

## The genus *Melanophloea*, an example of convergent evolution towards polyspory

André APTROOT and Felix SCHUMM

**Abstract:** The species described in or referred to the genus *Melanophloea*, traditionally referred to the *Thelocarpaceae*, are discussed. Detailed observations on two species, including the type species, show that they have not much more in common than their polysporous ascus. *Melanophloea* is reduced to the type species, *M. pacifica*. It shows a close resemblance to *Aptrootia* in the *Trypetheliaceae*, and it is therefore tentatively referred to this family. *Melanophloea americana* is shown to be close to *Thelenella* in the *Thelenellaceae*. The latter species and the related *M. montana* are newly combined into this genus as *Thelenella americana* and *T. montana*. *Thelocarpon nigrum*, which was recently compared to *Melanophloea*, is retained in *Thelocarpon* in the *Thelocarpaceae*.

Polyspory is suggested to facilitate dispersion, especially when compared to parent taxa that produce large muriform ascospores. Based on the current classification, polyspory originated at least 57 times within the lichenized ascomycetes, a clear example of convergent evolution.

**Key words:** *Aptrootia*, lichen, rainforest, taxonomy, *Thelenella*, *Thelenellaceae*, *Thelocarpaceae*, *Trypetheliaceae*

Accepted for publication 15 December 2011

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### Introduction

*Melanophloea* was described as a monotypic genus by James & Vězda (1971), based on two collections from the Solomon Islands. *Melanophloea pacifica* James & Vězda was the first, and for a long time the only, species to be described from among a sizeable collection of lichens from that region collected by D. J. Hill in 1965. It was clearly an unusual lichen, and the new genus was considered unique. It was attributed to the *Thelocarpaceae* because of the globose ascomata and the multispored asci. However, some quite fundamental differences with *Thelocarpon*, the type (and at that time only) genus of that family, were already pointed out in the original description. These include a fully carbonized (instead of hyaline to yellow) ascoma wall and anastomosing (as opposed to simple or branched) hamathecium filaments.

Here we will use the general descriptive terms ascoma and hamathecium rather than developmentally defined terms such as perithecia, apothecia, clypeus, pseudothecia, paraphyses, pseudoparaphyses or paraphysoids, as use of these terms would bias the setting of the research unnecessarily. In the results section we hope to be able to interpret the structures in special terms.

For several decades, no additional specimens were reported of the genus *Melanophloea*. It was, however, collected by B. J. Coppins in Sarawak (Malaysia) during the Mulu expedition in 1978 (cited in Aptroot *et al.* 1997), and subsequently in 1992 in Papua New Guinea (Aptroot *et al.* 1997). In Papua New Guinea, it is rather abundant in a lichenologically unique undisturbed rainforest that is still the only known locality of, for example, the genus *Wegea* (Aptroot & Tibell 1997) and of *Crustospathula cartilaginea* Aptroot (Aptroot 1998). More recently, *Melanophloea pacifica* has been reported from Cape Tribulation in Australia (McCarthy & Kantvilas 2009). A fleeting examination of

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A. Aptroot: ABL Herbarium, G.v.d.Veenstraat 107, NL-3762 XK Soest, The Netherlands.

Email: andreaptroot@gmail.com

F. Schumm: Mozartstr. 9, D-73117 Wangen, Germany.

the boxes with the still largely unidentified lichens from D. J. Hill's 1965 collection showed that the species is quite abundantly present in the Solomon Islands material, with at least a dozen specimens.

The specimens now known show some variation between them, chiefly in ascoma size and thallus colour, and in the degree of immersion of the ascomata in the thallus, but there is not enough differentiation to necessitate the distinction of different species. In fact, the type species is a well-characterized and, in the field, recognizable species which seems to indicate undisturbed lowland rainforests in the Malesian-Australasian region.

In 2008 the genus was expanded with a second species, *M. montana* P. M. McCarthy (McCarthy 2008; McCarthy & Kantvilas 2009), described from rainforest in Queensland, but from rock. It resembles the type of *Melanophloea* in several characters, chiefly the multispored ascus and the globose algae, but differs in so many characters that its inclusion made the genus quite heterogenous. The author was aware of the differences with the type species of the genus, but was unable to find a better disposition. Differences include the hyaline and less pigmented ascoma wall, the aligerous thallus covering most of the ascomata, the ellipsoid rather than globose ascospores, and the sparse, sparingly branched hamathecium filaments.

