750
T. epigaeum (Pers.) Wallr.	Family of uncertain position	—	AY607741	AY607751
Toninia sedifolia (Scop.) Timdal	*Lecanorales*	—	AY300868	AY300918
Trapelia coarctata (Turner ex Sm.) M. Choisy	*Agyriales*	—	AF274117	AY212874
T. placodioides Coppins & P. James	*Agyriales*	—	AF274103	AF431962
Trapeliopsis flexuosa (Fr.) Coppins & P. James	*Agyriales*	—	AF274118	AY212875
T. granulosa (Hoffm.) Lumbsch	*Agyriales*	—	AF274119	AF381561
Tremolecia atrata (Ach.) Hertel	*Lecanorales*	—	AY853347	AY853397
Wawea fruticulosa Henssen & Kantvillas	*Lecanorales*	Tasmania, *Kantvilas* (F, HO)	DQ007347	—
Xanthoria parietina (L.) Th. Fr.	*Lecanorales*	—	AF356687	AY143406

eventually have a multidivided disc, an amyloid ascus wall and a faintly amyloid tholus, 1–10 transversely septate ascospores, and a corticate thallus containing *Nostoc* as cyanobiont. Miądlikowska & Lutzoni (2004) did not include sequences of *Arctomiaceae* in their analyses, but suggested, based on structural similarities demonstrated by Henssen & Kantvilas (1985), that it may belong to *Peltigerineae* (as *Peltigerales*), closely related to *Collemataceae* and *Coccocarpiaceae* (placed in *Collematineae*). However, these similarities seemed to be mentioned merely to express doubts regarding the systematic placement of *Wawea* in the *Arctomiaceae* rather than being a statement on the phylogenetic relationships of the family (Henssen & Kantvilas 1985: 95). Previously, Henssen (1965, 1969) demonstrated considerable differences in the ascoma development of *Arctomia* and the *Collemataceae*, especially the external development in the former. Hence, Henssen (1969) suggested excluding *Arctomia* from the *Collemataceae* and to resurrect the *Arctomiaceae* as originally proposed by Fries (1860). In a study by Wedin *et al.* (2005) that included one species of *Arctomia* in a phylogenetic analyses using nuclear LSU and mitochondrial SSU rDNA sequences, *Arctomia* fell outside the peltigerinean lichens (including the *Collemataceae*) and had a sister-group relationship to *Moelleropsis humida*.

Moelleropsis humida was originally described as a *Biatora* species (Kullhem 1871) and subsequently as a *Leprocollema* species by Magnusson (1938). The species was placed in the formerly monotypic *Moelleropsis* by Coppins and Jørgensen (in Purvis *et al.* 1993) based on morphological similarities. Both the type species of *Moelleropsis* (*M. nebulosa*) and *M. humida* are terricolous lichens that often behave as pioneers. Both have a thin granular thallus but are anatomically quite different. *Moelleropsis* s. str. belongs to *Pannariaceae*, which is part of *Peltigerineae*. However, using ITS sequence data, Ekman & Jørgensen (2002) demonstrated that *Moelleropsis humida* does not belong here and not even to the *Pannariaceae*, an observation supported by Wedin *et al.* (2005).

As a consequence of this work, we have explored the phylogenetic position of *Moelleropsis humida* and the *Arctomiaceae*. We present here the results of a phylogenetic study including sequences of the nuclear LSU and mitochondrial SSU ribosomal DNA of all currently known species of *Arctomiaceae*. We have also studied the micromorphology of *Moelleropsis humida*, including the ontogeny of the ascomata, with the aim of investigating whether the molecularly inferred phylogenetic conclusions are supported by morphological evidence. Our molecular and morphological results indicate that *Moelleropsis humida* is indeed unrelated to the *Pannariaceae*, but belongs in a new genus of the *Arctomiaceae*. This new genus is described below.

