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Splitting or synonymizing – genus concept and taxonomy exemplified by the Parmeliaceae in the Nordic region

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The current use of a 30 million year dateline for accepting genera in the Parmeliaceae is evaluated. Its value is doubtful since evolution obviously went quicker in some lichen groups compared with others. Parallel evolution is also very common among lichens. Polyphyletic genera should always be split, while sister groups may remain split or be combined after considering non-molecular characters. Researchers dealing with the same groups should consult each other in an endeavour to achieve consensus. The most recent changes in taxonomy in the Nordic Parmeliaceae relate to the cetrarioid group, the last large clade to be revised. The division into two large genera, *Cetraria* and *Nephromopsis*, is supported, with a recommendation to retain *Masonhalea* due to its unique non-molecular characters. Three cases of parallel evolution in *Cetraria* and *Nephromopsis* are illustrated. Synonymization of *Gowardia* with *Alectoria* is supported, whereas synonymization of the parasitic genera *Raesaenenia* and *Nesolechia* with *Protousnea* and *Punctelia* respectively seems hardly necessary. Segregation of *Montanelia* from *Melanelia* is strongly supported, in contrast to the morphologically similar sister groups of *Usnea*, *Dolochousnea* and *Eumitria*, being recognised as separate genera.

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Introduction

The number of genera recognized and characters used for their recognition in the Parmeliaceae has varied considerably during the last few decades. In the well-known system for lichenized ascomycetes (Henssen & Jahns 1973), 18 genera were recognized for Parmeliaceae, all at that time distinguished by morphology. After numerous revisions by lichenologists, such as Mason Hale and Jack Elix during the 1970s to 1990s, the number of genera, based on supportive characters in cortex anatomy and secondary chemistry, was raised to c. 90 (Elix 1993, Thell et al 2012). In recent years a new taxonomy based entirely on phylogenetic analyses by means of DNA-characters has been established. The results from this analysis has reduced the number of genera to c. 70 and a large number of genera had to be synonymized; furthermore, several new genera were described based on DNA-phylogeny, only in some cases with correlating non-molecular characters. The number of genera in the Parmeliaceae in the Nordic countries consequently decreased from 44

to 37 between 2011 and 2017. Two genera, *Maronina* Hafellner & R.W.Rogers and *Protoparmelia* M.Choisy were transferred from Lecanoraceae to Parmeliaceae, thus, the number of genera in Parmeliaceae represented in the Nordic area is 37. Three parasitic genera with reduced morphology, *Nesolechia* A. Massal, *Phacopsis* Tul. and *Raesaenenia* D.Hawksw. et al., were not treated in the *Nordic Lichen Flora*, vol. 4, Parmeliaceae, released in 2011 and the review of Parmeliaceae the following year (Thell et al. 2012). Several changes have been proposed that concern the Nordic lichen flora recently; most of these relate to the cetrarioid group, since other main clades were revised earlier (Divakar et al. 2017). In this paper, we discuss and comment on taxonomic changes concerning the family within the *Nordic Lichen Flora* as proposed in 2011, and summarized in a classification of Parmeliaceae by Divakar et al. (2017), which accept that all branches diverged 30 million years ago as genera, an opinion which can hardly be left without problems or objections. To achieve a consensual conception in taxonomy, a discussion concerning the value of non-molecular characters in the genus concept is necessary.

This paper is dedicated to Tor Tønsberg, a good friend of all three of us for many years, on occasion of his 70th birthday.

Comments on the current taxonomy

Alectoria

The genus *Gowardia* Halonen et al. was segregated from *Alectoria* Ach. for morphological and chemical reasons by Halonen et al. (2009); except for the doubtful position of *Pseudevernia furfuracea* (L.) Zopf, the two genera were most closely related. *Gowardia* was accepted in the *Nordic Lichen Flora* (Velmala & Myllys 2011), but proposed as a synonym of *Alectoria* by Lumbsch & Huhndorf (2010: 19). We agree with the latter opinion since the two genera are sister clades, the split occurring in ‘recent’ times, i.e. less than 7 million years ago (Divakar et al. 2017). Furthermore, *Pseudevernia* Zopf is settled in the hypogymnioid clade and is treated by Divakar et al. (2017) as a separate genus although it actually originated 45 million years ago after the genus level threshold of 29. *Gowardia* enclosed two species, one of which, *Alectoria nigricans* (Ach.) Nyl. is present in the Nordic area. Considering all evidence, this synonymization seems reasonable (Table 1).

