

Molecular data support placement of *Cameronia* in Ostropomycetidae (Lecanoromycetes, Ascomycota)

H. Thorsten Lumbsch¹, Gintaras Kantvilas², Sittiporn Parnmen¹

¹ Department of Botany, Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, IL 60605, USA

² Tasmanian Herbarium, Private Bag 4, Hobart, Tasmania, Australia 7001

Corresponding author: *Thorsten Lumbsch* (tlumbsch@fieldmuseum.org)

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Abstract

The phylogenetic position of the Tasmanian endemic genus *Cameronia* Kantvilas is studied using partial sequences of nuclear LSU and mitochondrial SSU ribosomal DNA. Monophyly of the genus is supported, as is its placement in Ostropomycetidae, although its position within this subclass remains uncertain. Given the lack of close relatives to *Cameronia* and its morphological differences compared to other families with perithecioid ascomata in Ostropomycetidae, the new family Cameroniaceae Kantvilas & Lumbsch is proposed.

Keywords

Cameroniaceae, lichens, new family, Tasmania, taxonomy

Introduction

The lichen flora of Tasmania has a remarkable number of unique species, as well as several genera that are unknown or very rarely found in other regions. Examples include the genera *Jarmania* Kantvilas (Kantvilas 1996), *Meridianelia* Kantvilas & Lumbsch (Kantvilas and Lumbsch 2009), *Siphulella* Kantvilas, Elix & P. James (Kantvilas et al. 1992), *Tasmidella* Kantvilas, Hafellner & Elix (Kantvilas et al. 1999), and several species of *Cladia* (Kantvilas and Elix 1987, 1999) and thelotremoid Graphidaceae (Kantvilas and Vezda 2000; Mangold et al. 2009). In general, endemism can be either the result of survival of relict taxa (palaeoendemism) or recent speciation events (neoendemism) (Brandley et al. 2010; Brooks et al. 2006; Goldberg et al. 2005; Jans-

sen et al. 2008; Kier et al. 2009; Kraft et al. 2010; Lamoreux et al. 2006; Olson et al. 2001; Qian 2001). The reasons for the relatively large amount of endemic taxa in Tasmania are not well understood. In the genus *Cladia*, for example, molecular data are consistent with a recent speciation and suggest neoendemism (Lumbsch et al. 2010; Parnmen 2011), but for most endemic taxa there are currently insufficient data available to test whether they represent relict lineages or are the product of recent speciation events. In some cases, however, lichens that were believed to be endemic to Tasmania, were subsequently also discovered in New Zealand, e.g. *Bunodophoron flaccidum* (Wedin 1993; Wedin 2001).

Lichen taxa unique to Tasmania include the genus *Cameronia* (Kantvilas 2012), which was recently described with an unclear systematic position and placed tentatively in Ostropomycetidae. The genus includes two species that occur on siliceous rocks at high elevations. Although its thallus is superficially similar to that of a species of *Lecanora* or *Pertusaria*, the genus is readily distinguished by the presence of eumuriform ascospores in thick-walled, broadly obovate, hemiamyloid asci with a non-amyloid tholus, formed in a hamathecium consisting of richly branched, anastomosing paraphysoids. The ascomata are perithecioid. Secondary metabolites present in the genus include the 9-*O*-methylpannaric acid chemosyndrome and an unknown triphenyl.

Thick-walled asci having a hemiamyloid wall and non-amyloid tholus, anastomosing paraphysoids and muriform ascospores are all characters reminiscent of Arthoniales (Ertz and Tehler 2011; Grube 1998; Tehler 1990), but the perithecioid ascomata, chlorococcoid photobiont, and morphological details of the ascus differ from this order (Kantvilas 2012). Perithecioid ascomata and thick-walled asci in a hamathecium consisting of anastomosing paraphysoids are characteristic for Protothelenellaceae and Thelenellaceae in Ostropomycetidae (Fryday and Coppins 2004; Mayrhofer 1987a,b; Mayrhofer and Poelt 1985; Schmitt et al. 2005). However, these families differ in having cylindrical asci and, furthermore, Thelenellaceae lacks any amyloid reactions of the asci, whereas Protothelenellaceae have an amyloid tholus. Because phenotypic characters do not place *Cameronia* in any group unambiguously and the placement in Ostropomycetidae was tentative, we used freshly collected material of the two species of *Cameronia* to generate DNA sequences of two loci (mtSSU and nuLSU rDNA) to test the monophyly of *Cameronia* and its placement of *Cameronia* in Ostropomycetidae, and to identify the closest relatives of the genus and place it in a family.