Materials and Methods

Specimens

New nu LSU and mt SSU rDNA sequences were obtained from three species and aligned with sequences of 61 other euascomycetes as listed in Table 1.

Additional comparative material examined. Arctomia delicatula Th. Fr.—**Canada:** *Northwest Territories*: Distr. of Franklin, Bathurst Island, Polar Pass area, *H. L. Dickson* 2286 (WIS); unnamed tributary of the Arctic Red River, *C. D. Bird & J. W. Thomson* 19742 (WIS).

Arctomia interfixa (Nyl.) Vain.—**Canada:** Northwest Territories: Artillery Lake, Rat Lodge, *J. W. Thomson* 12135 & *J. A. Larsen* (WIS).

Moelleropsis humida (Kullhem) Coppins & P.M. Jørg.—**Germany:** *Nordrhein-Westfalen*: Ihnetal near Listerscheid, 30 ix 2000, *Zimmermann* (F), Ratingen, 24 iii 2002, *Zimmermann* (F).

Morphological studies

Longitudinal sections 16–20 μm thick were obtained from thalli and apothecia of *Moelleropsis humida* using a Leica SH2000 R freezing microtome. The samples were first hydrated with alcohol and deionized water, and then mounted in an embedding medium (O.C.T. 4583 Compound) to be frozen at − 20 °C. The sections were stained in lactophenol cotton blue. For the ontogenetic study, serial sections through thallus parts with small apothecia were prepared. Asci and ascospores were studied using squash preparations of apothecial sections; these features were also studied in *Arctomia* and *Wawea* specimens.

Molecular techniques

Total DNA was extracted from herbarium specimens using the DNeasy Plant Mini Kit (Qiagen) following the instructions of the manufacturer. Dilutions (10^{-1}) or undiluted DNA was used for PCR amplifications of the genes coding for the nuclear LSU rRNA and the mitochondrial SSU rRNA. Primers for amplification and sequencing, and PCR and cycle sequencing conditions were as described in Lumbsch *et al.* (2004). Amplification products were viewed on 1% agarose gels stained with ethidium bromide and subsequently purified using the QIAquick PCR Purification Kit (Qiagen). Sequence fragments obtained were assembled with SeqMan 4.03 (DNASTAR) and manually adjusted.

Sequence alignment

Because the mitochondrial data set contains highly variable sequence portions, we employed an alignment procedure that uses a linear Hidden Markov Model (HMM) as implemented in the software SAM (Sequence Alignment and Modelling system) (Karplus *et al.* 1998). Regions that were not aligned with statistical confidence were excluded from the phylogenetic analysis.

Phylogenetic analysis

The alignments were analyzed by maximum parsimony (MP) and a Bayesian approach (B/MCMC) (Huelsenbeck *et al.* 2001; Largет & Simon 1999).

MP analyses were performed using the program PAUP* (Swofford 2003). A heuristic search with 200 random taxon addition replicates was conducted with TBR branch swapping and MulTrees option in effect, equally weighted characters and gaps treated as missing data. Bootstrapping (Felsenstein 1985) was performed based on 2000 replicates with random sequence additions.

The Bayesian analyses were conducted using the MrBayes 3.0 program (Huelsenbeck & Ronquist 2001). The posterior probabilities of each branch were calculated by counting its occurrence in trees that were visited during the course of the MCMC analysis. For all data sets the general time reversible model of nucleotide substitution (Rodriguez *et al.* 1990), including estimation of invariant sites and assuming a discrete gamma distribution with six rate categories (GTR+I+G), was used. Parameters were calculated for each partition separately as proposed by Nylander *et al.* (2004). MrBayes was run on each data set producing 2 000 000 generations. Twelve chains were run simultaneously. Trees were sampled every 100 generations for a total of 20 000 trees. The first 200 000 generations (i.e. the first 2000 trees) were deleted as the 'burn in' of the chain. We plotted the log-likelihood scores of sample points against generation time using TRACER 1.0 (http://evolve.zoo.ox.ac.uk/software.html?id=tracer) to ensure that stationarity was achieved after the first 200 000 generations by checking whether the log-likelihood values of the sample points reached a stable equilibrium value. The remaining 18 000 trees were used to construct a majority rule consensus tree with average branch lengths using the sumt option of MrBayes. Posterior probabilities were obtained for each clade. Clades that received bootstrap support equal or above 75% under MP and posterior probabilities above 0·94, were considered as strongly supported. Phylogenetic trees were visualized using the program Treeview (Page 1996).