Cetraria and *Nephromopsis*

The cetrarioid group was the last large clade that needed a taxonomic revision. The phylogeny presented by Thell et al. (2009) undoubtedly showed that several genera had to be synonymized to avoid having to describe a large number of new genera in a group that already had a rather narrow genus concept. Two alternatives remained. One was to include all c. 80 species worldwide in one large genus, *Cetraria* Ach. The second possible alternative, according to cladistic rules, was to keep two genera, *Cetraria* and *Nephromopsis* Müll Arg., with a very large and similar morphological variation in both groups, but usually with different shaped conidia: the *Cetraria* clade has conidia with one swelling and the *Nephromopsis* clade has, almost entirely, conidia with two more-or-less apical swellings (Thell et al. 2005, 2009). In fact, a third genus of two species that we propose to save, *Masonhalea* Kärnefelt, has conidia without swellings, although it diverged only c. 25 million years ago according to Divakar et al. (2017). *Masonhalea* was synonymized with *Nephromopsis* along with the genera *Arctocetraria*, *Flavocetraria* and *Tuckermannopsis*. The division of the cetrarioid lichens in two genera resulted in several similar morphotypes being present in both genera since *Cetraria* now includes *Allocetraria*, *Cetrariella*,

Table 1. Parmeliaceae taxonomy used in the *Nordic Lichen Flora 4* (Thell & Moberg 2011) compared with current taxonomy (Divakar et al. 2017).

Taxonomy in <i>Nordic Lichen Flora 4</i> (Thell & Moberg 2011)	Current taxonomy (Divakar et al. 2017)	Comments and recommendations to the current taxonomy
<i>Alectoria</i> Ach.	<i>Alectoria</i> Ach., <i>Gowardia</i> Halonen et al.	<i>Alectoria</i> and <i>Gowardia</i> are sister groups with similar morphology.
<i>Allantoparmelia</i> (Vain.) Essl.	<i>Allantoparmelia</i> (Vain.) Essl.	
<i>Allocetraria</i> Kurok. Et M.J.Lai	<i>Cetraria madreporiformis</i> (With.) Müll.Arg.	Synonymization recommended.
<i>Arctocetraria</i> Kärnefelt & A.Thell	<i>Nephromopsis andrejevii</i> (Oxner) Divakar et al., <i>N. nigricascens</i> (Nyl.) Divakar et al.	Synonymization recommended.
<i>Arctoparmelia</i> Hale	<i>Arctoparmelia</i> Hale	
<i>Asahinea</i> W.L.Culb. & C.F.Culb.	<i>Asahinea</i> W.L.Culb. & C.F.Culb.	
<i>Brodoa</i> Goward	<i>Brodoa</i> Goward	
<i>Bryocaulon</i> Kärnefelt	<i>Bryocaulon</i> Kärnefelt	
<i>Bryoria</i> Brodo & D.Hawksw.	<i>Bryoria</i> Brodo & D.Hawksw.	
<i>Cetraria</i> Ach.	<i>Cetraria</i> Ach., <i>Allocetraria</i> Kurok. & M.J.Lai, <i>Cetrariella</i> Kärnefelt & A.Thell, <i>Vulpicida</i> J.-E.Mattsson & M.J.Lai	A monophyletic clade with <i>Allocetraria</i> , <i>Cetrariella</i> , <i>Usnocetraria</i> and <i>Vulpicida</i> nested within <i>Cetraria</i> .
<i>Cetrariella</i> Kärnefelt & A.Thell	<i>Cetraria commixta</i> (Nyl.) Th.Fr., <i>C. delisei</i> (Bory ex Schaer.) Nyl., <i>C. fastigiata</i> (Delise ex Nyl.) Kärnefelt	Synonymization recommended.
<i>Cetrelia</i> W.L.Culb. & C.F.Culb.	<i>Cetrelia</i> W.L.Culb. & C.F.Culb.	
<i>Cornicularia</i> (Schreb.) Hoffm.	<i>Cornicularia</i> (Schreb.) Hoffm.	
<i>Dactylina</i> Nyl.	<i>Dactylina</i> Nyl.	
<i>Usnea 132orediate132</i> Ach.	<i>Dolichousnea</i> (Y.Ohmura) Articus	Segregation from <i>Usnea</i> not recommended.
<i>Evernia</i> Ach.	<i>Evernia</i> Ach.	
<i>Flavocetraria</i> Kärnef. & A.Thell	<i>Nephromopsis cucullata</i> (Bellardi) Divakar et al., <i>N. nivalis</i> (L.) Divakar et al.	Synonymization recommended.
<i>Flavoparmelia</i> Hale	<i>Flavoparmelia</i> Hale	
<i>Gowardia</i> Halonen et al.	<i>Alectoria nigricans</i> (Ach.) Nyl.	Synonymization recommended.
<i>Hypogymnia</i> (Nyl.) Nyl.	<i>Hypogymnia</i> (Nyl.) Nyl.	
<i>Hypotrachyna</i> (Vain.) Hale	<i>Hypotrachyna</i> (Vain.) Hale	
<i>Imshaugia</i> S.L.F.Mey.	<i>Imshaugia</i> S.L.F.Mey.	
<i>Letharia</i> (Th.Fr.) Zahlbr.	<i>Letharia</i> (Th.Fr.) Zahlbr.	
–	<i>Maronina</i> Hafellner & R.W.Rogers**	Subfamily Protoparmelioidae, previously in the Lecanoraceae.
<i>Masonhalea</i> Kärnefelt	<i>Nephromopsis richardsonii</i> (Hook.) Divakar et al., <i>N. inermis</i> (Nyl.) Divakar et al.	Synonymization not recommended.
<i>Melanelia</i> Essl.	<i>Melanelia</i> Essl.	Including <i>Montanelia</i> Divakar et al. in NLF4.
<i>Melanelixia</i> O.Blanco et al.	<i>Melanelixia</i> O.Blanco et al.	
<i>Melanohalea</i> O.Blanco et al.	<i>Melanohalea</i> O.Blanco et al.	
<i>Menegazzia</i> A.Massal.	<i>Menegazzia</i> A.Massal.	

