

The lichen genus *Kroswia* is a synonym of *Fuscopannaria* (*Pannariaceae*)

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Abstract: Molecular inferences of three loci within a phylogenetic framework of a subset of the *Pannariaceae* confirm that the genus *Kroswia* is nested within the genus *Fuscopannaria*. The formal combination of the type species of *Kroswia* into *Fuscopannaria* is therefore made here, and *Kroswia* is reduced into synonymy with the latter genus.

Key words: ascomycota, cyanolichens, morphology, *Nostoc*, *Peltigerales*, taxonomy

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Introduction

A persistent question in the *Pannariaceae*, a well-known and cosmopolitan lichen family, lies with the assignment of taxa with collematoid thalli, that swell considerably and form gelatinous masses when wet and quickly return to a crispy and fragile form when dry, unlike typical members of the family that develop a ‘pannarioid’ thallus that does not swell when wet (Wedin *et al.* 2009; Otálora *et al.* 2010). Species in the genus *Kroswia* P. M. Jørg. develop thalli of the former type, typically homoiomerous with an indistinct cortex, the photobiont forming chains of cells with much swelling sheaths and present throughout the thallus; species with a typical ‘pannarioid’ thallus such as in the genus *Fuscopannaria* P. M. Jørg. develop heteromerous thalli with a distinct upper cortex and a very distinct photobiont layer with photobiont cells compacted and assembled in clusters.

A further interesting matter within the same family is the occurrence of tripartite thalli, which are lichenized with green algae but produce well-differentiated structures, usually referred to as cephalodia, which are

lichenized with cyanobacteria usually belonging to the genus *Nostoc*. Such cephalodia may develop thalloid forms, sometimes produce fragments that act as vegetative diaspores (Jørgensen & Wedin 1999), or may resemble autonomous entities recognized as a different genus, namely *Santessoniella* Henssen.

A recent study conducted by the authors (Magain & Sérusiaux 2014) could provide strong support for two interesting evolutionary patterns within that family. Indeed, a photobiont switch between two different strains of *Nostoc* is suspected to be the driver for the change in thallus type (pannarioid thallus to collematoid type) within a strongly supported clade comprising the genera *Fuscopannaria*, *Kroswia*, *Leciophysma* Th. Fr. and *Protopannaria* (Gyeln.) P. M. Jørg. & S. Ekman. Photobiont switches have been shown or are suspected to play a crucial role in speciation processes of lichens (examples in Baloch & Grube 2006; Nelsen & Gargas 2008; Fernández-Mendoza *et al.* 2011; Printzen *et al.* 2013) and the molecular inferences in a phylogenetic context do support such a scenario for the genus *Fuscopannaria*.

Furthermore, cephalodia emancipation from ancestral tripartite thalli followed by divergence is supported by the data and may represent an evolutionary pattern present throughout the family; it may explain the

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morphological resemblance between the thalli of several genera with cephalodia of others, as well as the complex phylogenetic relationships between species with tripartite thalli and others with collematoid or pannarioid thalli. A convincing example of this evolution pattern is provided by the free-living *Santessoniella polychidioides* (Zahlbr.) Henssen, lichenized with *Nostoc*, which is nested with strong support within the tripartite genus *Psoroma* Ach. ex Michx. (Ekman *et al.* 2014) and can be interpreted as the emancipated cephalodia of its tripartite ancestor which eventually diverged.

This study aims to confirm the finding by Magain & Sérusiaux (2014) that the collematoid genus *Krosowia* is nested in *Fuscopannaria* and to resolve their relationships by producing a phylogenetic tree including all data available in *Fuscopannaria*. As three accessions of its type species (*K. crystallifera* P. M. Jørg.) are found nested within *Fuscopannaria* with strong support, the taxonomic and nomenclatural conclusions are drawn in this paper.

Material and Methods

All sequences used in the phylogenetic analyses were downloaded from GenBank (Table 1). Those produced by Ekman *et al.* (2014) in a revised classification of *Pannariaceae* and Magain & Sérusiaux (2014) for the taxa dealt with in this paper are thus included. We assembled a concatenated matrix of three loci: mtSSU, nuLSU and *RPB1* using MacClade v. 4.08 (Maddison & Maddison 2005). Ambiguously aligned positions were delimited by eye and excluded from the phylogenetic analyses. The alignment was divided into six subsets: mtSSU, nuLSU, *RPB1* 1st, 2nd and 3rd codon positions, and the intron in *RPB1*. The best partition for the dataset was estimated using PartitionFinder (Lanfear *et al.* 2012) using AICc as a criterion and testing all models available with the greedy algorithm. The partition selected consisted of 5 subsets: LSU and the 1st codon of *RPB1* together, and every other subset by itself.