Results

Phylogeny based on molecular data

Three new nu LSU and two new mt SSU rDNA sequences were generated for this study (Table 1). These sequences were each aligned with 61 sequences obtained from GenBank to produce a matrix of 861 unambiguously aligned nucleotide positions in the LSU and 792 in the mt SSU rDNA. 394 characters were variable in the nu LSU and 530 in the mt SSU data set. The topology of the 95%-majority rule consensus trees of the two Bayesian single-partition analyses was congruent (data not shown) and hence a combined analysis was performed. The alignment is available in TreeBase (http://www.treebase.org/treebase/).

The likelihood parameters in the sample had the following average values (± one standard deviation): likelihood Ln= $-2586{\cdot}323$ ($\pm 0{\cdot}32$), base frequencies $\pi(A)=0{\cdot}306$ ($\pm 0{\cdot}003$), $\pi(C)=0{\cdot}174$ ($\pm 0{\cdot}003$), $\pi(G)=0{\cdot}239$ ($\pm 0{\cdot}003$), $\pi(T)=0{\cdot}281$ ($\pm 0{\cdot}004$), rate matrix $r(AC)=1{\cdot}07$ ($\pm 0{\cdot}059$), $r(AG)=3{\cdot}25$ ($\pm 0{\cdot}127$), $r(AT)=1{\cdot}91$ ($\pm 0{\cdot}086$), $r(CG)=1{\cdot}05$ ($\pm 0{\cdot}055$), $r(CT)=5{\cdot}38$ ($\pm 0{\cdot}262$), $r(GT)=1{\cdot}0$ ($\pm 0{\cdot}0$), gamma shape parameter $\alpha=0{\cdot}747$ ($\pm 0{\cdot}015$), and the proportion of invariable site $p(invar)=0{\cdot}303$ ($\pm 0{\cdot}006$). In the MP analysis, one most parsimonious tree with a tree length of 5045 steps, with CI=0·32 and RI=0·58, was found. The topologies of the phylogenetic trees obtained in the MP and Bayesian analyses were identical and thus the majority-rule consensus tree of 18 000 sampled trees in the Bayesian analysis is shown in Fig. 1. Only clades that received strong support (i.e. more than 74% MP bootstrap and more than 0·94 posterior