<i>Melanelia disjuncta</i> (Erichsen) Essl., <i>M. panniformis</i> (Nyl.) Essl., <i>M.</i> <i>133orediate</i> (Ach.) Goward & Ahti, <i>M. tominii</i> (Oxner) Essl.	Montanelia Divakar et al.	Segregation of <i>Montanelia</i> recommended.
<i>Arctocetraria</i> Kärnefelt & A. Thell, <i>Flavocetraria</i> Kärnefelt & A. Thell, <i>Tuckermannopsis</i> Gyelnik	Nephromopsis Müll.Arg.	A monophyletic clade with <i>Arctocetraria</i> , <i>Flavocetraria</i> and <i>Tuckermannopsis</i> nested within <i>Nephromopsis</i> . <i>Masonhalea</i> is a sister group and recommended as a separate genus.
<i>Nesolechia</i> A.Massal. / <i>Phacopsis</i> Tul.*	<i>Punctelia oxyspora</i> (Tul.) Divakar et al.	Synonymization not recommended. Separation between <i>Nesolechia</i> and <i>Phacopsis</i> poorly known (Divakar et al. 2017)
Parmelia Ach.	Parmelia Ach.	
Parmelina Hale	Parmelina Hale	
Parmeliopsis (Nyl.) Nyl.	Parmeliopsis (Nyl.) Nyl.	
Parmotrema A.Massal.	Parmotrema A.Massal.	
<i>Phacopsis</i> Tul.*	(<i>Phacopsis</i> Tul.)	See <i>Nesolechia</i> .
Platismatia W.L.Culb. & C.F.Culb.	Platismatia W.L.Culb. & C.F.Culb.	
Pleurosticta Petr.	Pleurosticta Petr.	
–	Protoparmelia M.Choisy**	Subfamily Protoparmelioidae, previously in the Lecanoraceae.
Protousnea huuskonenii (Räsänen) Divakar et al.	Protousnea Krog	See <i>Raesaenenia</i> .
Pseudephebe M.Choisy	Pseudephebe M.Choisy	
Pseudevernia Zopf	Pseudevernia Zopf	Should have been synonymized with <i>Hypogymnia</i> by Divakar et al. (2017), if following the 30 million dateline, however, the status as separate genus is recommended.
Punctelia Krog	Punctelia Krog	
Raesaenenia D.Hawksw. et al.*	<i>Protousnea</i> Krog; <i>P. huuskonenii</i> (Räsänen) Divakar et al.	<i>Protousnea</i> and <i>Raesaenenia</i> are sister groups. Synonymization not recommended.
<i>Tuckermannopsis</i> Gyeln.	<i>Nephromopsis chlorophylla</i> (Willd.) Divakar et al., <i>N. ciliaris</i> (Ach.) Hue	Synonymization recommended.
Usnea Adans.	Usnea Adans.	Including the sister group <i>Dolichousnea</i> .
Usnocetraria M.J.Lai & J.C.We	<i>Cetraria oakesiana</i> Tuck.	Synonymization recommended.
Vulpicida J.-E.Mattsson & M.J.Lai	<i>Cetraria juniperina</i> (L.) Ach., <i>C.</i> <i>pinastri</i> (Scop.) Gray, <i>C. tubulosa</i> (Schaer.) Zopf	Synonymization recommended.
Xanthoparmelia (Vain.) Hale	Xanthoparmelia (Vain.) Hale	