We produced a best ML tree using RaxML-HPC2 v. 8.0.24 (Stamatakis 2006; Stamatakis *et al.* 2008) as implemented on the CIPRES portal (Miller *et al.* 2010), using the GTRGAMMA model and 1000 bootstrap iterations. A Bayesian analysis was performed using MrBayes v. 3.2.2 (Huelsenbeck & Ronquist 2001) as implemented on the CIPRES portal, running for 20 million generations with two runs of three cold chains and one heated chain each, and sampling every 1000th generation. The first

25% of the trees sampled were discarded as burn-in, and a 50% consensus tree was produced using the remaining trees. Convergence of the analyses was assessed using Tracer (Rambaut & Drummond 2007) and AWTY (Nylander *et al.* 2008) as implemented on the website <http://king2.scs.fsu.edu/CEBProjects/awty>.

Results

The phylogenetic tree (Fig. 1) presented here is the Bayesian 50% consensus tree with evaluation of branch support from the Maximum Likelihood results and the posterior probabilities of the Bayesian search; 2666 characters from four loci (5.8 S, mtSSU, nuLSU and *RPB1*) are included for 42 accessions representing 38 taxa.

As in earlier studies (Ekman *et al.* 2014; Magain & Sérusiaux 2014), the genus *Fuscopannaria* is retrieved as a monophyletic group, divided into two strongly supported clades, accepting that *F. sampaiana* (Tav.) P. M. Jørg. is assigned to a different genus (*Nevesia*: Ekman *et al.* 2014) and with the exception of *F. laceratula* (Hue) P. M. Jørg. which is resolved within a strongly supported and related lineage comprising *Protopannaria pezizoides* P. M. Jørg. & S. Ekman. The first clade within *Fuscopannaria* includes, among others, the type species [*F. leucosticta* (Tuck.) P. M. Jørg.] and the three accessions of *Krosowia crystallifera*, whilst the second one includes, among others, the monotypic genus *Moelleropsis nebulosa* (Hoffm.) Gyeln.

Synonymy of *Krosowia* and new combination in the genus *Fuscopannaria*

The phylogenetic relationship of *Krosowia crystallifera*, the type species of *Krosowia*, is similar to *Moelleropsis nebulosa*: although the overall morphology strongly deviates from the typical pannarioid thallus type of all species assigned to that genus, the molecular data leave no doubt that both species must be subsumed into *Fuscopannaria* (Ekman *et al.* 2014; Magain & Sérusiaux 2014). Data on apothecial characters provided by Jørgensen (2007a) on another species [*K.*

TABLE 1. Table of the voucher specimens used in this study, with the species names and references to original publications; GenBank accessions of the sequences.