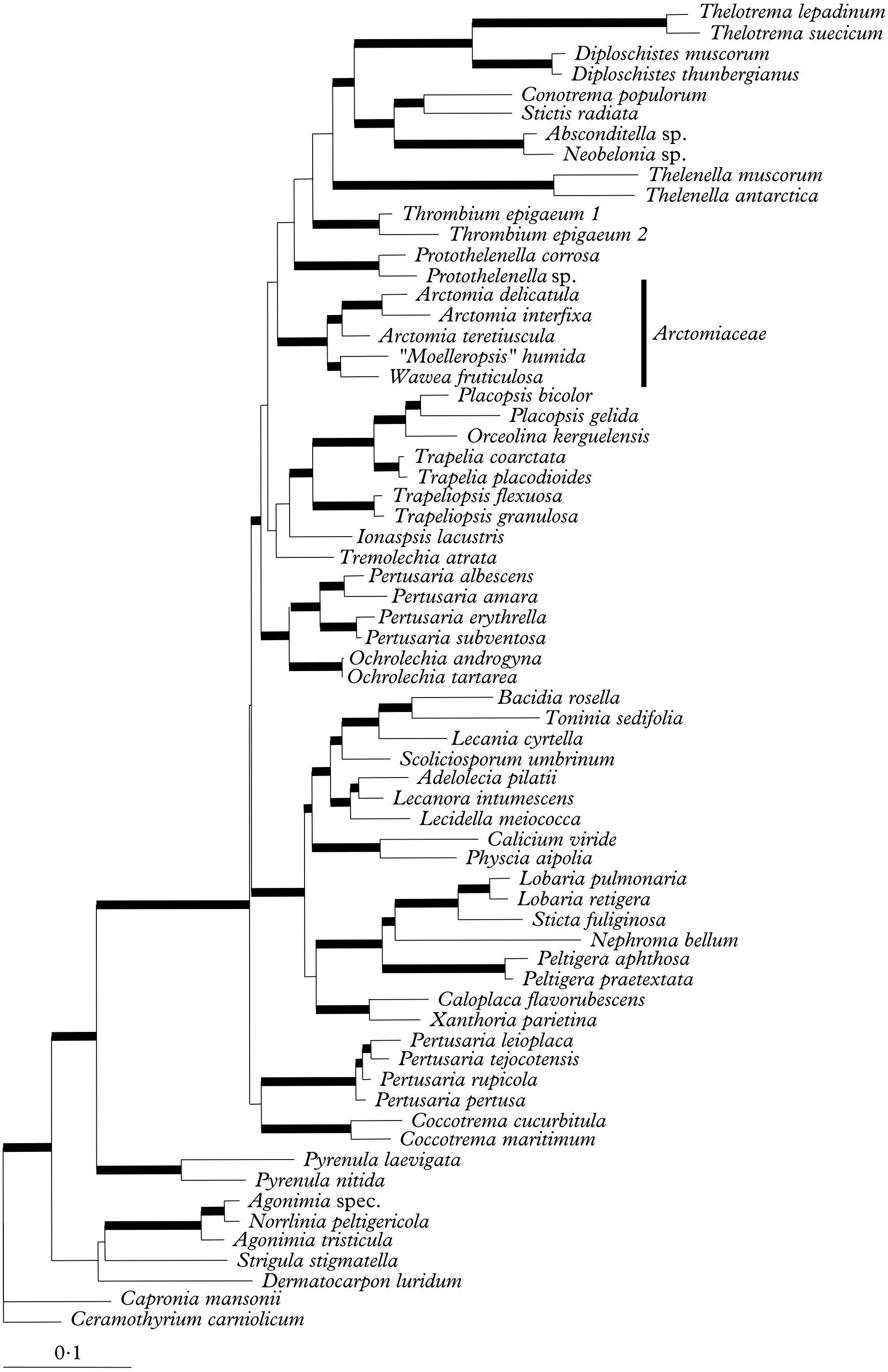

FIG. 1. Phylogeny of *Arctomiaceae* and related Lecanoromycetes as inferred from a combined analysis of nuclear LSU rDNA and mitochondrial SSU rDNA. This is a 50% majority-rule consensus tree based on 18 000 trees from a Bayesian MCMC tree sampling procedure. Branches with posterior probabilities equal or above 0·95 and MP bootstrap support values above 74% are indicated in **bold**.

probability) in both analyses are indicated in bold in Fig. 1.