Materials and methods

Taxon sampling and molecular methods

The study is based on fresh material collected by GK and deposited in the Tasmanian Herbarium (HO) and the Field Museum of Natural History (F), and on DNA sequences downloaded from Genbank. Sequences of Umbilicariaceae were included as outgroup since this family has been shown previously to be sister to Lecanoromycetida

e+Ostropomycetidae (Lumbsch et al. 2007a; Miadlikowska et al. 2006; Spatafora et al. 2006; Wedin et al. 2005). Sequence data of the two species of *Cameronia* were assembled with sequences of mitochondrial small subunit (mtSSU) and nuclear LSU rDNA downloaded from Genbank (Table 1). Sample preparation, DNA isolation, PCR and direct sequencing were performed as described previously (Mangold et al. 2008; Rovas-Plata and Lumbsch 2011). Primers for amplification were: mr SSU1 (Zoller et al. 1999) and MSU7 (Zhou and Stanosz 2001) for mtSSU, and AL2R (Mangold et al. 2008) and nu-LSU-1125-3' (= LR6) (Vilgalys and Hester 1990) for nuLSU rDNA. Sequence fragments obtained were assembled with SeqMan 4.03 (DNASTAR) and manually adjusted.

Table 1. Sequences obtained from Genbank for the study. Family or generic group as in figure 1, largely following (Lumbsch and Huhndorf 2010). Newly obtained sequences are indicated in bold.

Species	Family/generic group as in Fig. 1	nuLSU	mtSSU
<i>Acarosporina microspora</i>	Stictiaceae	AY584643	AY584612
<i>Agyrium rufum</i>	-	EF81824	EF81821
<i>Ainoa mooreana</i>	-	AY212850	AY212828
<i>Anzina carneonivea</i>	-	AY212829	AY212851
<i>Arctomia delicatula</i>	Arctomiaceae	AY853307	AY853355
<i>Arctomia teretiuscula</i>	Arctomiaceae	DQ007346	DQ007349
<i>Aspicilia caesiocinerea</i>	Megasporaceae	DQ780303	DQ780271
<i>Aspicilia cinerea</i>	Megasporaceae	DQ780304	DQ780272
<i>Aspicilia contorta</i>	Megasporaceae	DQ986782	DQ986876
<i>Aspicilia hispida</i>	Megasporaceae	DQ780305	DQ780273
<i>Baeomyces placophyllus</i>	-	AY300878	AF356658
<i>Baeomyces rufus</i>	-	DQ871008	DQ871016
<i>Belonia russula</i>	Gyalectaceae	FJ941887	AY648888
<i>Bryophagus gloeocapsa</i>	Gyalectaceae	AF465440	AY300880
<i>Cameronia pertusarioides</i> 6504	-	JX977114	JX977110
<i>Cameronia pertusarioides</i> 6505	-	JX977115	JX977111
<i>Cameronia pertusarioides</i> 6506	-	JX977116	JX977112
<i>Cameronia tecta</i>	-	JX977117	JX977113
<i>Chapsa phlyctidioides</i>	Graphidaceae	JX465300	EU675275
<i>Chapsa pulchra</i>	Graphidaceae	EU075619	EU075571
<i>Coccomycetella richardsonii</i>	Odontotremataceae	HM244761	HM244737
<i>Coccotrema cucurbitula</i>	Coccotremataceae	AF274092	AF329161
<i>Coccotrema pocillarium</i>	Coccotremataceae	AF274093	AF329166
<i>Coenogonium leprieurii</i>	Coenogoniaceae	AF465442	AY584698
<i>Coenogonium luteum</i>	Coenogoniaceae	AF279387	AY584699
<i>Coenogonium pineti</i>	Coenogoniaceae	AY300834	AY300884
<i>Cryptodiscus pallidus</i>	Stictiaceae	FJ904677	FJ904701
" <i>Cryptodiscus</i> " <i>rhopaloides</i>	-	FJ904685	FJ904707
<i>Dibaeis baeomyces</i>	Icmadophilaceae	AY789291	AY584704
<i>Diploschistes cinereocaesius</i>	Graphidaceae	AY300835	AY300885
<i>Diploschistes scruposus</i>	Graphidaceae	AF279389	AY584692
<i>Dyplolabia afzelii</i>	Graphidaceae	HQ639628	HQ639594
<i>Elixia flexella</i>	-	AY853368	AY853320