In 2011, Knudsen and Lendemer added a third species to the genus, viz. *M. americana* K. Knudsen & Lendemer (Knudsen *et al.* 2011). The type is a duplicate specimen of *Aptroot* 21389 which was left by the collector in NY. This species has virtually nothing in common with the type of *Melanophloea*, and it is unclear why it has been published in such a remote genus. This species has, for example, a dark brown outer ascoma wall that is curved inward below, apically (slightly) thickened asci, branched but not anastomosing hamathecium filaments and short-cylindrical ascospores.

As an afterthought, Knudsen and Lendemer suggest that *Thelocarpon nigrum* Aptroot & K. H. Moon from Korea (Moon & Aptroot 2009) might be a further species of *Melanophloea*, and mention that it differs from *M. americana* by the thicker hamathecium fila-

ments and larger ascospores. To this, one might add several other characters, notably the ascoma wall that is greenish outside and yellow to hyaline inside, the presence of paraphyses, as well as its occurrence on bark in East Asia.

So, what was for decades a very characteristic monotypic genus with a well-defined ecology and distribution, and one of the few easily recognizable lichens that are restricted to primary rainforest, has within a few years become a fairly heterogenous assemblage of species, each with a limited known ecology and distribution without any overlap, and occurring in discrete climatic zones.

As we have easy access to good material of most species, we endeavoured to make a detailed study of the morphology in order to present an alternative hypothesis for the classification of the various species now thrown together in *Melanophloea*.

## Material and Methods

Identification and descriptive work was carried out in Soest using an Olympus SZX7 stereomicroscope and an Olympus BX50 compound microscope with interference contrast, connected to a Nikon Coolpix digital camera, and in Wangen using a Wild M3 stereomicroscope, an Olympus BX51 compound microscope with interference contrast, a Canon EOS 40D camera with MP-E 65 mm and a Mic HM 560 cryotome. Specimens were measured and illustrated using material mounted in tap water, unless marked with IKI (mounted in iodine) or LCB (mounted in lactophenol Cotton Blue). The materials are preserved in ABL, B, BM, BR, E, F and hb. Diederich.

## Results

### *Melanophloea pacifica* P. James & Vězda

*Lichenologist* 5: 89 (1971); type: Solomon Islands, Kolombangara, on bark, 29 August 1965, D. J. Hill 10376 (BM—holotype).

(Fig. 1)

*Thallus* expanding, of smooth, whitish to green granules 0.05–0.1 mm diam. Algae chlorococcoid, globose, 4.8–6.5 µm diam.

*Ascomata* pyrenocarpous, wall carbonized throughout, closed below, mostly globose