Moelleropsis humida clusters within the *Arctomiaceae* as sister-group to *Wawea fruticulosa* with strong support. These two species are sister to the three species of *Arctomia*. The Himalayan *A. teretiuscula* is basal within *Arctomia*. All relationships within the *Arctomiaceae* and the family itself are strongly supported in both analyses. However, the phylogenetic relationship of the family to other groups of lichenized ascomycetes remains unresolved. While the placement of *Arctomiaceae* together with *Agyriales*, *Graphidales*, *Ostropales*, *Pertusariales* p.p., *Hymeneliaceae*, *Protothelenellaceae*, and *Thelenellaceae* within the Ostropomycetidae is strongly supported, most relationships of orders and families in that subclass are not supported. The *Graphidales* (*Diploschistes*, *Thelotrema*) and *Ostropales* s. str. (*Absconditella*, *Conotrema*, *Neobelonia*, *Stictis*) are strongly supported and have a strongly supported sister-group relationship. The *Protothelenellaceae* (*Protothelenella*, *Thrombium*) is paraphyletic, but this lacks support. *Agyriales* (*Orceolina*, *Placopsis*, *Trapelia*, *Trapeliopsis*) are strongly supported as monophyletic, whereas the basal position of *Ionaspis* and *Tremolecia* to this order is not supported. The *Variolaria*-group of *Pertusaria* (Schmitt & Lumbsch 2004) is strongly supported and forms a well supported clade with *Ochrolechia*. The genus *Pertusaria* s. str. and *Coccotrema* are basal to remaining Lecanoromycetes. However, this placement and the sister-group relationship of the two genera lacks support. The *Lecanorales*, including the *Peltigerineae* and *Teloschistineae*, are strongly supported as monophyletic. The Lecanoromycetes are also strongly supported. Nine taxa belonging to Chaetothyriomycetes were used as an outgroup.

Ascoma development of *Moelleropsis humida*

The development of the ascomata takes place in an outgrowth of the thallus. In the earliest stages observed (Fig. 2A), ascogonia are visible in the upper part of the primordium with paraphysoids. No trichogynes were found. The primordium is only slightly elevated from the thallus. In a later stage (Fig. 2B) the inner part of the primordium is filled with richly branched paraphysoids and the margins of the primordium are slightly brownish pigmented. In the lower part, there are ascogenous hyphae present that are more easily seen in later stages of development. The young asci grow into the hymenium comprised of paraphyses. The mature apothecia are sessile (Fig. 2C) on the goniocyst thallus. The proper exciple (Fig. 2D) consists of paraplectenchymatous, thin-walled hyphae. The asci have a faintly amyloid wall and a non-amyloid tholus and contain eight single-celled or rarely 1-septate ascospores (Fig. 2E). The overall ascoma development in *Moelleropsis humida* is gymnocarpous.

Discussion

The phylogenetic analysis of an extended molecular data set of *Arctomiaceae* strongly supports the placement of *Moelleropsis humida* in this family and confirms the previous results by Wedin *et al.* (2005) that these lichen-forming fungi do not belong in the *Lecanorales*. Instead the *Arctomiaceae* belong to Ostropomycetidae and are a further clade of lichen-forming fungi, in addition to the Lichinomycetidae and *Peltigerineae* (or *Peltigerales*), that employ cyanobacteria as their primary photobiont. Unfortunately, our data set was not sufficient to clarify the phylogenetic placement within the Ostropomycetidae, but morphological characters, such as the ascus-type, suggest a relationship to the *Agyriales*. Additional molecular data are necessary to evaluate this hypothesis.

The placement of *Moelleropsis humida* in the *Arctomiaceae* is supported by morphological evidence. This includes cyanobacteria as primary photobiont, an external ascoma ontogeny and the ascus with an amyloid wall and non-amyloid tholus. At one stage, alternative classifications of *Moelleropsis humida* in the *Arctomiaceae* were