Taxon	Country	Publication	GenBank mtSSU	Accession LSU	Number RPB1
<i>Fuscoderma applanatum</i>	New Zealand	Wedin <i>et al.</i> 2009	GQ259024	GQ258994	GQ259053
<i>Fuscopannaria ahlneri</i>	South Korea	Wedin <i>et al.</i> 2009	GQ259025	GQ258995	GQ259054
<i>F. cheiroloba</i>		Ekman <i>et al.</i> 2014	—	—	KC608113
<i>F. confusa</i>	Norway	Carlsen <i>et al.</i> 2012	GU570043	—	—
<i>F. ignobilis</i>		Miądlikowska <i>et al.</i> 2006	DQ917416	DQ917417	DQ986839
<i>F. lacerulata</i>		Ekman <i>et al.</i> 2014	KC608070	—	KC608115
<i>F. leucosticta</i> 1	Reunion Island	Magain & Sérusiaux 2014	JX494238	JX494264	JX494284
<i>F. leucosticta</i> 2	USA	Wedin <i>et al.</i> 2009	DQ900630	DQ900640	GQ259055
<i>F. leucostictoides</i>		Ekman <i>et al.</i> 2014	KC608071	—	KC608116
<i>F. maritima</i>		Ekman <i>et al.</i> 2014	KC608072	—	KC608117
<i>F. mediterranea</i>		Miądlikowska <i>et al.</i> 2006	DQ917418	DQ917419	—
<i>F. olivacea</i>		Ekman <i>et al.</i> 2014	KC608073	—	—
<i>F. pacifica</i>		Ekman <i>et al.</i> 2014	KC608074	—	KC608118
<i>F. praetermissa</i> 1	Reunion Island	Magain & Sérusiaux 2014	JX494239	—	JX494285
<i>F. praetermissa</i> 2	Sweden	Wedin <i>et al.</i> 2009	GQ259026	GQ258996	GQ259056
<i>F. protensa</i>		Ekman <i>et al.</i> 2014	—	—	KC608119
<i>F. soreidiata</i>		Ekman <i>et al.</i> 2014	KC608067	—	—
<i>Kroszwia crystallifera</i> 1	Madagascar	Magain & Sérusiaux 2014	JX494235	JX494261	JX494281
<i>K. crystallifera</i> 2	Reunion Island	Magain & Sérusiaux 2014	JX494236	JX494262	JX494282
<i>K. crystallifera</i> 3	Reunion Island	Magain & Sérusiaux 2014	JX494237	JX494263	JX494283
<i>Lecioophysma furfurascens</i>	Sweden	Wedin <i>et al.</i> 2009	GQ259028	GQ258998	GQ259058
<i>Moelleropsis nebulosa</i>		Ekman <i>et al.</i> 2014	KC608079	—	KC608122
<i>Nevestia sampaiana</i>	Norway	Carlsen <i>et al.</i> 2012 / Ekman <i>et al.</i> 2014	GU570030	—	KC608120
<i>Pannaria calophylla</i>	Argentina	Passo <i>et al.</i> 2008	EU885318	—	—
<i>P. implexa</i>	Argentina	Passo <i>et al.</i> 2008	EU885333	—	—
<i>P. lurida</i>	Reunion Island	Magain & Sérusiaux 2014	JX494248	JX494273	—
<i>P. microphyllizans</i>	Argentina	Passo <i>et al.</i> 2008	EU885322	—	—
<i>P. multifida</i>	Reunion Island	Magain & Sérusiaux 2014	JX494241	JX494266	KF704308
<i>P. pallida</i>	Argentina	Passo <i>et al.</i> 2008 / Elvebakk <i>et al.</i> 2010	EU885323	GQ927270	—
<i>P. rubiginella</i>		Wedin <i>et al.</i> 2009	GQ259037	GQ259007	GQ259074
<i>P. rubiginosa</i>	Portugal	Wedin <i>et al.</i> 2009	AY340513	AY340558	GQ259073
<i>P. sp.</i>	Thailand	Magain & Sérusiaux 2014	KF704289	KF704290	KF704306
<i>P. sphinctrina</i>	Argentina	Passo <i>et al.</i> 2008 / Elvebakk <i>et al.</i> 2010	EU885324	GQ927271	—
<i>P. tavaresii</i>	Argentina	Passo <i>et al.</i> 2008	EU885316	—	—
<i>Parmeliella parvula</i>	Norway	Carlsen <i>et al.</i> 2012	GU570031	—	—
<i>Protopannaria pezizoides</i>	Sweden	Wedin <i>et al.</i> 2009	AY340519	AY340561	GQ259081
<i>Psoroma hypnorum</i>	Sweden	Wedin <i>et al.</i> 2009	AY340523	AY340565	GQ259085
<i>P. palaceum</i>	Argentina	Passo <i>et al.</i> 2008	EU885327	GQ927305	—
<i>Ramalodium succulentum</i>	Australia	Wedin <i>et al.</i> 2009	GQ259043	GQ259013	GQ259086
<i>Santessoniella</i> sp.		Ekman <i>et al.</i> 2014	KC608105	—	KC608146
<i>Staurolemma omphalarioides</i>	Norway	Wedin <i>et al.</i> 2009	GQ259044	GQ259014	—
<i>S. sp.</i>	Reunion Island	Magain & Sérusiaux 2014	KF704288	KF704291	—

gemmascens (Nyl.) P. M. Jørg.] referred to that genus are congruent: hymenium I+ blue-green rapidly turning red-brown, asci with an amyloid ring structure. Two characters of the ascospores do deviate as they are globose and pale brown in *K. gemmascens*, while they are ellipsoid without any colour in *Fuscopannaria leucosticta*, *F. praetermissa*

(Nyl.) P. M. Jørg. and other related species (Jørgensen 2007b). Furthermore they lack a perispore, which makes a difference for many species of *Fuscopannaria*. The value of these characters have never been tested in a phylogenetic context, and they are thus difficult to interpret. They might be species-specific within the genus, or represent