Species	Family/generic group as in Fig. 1	nuLSU	mtSSU
<i>Fissurina insidiosa</i>	Graphidaceae	DQ973045	DQ972995
<i>Glyphis cicatricosa</i>	Graphidaceae	HQ639630	HQ639610
<i>Graphis scripta</i>	Graphidaceae	AY853322	AY853370
<i>Gregorella humida</i>	Arctomiaceae	AY853329	AY853378
<i>Gyalecta flotowii</i>	Gyalectaceae	AY300838	AY300889
<i>Gyalecta hypoleuca</i>	Gyalectaceae	AF465453	HQ659180
<i>Gyalecta truncigena</i>	Gyalectaceae	HM244766	HM244743
<i>Gyalecta ulmi</i>	Gyalectaceae	AF465463	AY300888
<i>Gyalectaria gyalectoides</i>	Coccotremataceae	GU980983	GU980975
<i>Gyalectaria jamesii</i>	Coccotremataceae	GU980984	GU980976
<i>“Gyalidea” praetermissa</i>	-	HM244768	HM244745
<i>Hymenelia lacustris</i>	Hymeneliaceae	AY853371	AY853323
<i>Icmadophila ericetorum</i>	Icmadophilaceae	DQ883694	DQ986897
<i>Lobothallia radiosa</i>	Megasporaceae	DQ780306	DQ780274
<i>Myriotrema olivaceum</i>	Graphidaceae	EU075627	EU075579
<i>Nadvornikia hawaiiensis</i>	Graphidaceae	AY605080	EU075581
<i>Ocellularia chiriquiensis</i>	Graphidaceae	EU075629	EU075582
<i>Ocellularia endoxantha</i>	Graphidaceae	AY605082	EU075589
<i>Ochrolechia androgyna</i>	<i>Ochrolechia</i>	AY300846	AY300897
<i>Ochrolechia balcanica</i>	<i>Ochrolechia</i>	AF329171	AF329170
<i>Ochrolechia frigida</i>	<i>Ochrolechia</i>	AY300847	AY300898
<i>Ochrolechia oregonensis</i>	<i>Ochrolechia</i>	DQ780308	DQ780276
<i>Ochrolechia pallescens</i>	<i>Ochrolechia</i>	DQ780310	DQ780277
<i>Ochrolechia parvella</i>	<i>Ochrolechia</i>	AF274097	AF320173
<i>Ochrolechia peruensis</i>	<i>Ochrolechia</i>	DQ780311	DQ780279
<i>Ochrolechia turneri</i>	<i>Ochrolechia</i>	AY568002	AY567982
<i>Ochrolechia yasudae</i>	<i>Ochrolechia</i>	DQ986776	DQ986902
<i>Ochrolechia</i> sp.	<i>Ochrolechia</i>	DQ986777	DQ986886
<i>Odontotrema phacidiellum</i>	Odontotremataceae	HM244769	HM244748
<i>Odontotrema</i> sp.	Odontotremataceae	HM244772	HM244751
<i>Orceolina antarctica</i>	Trapeliaceae	AY212852	AF274115
<i>Orceolina kerguelensis</i>	Trapeliaceae	AY212830	AF381561
<i>Paschelkiella pini</i>	Stictidaceae	HM244762	HM244738
<i>“Pertusaria” albescens</i>	Variolaria-group	AF329176	AF329175
<i>“Pertusaria” amara</i>	Variolaria-group	AF274101	AY300900
<i>Pertusaria coccodes</i>	Pertusariaceae	AF2741095	AY567984
<i>“Pertusaria” corallina</i>	Variolaria-group	AY300850	AY300901
<i>“Pertusaria” corallophora</i>	Variolaria-group	DQ780316	DQ780285
<i>Pertusaria coronata</i>	Pertusariaceae	AY300851	AY300902
<i>Pertusaria gibberosa</i>	Pertusariaceae	DQ780322	DQ780289
<i>Pertusaria lecanina</i>	Pertusariaceae	AF274296	AY567991
<i>Pertusaria leioplaca</i>	Pertusariaceae	AY300852	AY300903
<i>“Pertusaria” mammosa</i>	Variolaria-group	AY212831	AY212854
<i>Pertusaria mesotropa</i>	Pertusariaceae	DQ780325	DQ780292
<i>“Pertusaria” ophthalmiza</i>	Variolaria-group	AY568006	AY567993
<i>Pertusaria paramerae</i>	Pertusariaceae	DQ780326	DQ780293
<i>Pertusaria pertusa</i>	Pertusariaceae	AF279300	AF381565
<i>Pertusaria plittiana</i>	Pertusariaceae	DQ780328	DQ780294