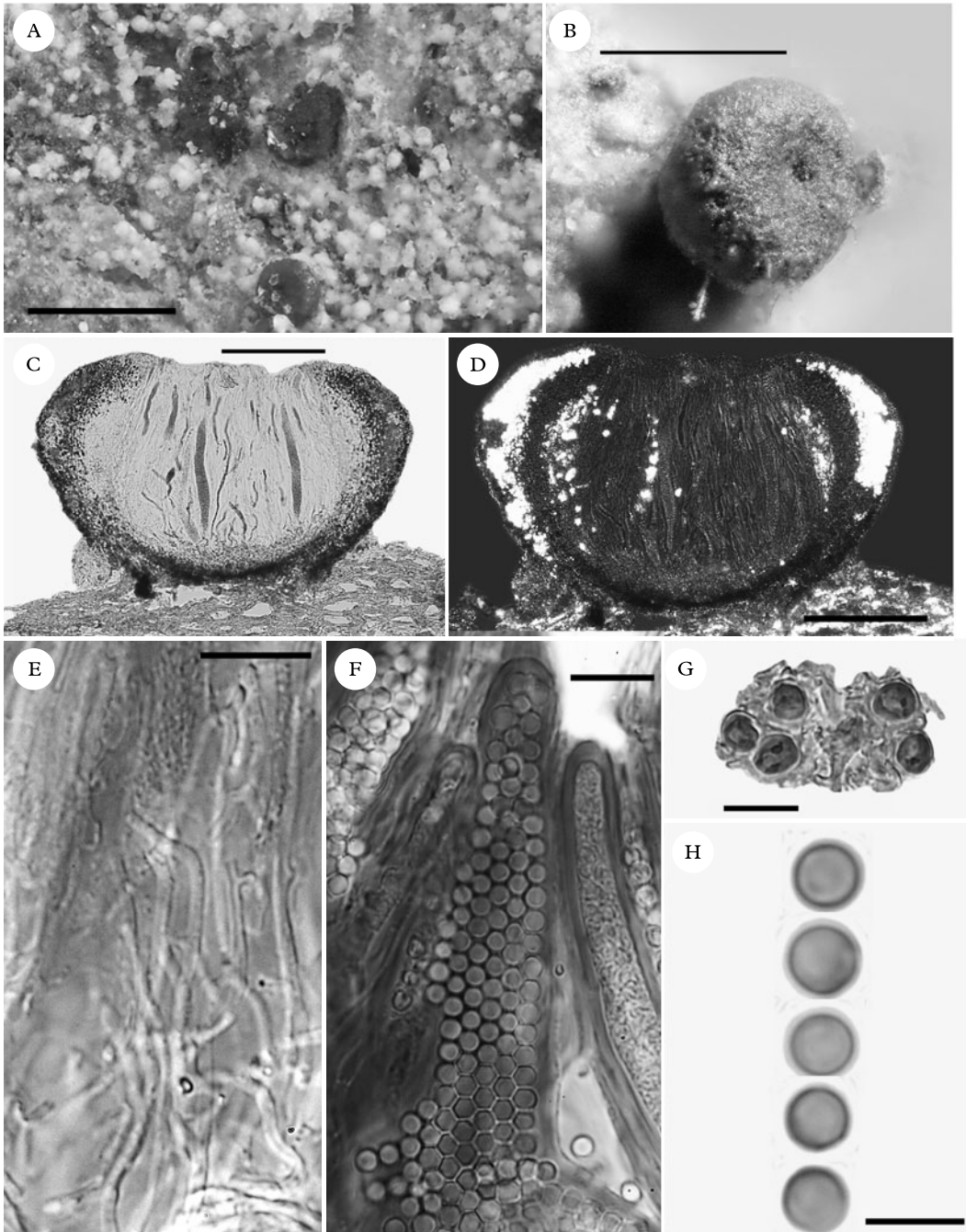


FIG. 1. *Melanophloea pacifica* (Aptroot 36520). A, habit; B, ascoma in surface view; C, ascoma in transverse section; D, ascoma in transverse section with polarized light; E, hamathecium filaments; F, ascus tips; G, photobiont cells; H, ascospores. C, G & H in LCB, E & F in IKI. Scales: A = 500  $\mu\text{m}$ ; B = 200  $\mu\text{m}$ ; C & D = 100  $\mu\text{m}$ ; E–G = 10  $\mu\text{m}$ ; H = 5  $\mu\text{m}$ .

but flattened at the top, 0.15–0.2 mm diam., with preformed ostiole, carbonized wall equally thick in most places, 33–44 µm wide, but thinned towards the ostiole and sometimes thickened in a ring-like zone around the depression towards the ostiole; inside the carbonized wall a thin layer of hyaline cells and, especially towards the top, many polarizing crystals.

*Hamathecium* K/I+ blue, copious, filaments paraphysoid, anastomosing, *c.* 1 µm wide, without discernable septa, tips unchanged, not forming an epithecium but ending in the ostiole; periphysis absent.

*Asci* uniformly thick-walled, up to 160 × 12 µm, with wall *c.* 2 µm wide, tip when young with flat and wide ocular chamber, bitunicate. *Ascospores* >500 per ascus, hyaline, globose, 2.7–3.0 µm diam.