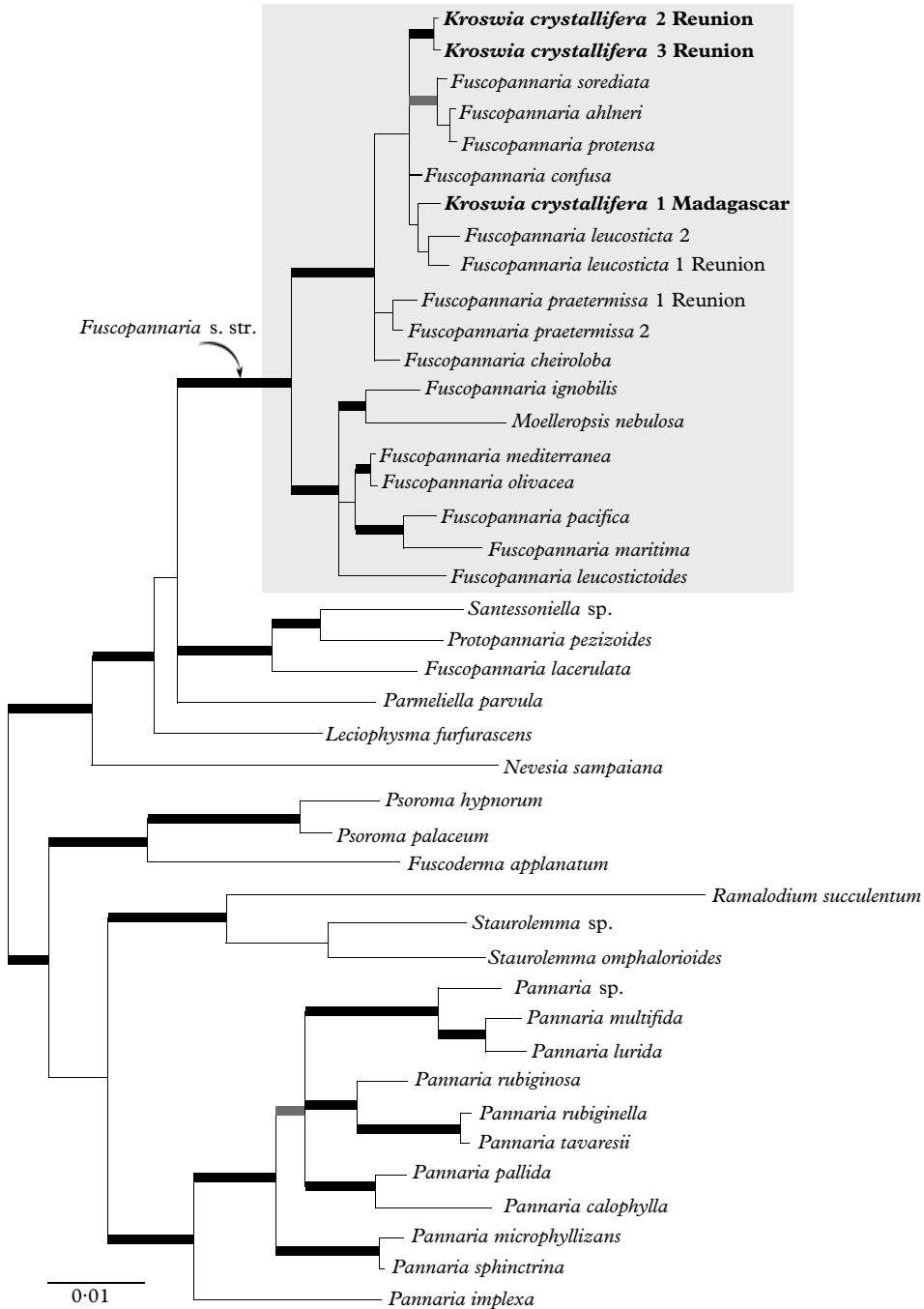


FIG. 1. 50% consensus tree resulting from the Bayesian analysis of mtSSU, LSU and *RPB1* on representatives of the family Pannariaceae. The genus *Fuscopannaria* is highlighted. Rooting follows Magain & Sérusiaux (2014). Thick black branches have a Posterior probability > 0.95 and a Maximum Likelihood bootstrap > 70. Thick grey branches have a PP > 0.95 but MLBS < 70.

autapomorphies for a further generic entity within the *Fuscopannaria* clade. Certainly, the genus has no close relationship with the *Pannaria lurida* (Mont.) Nyl. group as previously assumed (Jørgensen 2002), as this group is resolved with strong support within *Pannaria* Delise ex Bory s. str.