Species	Family/generic group as in Fig. 1	nuLSU	mtSSU
<i>Pertusaria pustulata</i>	Pertusariaceae	DQ780332	DQ780297
" <i>Pertusaria</i> " <i>scaberula</i>	<i>Variolaria</i> -group	AF274099	AF431959
" <i>Pertusaria</i> " <i>subventosa</i>	<i>Variolaria</i> -group	AY300854	AY300905
<i>Phlyctis agelaea</i>	Phlyctidaceae	AY853381	AY853332
<i>Phlyctis argena</i>	Phlyctidaceae	DQ986771	DQ986880
<i>Phyllobaeis erythrella</i>	-	DQ986780	DQ986888
<i>Placopsis cribellans</i>	Trapeliaceae	DQ871010	DQ871018
<i>Placopsis gelida</i>	Trapeliaceae	AY212836	AY212859
<i>Placopsis santessonii</i>	Trapeliaceae	AY212845	AY212867
<i>Placynthiella icmalea</i>	Trapeliaceae	AY212846	AY212870
<i>Placynthiella uliginosa</i>	Trapeliaceae	DQ986774	DQ986877
<i>Protothelenella corrosa</i>	Protothelenellaceae	AY607734	AY607746
<i>Protothelenella sphinctrinoidella</i>	Protothelenellaceae	AY607735	AY607747
<i>Pycnotrema pynoporellum</i>	Graphidaceae	JX421615	JX421295
<i>Rhexiophiale rhexoblephara</i>	-	AY853391	AY853341
<i>Schizoxylon albescens</i>	Stictidaceae	DQ401144	DQ401142
<i>Siphula ceratites</i>	Icmadophilaceae	AY853394	AY853344
<i>Schaereria corticola</i>	-	AY300909	AY300859
<i>Stegobolus subcavatus</i>	Graphidaceae	EU075641	EU075595
<i>Stictis populorum</i>	Stictidaceae	AY527327	AY300882
<i>Stictis radiata</i>	Stictidaceae	AY300864	AY584727
<i>Thamnotia vermicularis</i>	Icmadophilaceae	AY853345	AY853395
<i>Thecaria quassicolae</i>	Graphidaceae	HQ639667	JF828971
<i>Thelotrema lepadinum</i>	Graphidaceae	AY300866	AY300916
<i>Thelotrema subtile</i>	Graphidaceae	DQ871013	DQ871020
<i>Thelotrema suecicum</i>	Graphidaceae	AY300867	AY300917
<i>Topeliopsis decorticans</i>	Graphidaceae	EU075654	EU075609
<i>Trapelia chiodectonoides</i>	Trapeliaceae	AY212847	AY212873
<i>Trapelia placodioides</i>	Trapeliaceae	AF274103	AF431962
<i>Trapeliopsis flexuosa</i>	Trapeliaceae	AF274118	AY212875
<i>Trapeliopsis granulosa</i>	Trapeliaceae	AF274119	AF381561
<i>Trapeliopsis percrenata</i>	Trapeliaceae	AF279302	AY212876
<i>Umblicaria crustulosa</i>	Umblicariaceae	AY300869	AY300919
<i>Umblicaria decussata</i>	Umblicariaceae	HM161603	HM161628
<i>Umblicaria hyperborea</i>	Umblicariaceae	AY853399	AY853349
<i>Varicellaria hemisphaerica</i>	<i>Varicellaria</i>	AF381563	AF381556
<i>Varicellaria lactea</i>	<i>Varicellaria</i>	AF381557	AF381564
<i>Varicellaria velata</i>	<i>Varicellaria</i>	AY300855	AY300906
<i>Waweia fruticulosa</i>	Arctomiaceae	DQ007347	DQ871023