*Notes.* A detailed investigation of the morphology shows that this is clearly a pyrenocarpous lichen with an ostiole (Fig. 1B) and thick-walled, bitunicate asci (Fig. 1E) that resemble those of members of the *Trypetheliaceae* when young. The hamathecium consists of strongly anastomosing paraphysoids without septa and is indistinguishable from the hamathecium in many *Trypetheliaceae*. This species may in fact be quite close to the genus *Aptrootia*, a genus of three known species (Aptroot 2009), all known from Australasia, with one extending to the neotropics. The main differences are the polyspory, the simple globose ascospores that remain hyaline, and the chlorococcoid (not trentepohlioid) algae. However, the thallus in the genus *Aptrootia* is quite variable, and associated algae are even nearly absent in *A. terricola* (Aptroot) Lücking *et al.* (Aptroot 1999; Lücking *et al.* 2007). *Aptrootia* is currently classified in the *Trypetheliaceae* (*Trypetheliales*, Dothideomycetes). The genus *Melanophloea* (of which *M. pacifica* is the type) is herewith suggested to belong to this family, but the genus *Aptrootia* is not synonymized with it, as the differences between them seem firm. Moreover, *Aptrootia* is, in its current circumscription, an ecologically informative taxon, restricted to tropical mountains or wet subtropical lowlands.

*Selected additional specimens examined.* **Papua New Guinea:** Madang: foothills of Finisterre Range along road Madang–Lae, 1997, *A. Aptroot* 36520 (ABL, BR); *ibid.*, 1992, *P. Diederich* 12149 (ABL, hb. Diederich).—**Borneo:** Sarawak: Gunong Mulu National Park, 1978, *B. J. Coppins* 5123 (ABL, E).—**Solomon Islands:** Kolombangara, 1965, *D. J. Hill* (BM).

### ***Thelenella americana* (K. Knudsen & Lendemer) Aptroot comb. nov.**

MycoBank No.: MB563999

*Melanophloea americana* K. Knudsen & Lendemer in Knudsen, Lendemer & Harris, *Opuscula Philolichenum* 9: 61 (2011); type: USA, Pennsylvania, Montgomery Co., Pennypack Watershed, on siliceous rock, November 1987, *A. Aptroot* 21376 (ABL, BR—*isotypes*) & *A. Aptroot* 21389 (ABL, BR—*isotypes*).

*Notes on typification.* The plate of the new species in the paper by Knudsen *et al.* depicts the collection *Aptroot* 21389, which is however not mentioned in the text at all. This collection is an *isotype*, but only the authors and the collector could know as it is not cited as such. It is illustrated in the original description and the illustration is part of the protologue. It would have been easier to just cite the specimen in the text, and it remains strange that only a duplicate in NY is mentioned as original material; more and larger material is present in ABL and BR. All type specimens examined are enumerated above.

(Fig. 2)

*Thallus* absent. Algae chlorococcoid, 12 µm diam., angular to ellipsoid, present chiefly inside the inner ascoma wall at the basis of the hymenium.

*Ascomata* consisting of a hyaline inner wall, surrounded by a black (in section dark brown) pseudostromatic clypeus wall, 15–20 µm wide, that curves inward below, enclosing the alga.

*Hamathecium* K/I–, copious, filaments paraphysoid, branched, up to 1.2 µm wide, with clearly discernable septa, tips unchanged, not forming an epithecium but ending as a wide ostiole; periphyses absent.

*Asci* with thickened IKI+ blue tip with round ocular chamber, bitunicate. *Ascospores* >500 per ascus, hyaline, short cylindrical, 3.3–4.4 × 1.3–1.5 µm.

*Notes.* A detailed morphological analysis shows that the overall ascoma shape, ascomal wall, ostiole, ascus, hamathecium and algae are all in perfect accordance with the genus