*The genera *Nesolechia*, *Phacopsis* and *Raesaenenia* were excluded from the *Nordic Lichen Flora 4* due to their special morphology. These particular species are planned for a separate volume of lichens with a parasitic and lichenicolous habit.

**The genera *Maronina* and *Protoparmelia* was excluded from *Nordic Lichen Flora 4* because they were then positioned in the Lecanoraceae, now constituting the subfamily Protoparmelioidae in the Parmeliaceae (Divakar et al. 2017).

Usnocetraria and *Vulpicida* (Divakar et al. 2017). Three cases of parallel evolution in *Cetraria* and *Nephromopsis* are illustrated, *Cetraria islandica* (L.) Ach. and *Nephromopsis andrejevii* (Oxner) Divakar et al., *Cetraria fastigiata* (Delise ex Nyl.) Kärnefelt and *Nephromopsis cucullata* (Bellardi) Divakar et al., and *Cetraria pinastri* (Scop.) Gray and *Nephromopsis chlorophylla* (Willd.) Divakar et al. (Figs 1–6). The solution with three genera proposed here would still include a problem since *C. sepincola* (Ehrh.) Ach., nested within *Cetraria*, has conidia with two swellings (Thell et al. 2002).

Melanelia* and *Montanelia

The segregation of the two large genera *Melanelixia* Blanco et al. and *Melanohalea* Blanco et al., from *Melanelia* Essl. (Blanco et al. 2004), later resulted in a third segregate with Nordic representatives, *Montanelia* Divakar et al.. It appeared as a sister group to *Melanelixia* and *Melanohalea* and the non-Nordic genera *Emodomelanelia* Divakar & A. Crespo and *Austromelanelixia* Divakar et al. This entire clade of five genera, is distantly related to *Melanelia*, a genus positioned close to the cetrarioid core (Thell et al. 2009, Divakar et al. 2017). The segregation of *Montanelia* with the Nordic species *M. disjuncta* (Erichsen) Divakar et al., *M. panniformis* (Nyl.) Divakar et al. and *M. soredata* (Ach.) Divakar et al., from *Melanelia* was necessary (Divakar et al. 2012).

Protousnea* and *Punctelia

Protousnea (Motyka) Krog is primarily a subtropical genus that only recently included a Nordic member when the parasite *Raesaenenia huuskonenii* (Räsänen) D.Hawksw. et al. was synonymized (Divakar et al. 2017). Most of the c. 30 species of *Punctelia* are distributed in temperate regions of Africa and South America. Three species occur in the Nordic area, *P. jeckeri* (Roum.) Kalb, *P. stictica* (Duby) Krog and *P. subrudecta* (Nyl.) Krog (Thell 2011). The genus was morphologically defined by its punctiform pseudocyphellae, but recent synonymization of the reduced parasitic and monotypic genus *Nesolechia* invalidates this. Parasitic and lichenicolous genera were not included in the Parmeliaceae volume of the *Nordic Lichen Flora*, although it was acknowledged at that time that *Nesolechia* A.Massal. and *Phacopsis* Tul. were members of this family. A third genus, *Raesaenenia* D.Hawksw. et al. was described later (Divakar et al. 2015). The borders between the three genera are not finally settled, but phylogenetic analyses of *Nesolechia* and *Raesaenenia* have shown that these genera are morphologically reduced members of the *Punctelia* Krog and *Protousnea* clades respectively, and they were subsequently synonymized with them (Divakar et al. 2017). The type species of the polyphyletic genus *Phacopsis* Tul., namely *P. oxyspora* (Tul.) Triebel & Rambold, was combined in *Punctelia* by Divakar et al. (2017), but currently combined in *Nesolechia*, as *N. oxyspora* (Tul.) A. Massal. *Raesaenenia* and *Protousnea* diverged c. 23 million years ago, whereas *Nesolechia/Phacopsis* and *Punctelia* diverged c. 25 million years ago according to calculations by Divakar et al. (2017), in both cases close to the decisive 30 million dateline. Furthermore, since the parasitic genera appear as sister groups to *Protousnea* and *Punctelia*, synonymization feels hardly necessary.