Sequence alignments and phylogenetic analysis

We assembled partial sequences using Geneious Pro 5.4.3 (Drummond et al. 2011) and edited conflicts manually. Alignments were done using Clustal W (Thompson et al. 1994). Ambiguously aligned regions were removed manually. The single locus and concatenated alignments were analyzed by maximum likelihood (ML) and a Bayesian approach (B/MCMC). To test for potential conflict, ML bootstrap analyses were per-

formed on the individual data sets, and 75% bootstrap consensus trees were examined for conflict (Lutzoni et al. 2004). Maximum likelihood analyses were performed using the program GARLI (Zwickl 2006), employing 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 as in Lumbsch et al. (2007b). Bootstrapping (Felsenstein 1985) was performed based on 2000 replicates. The B/MCMC analysis was conducted on the concatenated data set using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001), with the same substitution model as in the ML analysis. The dataset was partitioned into two (mtSSU, nuLSU) and each part was allowed to have its own parameters (Nylander et al. 2004). A run with 20,000,000 generations, starting with a random tree and employing 4 simultaneous chains, was executed. Every 100th tree was saved. The first 500,000 generations (i.e. the first 5000 trees) were deleted as the “burn in” of the chain. We used AWTY (Nylander et al. 2007) to compare split frequencies in the different runs and to plot cumulative split frequencies to ensure that equilibrium was reached. Of the remaining trees, a majority rule consensus tree with average branch lengths was calculated using the sumt option of MrBayes. Posterior probabilities were obtained for each clade. Only clades that received bootstrap support equal or above 70% under ML and posterior probabilities ≥ 0.95 were considered as strongly supported. Phylogenetic trees were depicted using the program FigTree 1.3.1 (Rambaut 2009).

Results and discussion

Eight new sequences were generated for this study and aligned with sequences downloaded from Genbank (Table 1). The single gene locus trees did not show any conflicts and hence the concatenated data set was analyzed. Our combined data set included 1313 unambiguously aligned positions, 370 of which were constant. The ML tree had a likelihood value of -26318.540 and in the B/MCMC analysis of the combined data set, the likelihood parameters in the sample had the following mean (Variance): LnL = -27045.138 (0.35). The ML tree and the tree from the B/MCMC tree sampling were almost identical, with no differences in well-supported clades. Furthermore, taxon sampling was very similar to that of previous studies focusing on the phylogeny of Ostropomycetidae (Baloch et al. 2010; Lumbsch et al. 2007a; Lumbsch et al. 2007b; Wedin et al. 2005). Thus, only a simplified ML tree, with samples of well-supported families, genera or generic groups collapsed, is shown here (Fig. 1). Individual OTUs are shown only for the species of *Cameronia* and its sister groups. In our analysis, the four samples of the two *Cameronia* species form a strongly supported, monophyletic group within the well-supported Ostropomycetidae, confirming the monophyly of the genus and its placement in Ostropomycetidae. The genus *Cameronia* is another example of a group of lichenized ascomycetes with perithecioid ascomata in this subclass, with others being Porinaceae (Baloch and Grube 2006; Grube et al. 2004), Protothelenellaceae and Thelenellaceae (Schmitt et al. 2005). There are additional families