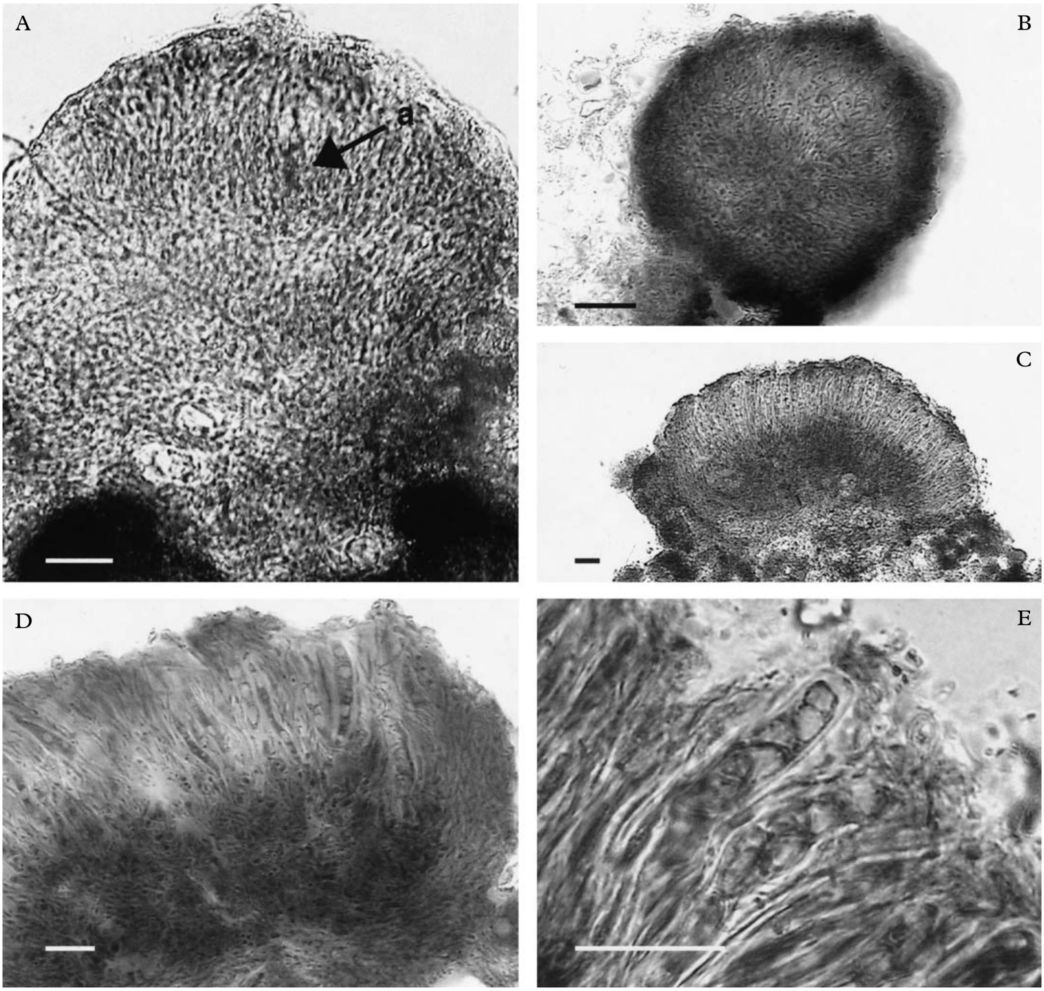

FIG. 2. Ascoma development in *Moelleropsis humida*. A, primordium with ascogonia (arrow) and paraphysoids; B, primordium filled with richly branched paraphysoids; C–E, cross section through mature apothecium; C, overview; D, detail showing the true exciple; E, detail showing the hymenium with asci and ascospores. Scales: A–E = 30 µm.

considered, such as placing *Gregorella humida* in *Wawea* or merging all species of *Arctomiaceae* within the one genus in order to avoid having two monotypic genera in the family. However, our phylogenetic analysis does not contradict the current generic concepts in the family. The genus *Arctomia* is monophyletic in our analysis and has a sister-group relationship to *Moelleropsis humida* + *Wawea*. We feel that the differences between the genera, of which the most important features are listed in Table 2, further confirm the current generic concept. Thus we decided to describe *Moelleropsis humida* in a new genus.

Gregorella—a new genus for *Moelleropsis humida*

Gregorella Lumbsch, gen. nov.