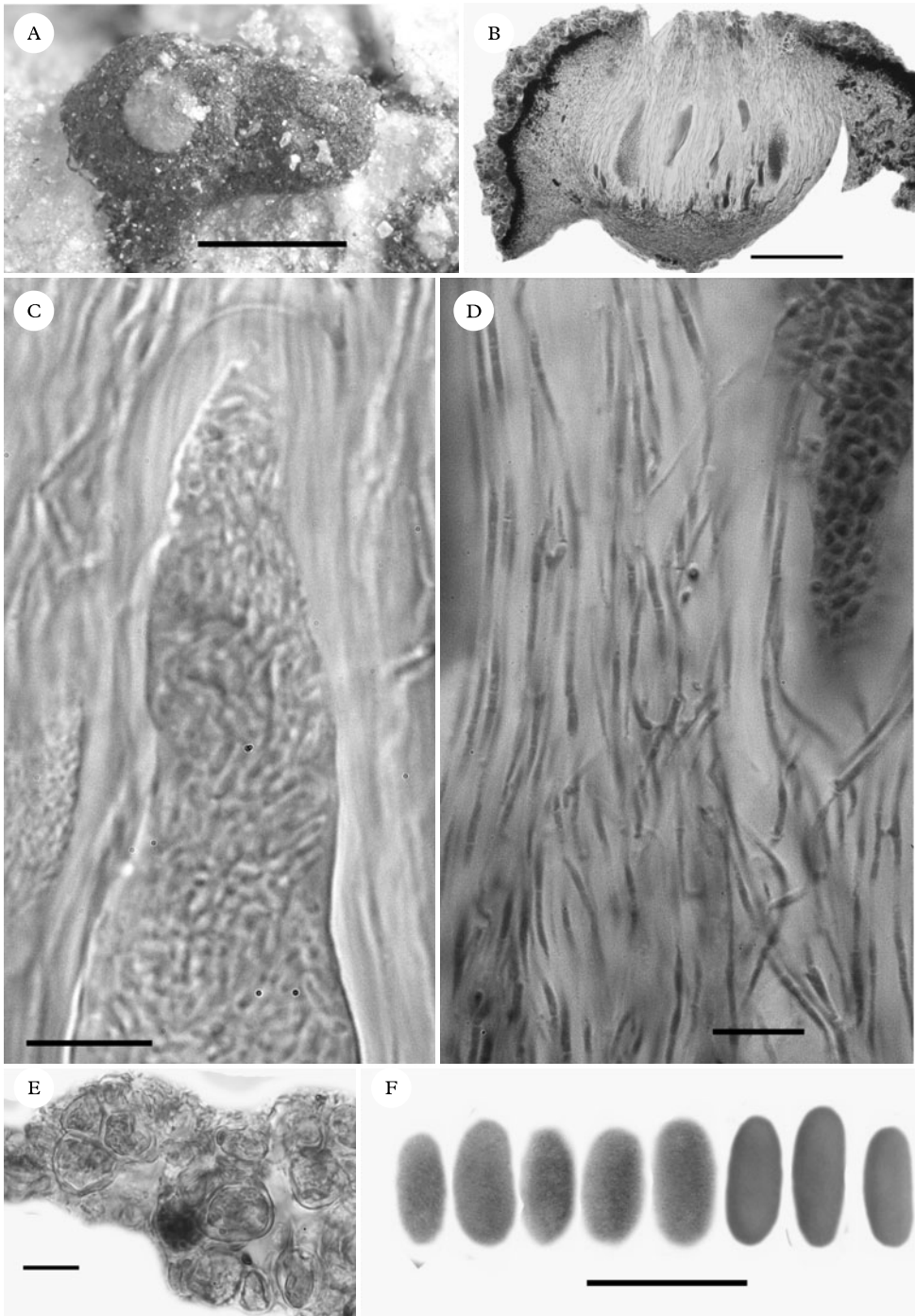


FIG. 2. *Thelenella americana* (Aptroot 21376). A, habit; B, ascoma in transverse section; C, ascus tip; D, hamathecium filaments; E, photobiont cells; F, ascospores. B & D in LCB, C & E in IKI. Scales: A = 500  $\mu\text{m}$ ; B = 100  $\mu\text{m}$ ; C–E = 10  $\mu\text{m}$ ; F = 5  $\mu\text{m}$ .

*Thelenella* (Mayrhofer 1987; Smith *et al.* 2009), which is currently classified in the *Thelenellaceae* and belongs to the Ostropomycetidae. It is the first polysporous species in this genus.

***Thelenella montana* (P. M. McCarthy)  
Aptroot comb. nov.**

MycoBank No.: MB564000

*Melanophloea montana* P. M. McCarthy, *Australasian Lichenology* **62**: 26 (2008); type: Australia, Queensland, Atherton Tableland, Tully Falls, on siliceous rock, 7 August 2006, P. M. McCarthy 2520 (CANB—holotype n.v.).

*Notes.* This species was not studied by us, but the beautiful illustrations and detailed descriptions and discussion of the type and only specimen (McCarthy 2008; McCarthy & Kantvilas 2009) leave little doubt that it is close to the previous species. The main difference seems to be that the ascospores are wider and oblong to ellipsoid, and that the algae are also present somewhat higher up in between the inner ascoma wall and the outer wall. It is the second species in the genus *Thelenella* with polysporous asci.