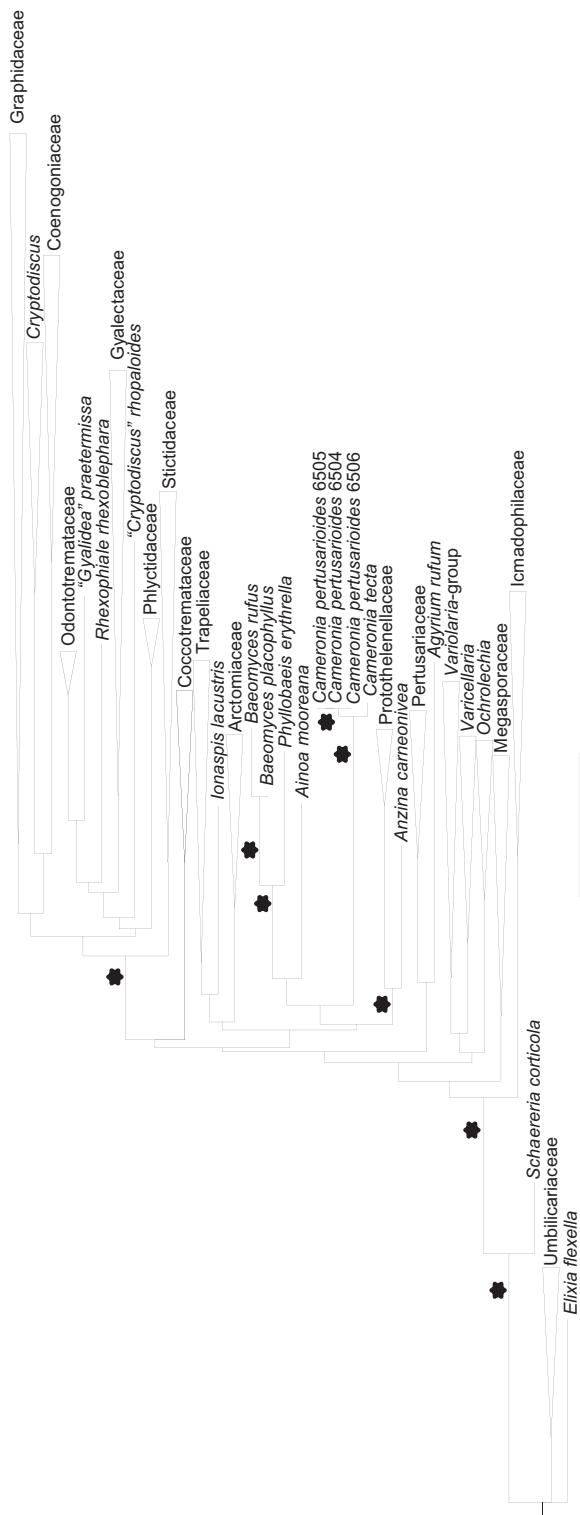


Figure 1. Phylogenetic placement of *Cameronia* as inferred from a concatenated alignment of mtSSU and nuLSU DNA sequences. This is a simplified cartoon of the optimal tree under maximum likelihood with well supported families and species groups collapsed that were shown in previous studies (Baloch et al. 2010; Lumbsch et al. 2007a; Lumbsch et al. 2007b; Wedin et al. 2005). Asterisks indicate branches with likelihood bootstrap support values above 70% and posterior probabilities equal or above 0.95.

in this subclass that also include taxa with more or less perithecioid ascomata, such as Coccotremataceae, Gyalectaceae, Pertusariaceae and Graphidaceae (Baloch et al. 2010; Lumbsch and Schmitt 2002; Lumbsch et al. 2001; Rivas-Plata et al. 2012; Rovas-Plata and Lumbsch 2011; Schmitt et al. 2010; Schmitt and Lumbsch 2004). The diversity of ascomatal morphologies in this subclass has been linked to the hemiangiocarpous type of ascoma development in the group as a whole (Schmitt et al. 2009).

The backbone of the Ostropomycetidae tree largely lacks support and the relationships of *Cameronia* within Ostropomycetidae remain unclear. *Cameronia* is the sister-group of Baeomycetaceae (*Ainoa*, *Baeomyces*, *Phyllobaeis*) but this relationship lacks support. This clade forms a sister-group to a well-supported clade that includes *Anzina* and Protothelenellaceae, but again, this relationship lacks support.