Genus *Arctomiacearum*, photobiontas ad *Nostoc* pertinentes in thallo continens. Thallus crustaceus, ex

TABLE 2. *Main characters that distinguish genera within the* Arctomiaceae

Genus	Thallus	Apothecia	Pycnoascocarps	Paraphyses	Hymenial gel	Ascal tholus	Ascospores	Distribution
Arctomia	Crustose to coralloid or squamulose, not goniocystal	Secondary multidivided	Absent	Lax, simple, apically thickened, brown pigmented	Hemi-amyloid	Faintly amyloid ring	Fusiform, 4–10-septate	Bipolar, arctic-alpine
Gregorella	Crustose, composed of goniocysts	Not multidivided	Absent	Lax, simple, apically not thickened and not pigmented	Non-amyloid	Non-amyloid	Ellipsoid, 1(–2)-celled	Temperate, western Europe
Wawea	Fruticose	Secondary multidivided	Present	Strongly conglutinate, sparingly branched and anastomosing, apically not thickened and not pigmented	Hemi-amyloid	Faintly amyloid ring	Fusiform, 2-celled	Tasmania and New Zealand

goniocystis constans. Apothecia sessilia, orbicularia, biatorina, gymnocarpia. Excipulum anulatum, hyalinum. Hymenium amyloideum. Paraphyses simplices vel ramosae. Asci ad typum *Trapeliae* dictum pertinentes, octospori. Ascosporae hyalinae, ellipsoideae, simpices vel 1-septatae, non-halonatae. Pycnidia non visa.

Typus generis: **Gregorella humida (Kullhem) Lumbsch, comb. nov.**

Basionym: *Biatora humida* Kullhem, *Not. Sallsk. Fauna Fl. Fenn. Förh.* **11:** 274 (1870).—*Lecidea humida* (Kullhem) Th. Fr., *Lich. Scand.* **2:** 477 (1874).—*Moelleropsis humida* (Kullhem) Coppins & P.M. Jørg., in Purvis, Coppins & James, *Bull. Br. Lich. Soc.* **72** (Suppl.)**:** 75 (1993).

Leprocollema europaeum H. Magn., *Hedwigia* **78:** 219 (1938).

Thallus crustose, thin, granular, olivaceous to dull grey-brown, bluish grey when wet, consisting of goniocysts. *Goniocysts* 30–60 μm in diam., roundish, covered by a layer of isodiametric cells, 6·0–8·5 μm wide. Prothallus not visible. *Photobiont* belonging to the genus *Nostoc*.

Apothecia numerous, sessile, roundish, constricted at base, 0·2–0·6 mm diam., discs red-brown, colourless when young, convex, immarginate or margins soon becoming excluded. *True exciple* annulate, yellowish, composed of long-celled, thin-walled hyphae. *Subhymenium* yellowish, 50–80 μm high. *Hymenium* 70–90 μm high, hyaline, non-amyloid. *Paraphyses* simple to slightly branched, easily separated, 1–1·5 μm thick, not thickened apically. *Asci* cylindrical to subclavate, *Trapelia*-type, 8-spored with ascus wall amyloid and tholus non-amloid. *Ascospores* ellipsoid, hyaline, non-septate or rarely 1-septate, non-halonate, 12·5–19·5 × 6·5–9·5 μm.

Pycnidia not seen.

Chemistry. No secondary metabolites found by TLC or HPLC.

Etymology. The new genus is described in honour of Dieter Gregor Zimmermann (Düsseldorf) who first introduced HTL to this fascinating lichen in the field.

Notes. *Gregorella humida* is a small crustose lichen composed of goniocysts containing a *Nostoc* cyanobiont. It is readily recognized when wet by its bluish grey thallus and glossy red-brown apothecia. The hymenial gel and ascus wall are amyloid, but the tholus is non-amyloid. The ascospores are hyaline and mostly single-celled. The species is a pioneer lichen on bare soil and detritus at roadsides and dump heaps. Its ecology and distribution were discussed by Poelt & Vězda (1990) and, more recently, by Cezanne *et al.* (2003).

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