Usnea

Usnea Dill. ex Adans. is a huge genus comprising several 100 species worldwide, but mainly in tropical and subtropical regions. The former genus *Neuropogon* Nees & Flot. has now been included within *Usnea* by Divakar et al. (2017) – an inclusion proposed much earlier by Walker (1985) – while *Dolichousnea* (Y.Ohmura) Articus and the non-Nordic *Eumitria* Stirt. were



Figure 1



Figure 4

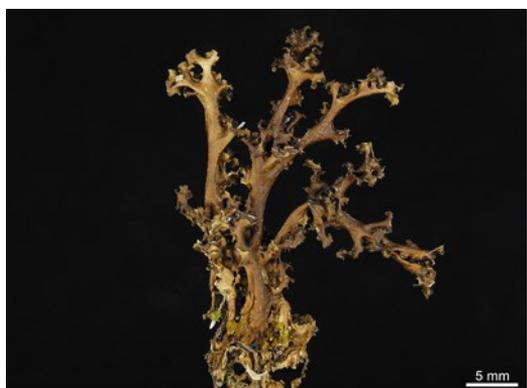


Figure 2



Figure 5



Figure 3



Figure 6

Figures 1–6. Morphological similarities between the genera *Cetraria* Ach. (Figs 1–3) and *Nephromopsis* Müll.Arg. (Figs 4–6) 1. *Cetraria islandica* (L.) Ach. ssp. *crispiformis* (Räsänen) Kärnefelt, Kärnefelt 580 (LD), 2. *C. fastigiata* (Delise ex Nyl.) Kärnefelt, Westberg 2695 (LD), 3. *C. pinastri* (Scop.) Gray, Mattsson 34 (LD), 4. *Nephromopsis andrejevii* (Oxner) Divakar, Crespo & Lumbsch, Kärnefelt 28c (LD), 5. *N. cucullata* (Bellardi) Divakar, Crespo & Lumbsch, Frödén 307 (LD), 6. *N. chlorophylla* (Willd.) Divakar, Crespo & Lumbsch, Thell SK9603 (LD). Photos: Patrik Frödén (LD).

resurrected as segregates since they diverged c. 40 million years ago, i.e. beyond the decisive 30 million year dateline (Divakar et al. 2017). All these taxa are characterized by an *Usnea*-morphology containing the typical cord within the medulla. The resurrection of the latter two genera therefore seems unnecessary and is not supported (Table 1).

Discussion

Parmeliaceae is a monophyletic family of more than 2700 species and thereby the largest of all lichen families, composed mainly of foliose and fruticose groups. It is, in addition, the most intensely studied of the large lichen families phylogenetically seen and its taxonomy has settled in most recent years (Divakar et al. 2017). The use of a fixed dateline for accepting genera is doubtful since evolution obviously went quicker in some lichen groups compared with others. The inclusion of additional genes in analyses may change the phylogenetic view that the strict 30 million dateline for accepting genera in the Parmeliaceae should be flexible: there is no reason to prevent morphology and other non-molecular characters to be considered, even after the paradigm shift, which implies that molecular characters determine the systematics, a topic discussed by Lumbsch and Leavitt (2011), which we generally agree with. Parallel evolution, e.g. when similar morphologies appear in non-related groups, is very common among lichens. Three examples within the cetrarioid core are illustrated (Figs. 1–6) but the list can be infinitely long in the Parmeliaceae; further examples among cetrarioid lichens are *Cetraria madreporiformis* (With.) Müll. Arg. and *Dactylina arctica* (Richardson) Nyl., *Cetraria commixta* (Nyl.) Th.Fr. and *Melanelia hepatizon* (Ach.) A.Thell, and *Cetraria aculeata* (Schreb.) Fr. and *Bryocaulon divergens* (Ach.) Kärnefelt. Well-known cases outside the cetrarioid group are *Imshaugia aleurites* (Ach.) S.L.F.Mey and *Parmeliopsis ambigua* (Wulfen) Nyl. and the genera *Alectoria* Ach. and *Bryoria* Brodo & D.Hawksw. Polyphyletic genera should always be split, while sister groups may remain split or be combined after considering non-molecular characters. Other researchers dealing with the same groups should be consulted in an endeavour to achieve consensus.

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