A detailed description of *Kroswia* is available in Jørgensen (2002). Three species are currently recognized in the genus: *K. crystallifera*, known from Kenya, South Africa, Reunion, India/Tamil Nadu, Sri Lanka, Taiwan, Papua New Guinea and Australia (Jørgensen & Sipman 2006) and also Madagascar (Magain & Sérusiaux 2014); *K. gemmascens*, reported from Japan and China/Sichuan and Xizang (Jørgensen 2007a); and *K. polydactyla* P. M. Jørg., described and known only from New Caledonia (Jørgensen & Gjerde 2012). The collematoid thallus of *K. crystallifera* (Fig. 2A) is homoiomerous, with a hardly distinct epicortex, or no cortex at all, with individual chains of *Nostoc* easily distinguished and spreading throughout the height of the thallus. Such a thallus is very different from the closely related species which have a distinct, multi-layered cortex and a well-delimited layer containing *Nostoc* cells, with hardly any chains distinguishable (Magain & Sérusiaux 2014).

Interestingly, *Kroswia crystallifera* is closely related to the type species of *Fuscopannaria* (*F. leucosticta*, Fig. 2A), and to other species grouped together as an unresolved polytomy [*F. ahlneri* (P. M. Jørg.) P. M. Jørg., *F. cheiroloba* (Müll. Arg.) P. M. Jørg., *F. confusa* (P. M. Jørg.) P. M. Jørg., *F. praetermissa*, *F. protensa* (Hue) P. M. Jørg., *F. sorediata* P. M. Jørg.]. The hypothesis that *F. crystallifera* evolved from a duo of photomorphs, formed by the very same fungus and lichenized with two different strains of *Nostoc* that eventually dissociated and diverged, cannot be ruled out. Both photomorphs may even have formed a single thallus, such as in the case of cyanochlorolichens (Henskens *et al.* 2012) or in cases of co-existence of two different photobionts within a single thallus [Casano *et al.* 2011; del Campo *et al.* 2013 for *Ramalina farinacea* (L.) Ach.]. Furthermore, another switch between different strains of *Nostoc*

within the clade of *Fuscopannaria* is likely to explain the very different thallus of *Moelleropsis nebulosa*, formed by coarse, usually dispersed granules, as this monotypic genus is nested within the second group recognized within *Fuscopannaria*.

As no molecular data are available for *Kroswia gemmascens* and *K. polydactyla*, we refrain from formally proposing the combination of both epithets to *Fuscopannaria*. Indeed, the *Pannariaceae* have reserved so many surprises regarding its evolutionary patterns that proposing hardly confirmed nomenclatural changes must be avoided.

Moelleropsis Gyeln. is a monotypic genus and is an older name than *Fuscopannaria*; a conservation proposal has been formally made (Jørgensen *et al.* 2013) and we therefore maintain the use of *Fuscopannaria* for this widespread and well-known species clade.

***Fuscopannaria* P. M. Jørg.**

J. Hattori Bot. Lab. 76: 198 (1994); type: *Fuscopannaria leucosticta* (Tuck.) P. M. Jørg.

Kroswia P. M. Jørg., *Lichenologist* 34: 297 (2002), **syn. nov.**; type: *Kroswia crystallifera* P. M. Jørg.

***Fuscopannaria crystallifera* (P. M. Jørg.) Magain & Sérus. comb. nov.**

MycoBank No.: 809865

Kroswia crystallifera P. M. Jørg., *Lichenologist* 34: 299 (2002); type: India, Tamil Nadu, Palmi Hills, 23 January 1975, *M. E. Hale* 43843 (US—holotype!)

(Fig. 2A)

Selected material examined of Fuscopannaria crystallifera:
Madagascar: Angavokely Forest Station, 18°55'37.9"S, 47°44'15.2"E, alt. 1770–1780 m, degraded ericaceous shrub near the summit, 2008, *E. Sérusiaux* s. n. with *E. Fischer*, *D. Ertz*, *D. Killmann* & *V. Razafindrahaja* (LG M788).—**Réunion:** Cirque de Cilaos, Forêt du Grand Matarum, 21°07.416'S, 55°28.983'E, alt. 1400–1450 m, disturbed montane forest, 2008, *E. Sérusiaux* with *M. Brand* & *P. van den Boom* (LG R1055); *ibid.*, Col de Taïbit, 21°06'42.5"S, 55°26'34.0"E, alt. 1800 m, disturbed montane forest, *N. Magain* & *E. Sérusiaux* (LG R1679).

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FIG. 2. *Fuscopannaria*, thalli of the species studied; A, *F. (Krosvia) crystallifera*; B, *F. leucosticta*. Scale = 1 cm. In colour online.

2008 was conducted with our colleagues and friends Maarten Brand and Pieter van den Boom. The field trip to Madagascar was organized with the logistical support of the “Parc Botanique et Zoologique de Tsimbazaza” in Antananarivo, and with collecting and export permits of scientific material issued by the “Ministère des Eaux &

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