Although the molecular data support the placement of *Cameronia* in Ostropomycetidae, they fail to identify any close relatives of the genus, which is also reflected in the similarities of Blast searches of the newly generated sequences (maximal identity - nuLSU: 94%, mtSSU: 93%). *Cameronia* is distinguished by several characters that are generally used to characterize families, as shown in Table 2 where salient features of *Cameronia* and other families of Ostropomycetidae with perithecioid ascomata (Porinaceae, Protothelenellaceae, Thelenellaceae) are compared. The ascus type is very different from any of the other perithecioid Ostropomycetidae and also different from the apotheciate Baeomycetaceae, which have cylindrical asci (Gierl and Kalb 1993). Nor is the rudimentary exciple seen in *Cameronia* found in any of the other perithecioid families. Morphologically, the most similar family in Ostropomycetidae is Protothelenellaceae, with which *Cameronia* shares a hamathecium of richly branched paraphysoids and a lack of periphyses. However, Protothelenellaceae have a different exciple, different asci with an amyloid apical apparatus in the tholus and an ocular chamber, and halonate ascospores. Furthermore, Protothelenellaceae form a well-supported clade with *Anzina* (Fig. 1) and are only distantly related to *Cameronia*. The isolated position of *Cameronia* is consistent with the hypothesis that this genus is a case of paleoendemism. It will be an exciting project to test this hypothesis at a later stage when more sequence data from Ostropomycetidae become available.

Given the dissimilarity in morphological characters and the lack of close relatives in the phylogenetic tree, we propose a new family Cameroniaceae below to accommodate the genus *Cameronia*. The new family is placed in Ostropomycetidae with unclear ordinal position.

Cameroniaceae Kantvilas & Lumbsch, fam. nov.

Mycobank: MB 802404

Type: *Cameronia* Kantvilas, Lichenologist 44: 92. 2012.

Description. Thallus crustose, photobiont a coccoid green alga. Ascomata perithecioid, immersed in the thallus, proper exciple rudimentary, hamathecium consisting of richly branched, anastomosing paraphysoids, interspersed with oil droplets, containing

Table 2. Diagnostic features of families with perithecioid ascomata in Ostropomycetidae (Baloch and Grube 2006; Fryday and Coppins 2004; Grube et al. 2004; Kantvilas 2012; Mayrhofer 1987b,2002; Mayrhofer and Poelt 1985; McCarthy 1995; McCarthy 2000).

Characters	<i>Cameronia</i>	Porinaceae	Protothelenellaceae	Thelenellaceae
Proper exciple	rudimentary	Well developed, consisting of periplektenchymatous cells	Well developed, consisting of periplektenchymatous to isodiametric cells	Well developed, consisting of periplektenchymatous cells
Hamathecium	Richly branched, anastomosing paraphysoids, no periphyses	Simple to sparsely branched Paraphyses, no periphyses	Richly branched, anastomosing paraphysoids, no periphyses	Richly branched, anastomosing paraphysoids, periphyses present
Asci	Broadly obovate	cylindrical	cylindrical	cylindrical
Tholus	Well-developed	Poorly developed	Well-developed	Poorly developed
Ascus amyloidity	Outer wall hemiamyloid, tholus non-amyloid	Non-amyloid	Outer and wall and tholus amyloid	Non-amyloid
Ocular chamber	-	-	+	+/-
Ascospores	Hyaline, non-halonate, thick-walled, muriform	Hyaline, halonate, thin- to thick-walled, transversely septate to muriform	Hyaline, halonate, thick-walled muriform	Hyaline to brownish, halonate, thin-walled, muriform
Chemistry	Dibenzofuranes, triphenyl	Nil or pigments	nil	nil

hymenial algae, periphyses absent. Asci broadly obovate, with outer wall hemiamyloid and with a well-developed, non-amyloid tholus; ocular chamber lacking. Ascospores hyaline, non-halonate, eumuriform. Conidiomata immersed in the thallus, forming baciliform to bone-shaped conidia.

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