***Thelocarpon nigrum* Aptroot &  
K. H. Moon**

in Moon & Aptroot, *Bibliotheca Lichenologica* **99**: 309 (2009); type: Korea, Chungchongbuk-do, Danyang-gun, Youngchun-myun, Backja-ri, around entrance parking area of Guin-sa temple, on tree, 19 May 2007, A. Aptroot 67727 (B—isotype).

*Notes.* This is without doubt a species of *Thelocarpon*; it shows all key characters, although it should be noted that the genus *Thelocarpon* in its present sense is quite variable as to hamathecium characters. It is specifically characterized by the dark green ascoma pigment, which is formed by a mixture of the greenish yellow pigment present in many *Thelocarpon* species, together with some sparse carbonization. We have not re-examined this species, which is still known only from the type. Just like all other species of *Thelocarpon*, it has thin-walled, closed perithecia with paraphyses, which in *T. nigrum* are unbranched and rather wide. It has no close relationships with any of the

other species which have been placed in *Melanophloea*. *Thelocarpon* is currently classified in the *Thelocarpaceae*, the position of which within the Pezizomycotina is uncertain.

**Discussion**

The only characters the abovementioned species have in common are their polyspory, hyaline ascospores and chlorococcoid algae (though all of different sizes and shapes). They do not share, for example, ascoma type, wall colour and texture, branching type of hamathecium filaments or ascus tip morphology. In fact, they could serve as an introduction to the main characters which are useful for distinguishing fungal subclasses with lichenized members, with the four species serving as probable examples of three different groups.

Even so, the classification proposed here is just an alternative hypothesis, based only on morphological comparison. Although it is possible that future work will show that the affinities of the taxa lie elsewhere, it can be safely ruled out that the different species described in *Melanophloea* are related. There are too many fundamental characters differentiating them. The main taxa under discussion here are listed in Table 1. Listed are the differentiating key characters that are generally rather stable in larger groups. In pyrenocarpous lichens, as in non-lichenized pyrenocarpous ascomycetes, this includes the general ascoma structure (including the presence of ostiole and clypeus), the hamathecium structure (filaments with differentiated apices meaning that they grew only from below or not and their septation) and the ascus structure (uni- or bitunicate, apical structure). The table shows that the main character in which the *Melanophloea* species differ from the families to which they are suggested to belong in this paper is the polysporous ascus, with the tiny, simple and sometimes globose ascospores as a more or less logical consequence of that single trait. It is impossible to accommodate >500 ascospores in an ascus if they are not at the same time tiny and simple.

TABLE 1. *Diagnostic characters of Melanophloea species and other lichen taxa discussed in this paper*

	<i>Melanophloea pacifica</i>	<i>Aprootia</i> and other <i>Trypetheliaceae</i>	<i>Melanophloea americana</i> & <i>M. montana</i>	<i>Thelenella</i> ( <i>ceae</i> )	<i>Thelocarpon nigrum</i>	<i>Thelocarpaceae</i>
Alga (if present)	chlorococcoid	trentepohlioid	chlorococcoid	chlorococcoid	chlorococcoid	chlorococcoid
Ascoma wall	carbonized	carbonized	carbonized outside	carbonized outside	green but carbonized outside	hyaline to green
Clypeus	absent	absent	present	present	absent	absent
Ostiole	punctiform	punctiform	punctiform	punctiform	often wide open	often wide open
Hamathecium	non-septate paraphysoids with- out preformed tips	non-septate paraphysoids with- out preformed tips	septate pseudoparaphyses without preformed tips	septate pseudo- paraphyses without preformed tips	paraphyses with preformed tips	paraphyses with preformed tips or absent
K/I reaction	blue	blue or negative	negative	negative	negative	blue or negative
Ascus	thick-walled	thick-walled	thick-walled	thick-walled	thin-walled	thin-walled
Ascus tip	(young) with ocular chamber	with ocular chamber	(young) with ocular chamber	with ocular chamber	thin, without differentiation	thin, without differentiation
No. ascospores	>500	1–8	>500	2–8	>100	12–300
Ascospores	simple, globose	septate, ellipsoid	simple, ellipsoid	septate, ellipsoid	simple, ellipsoid	simple, globose to ellipsoid

Polyspory is also probably what has led the respective authors to suppose a taxonomic relatedness of the species described in or referred to *Melanophloea*. However, only rarely are all members of a higher lichen taxon (up to family level) polysporous. Groups of lichenized ascomycetes with usually polysporous asci are the three families *Acarosporaceae*, *Biatorrellaceae* and *Thelocarpaceae* and the genera *Arthrosporium*, *Biatoridium*, *Lithoglyphia*, *Maronea*, *Melanophloea* s. str., *Neoheppia*, *Piccolia*, *Placothelium* (whatever it may be), *Sarcosagium*, *Sporastatia*, *Steinia*, *Strangospora*, *Thelopsis*, *Timdalia*, *Tylophorella*, and *Wadeana* (Martens 1937; Aptroot & Tibell 1997; Hafellner & Türk 2001; Reeb *et al.* 2004; Ahti *et al.* 2007; Lücking 2008; Smith *et al.* 2009). Often only one or a few members of a certain genus are polysporous. Many accepted lichen genera that largely have 8 ascospores (which is the most common number throughout) in the ascus include one or a few species with more ascospores in the ascus. Such genera are the totally unrelated *Anema*, *Anzia*, *Buellia*, *Bulbothrix*, *Caloplaca*, *Candelaria*, *Candelariella*, *Catillaria*, *Catinaria*, *Cryptolechia*, *Cryptothele*, *Epigloea*, *Fellhanera* (*F. duplex* Coppins & Aptroot), *Fellhaneropsis*, *Gyalidea*, *Lecania*, *Lecanora*, *Lecidea* s. lat. (e.g. *Lecidea dodecama* Müll. Arg., of unknown affinity), *Lichinella*, *Pachyphiale*, *Peccania*, *Peltula*, *Phylliscum*, *Placidium*, *Protoparmelia* (the species formerly placed in *Maronina*), *Psorotichia*, *Pterygiopsis*, *Pyrenopsis*, *Ramonia*, *Rinodina*, *Scoliciosporum*, *Strigula*, *Synalissa* (genus probably monotypic, but the type species is variably polysporous), *Thallinocarpon*, *Thelenella* (with the inclusion of the two species excluded above from *Melanophloea*), *Thelignya*, *Verrucaria* (the species formerly placed in *Trimmatothele*) and *Zahlbrucknerella* (Martens 1937; Reeb *et al.* 2004; Ahti *et al.* 2007; Lücking 2008; Smith *et al.* 2009; Papong *et al.* 2011). Obviously, the occurrence of multispored asci is multi-polyphyletic (Reeb *et al.* 2004), having already originated within the lichenized fungi at least 57 times independently, as each of the above represents at least one separate evolutionary pathway towards multispory. In fact, there must

be more than 57 separate origins, as polyspory sometimes occurs in several different, unrelated species within a genus.

The tendency to polyspory can be regarded as convergent evolution. There is obviously an ecological advantage in producing many tiny ascospores, especially when compared to large, muriform ascospores that do not disperse well. Two of the three species of *Aptrootia* are among the lichens with the largest ascospores known, and are recorded 3rd and 15th on a list of species with the largest ascospores (Sweetwood *et al.* 2012). There is no doubt it would be a huge evolutionary advantage if these ascospores (which are nearly 0.5 mm long) dissolved into tiny spores, which seems to have happened and led to the origin of *Melanophloea pacifica*.

It should also be realized that there is a huge variation in the numbers of ascospores in polysporous asci, which reflects, at least in part, their different origins. Asci with 16, 32 or 64 ascospores are obviously the result of one extra mitotic division, or a premature cleavage of, for example, mature 1-septate ascospores within the ascus. Asci with > 1000 tiny ascospores may at least in part result from a totally different phenomenon, the formation of ascoconidia, which can occasionally be observed, especially in tropical taxa with large hyaline muriform ascospores, such as *Brigantiaea* and *Gyalidea* (Martens 1937; Hafellner & Bellemère 1981; Aptroot & Lücking 2003). At some stage, often while still in the ascus, these ascospores disintegrate into numerous conidia with shapes and sizes indistinguishable from the elements that are described as the ascospores in *Thelenella americana* and *T. montana*.

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