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Observations on two marine and maritime “borderline” lichens: *Mastodia tessellata* and *Collemopsidium pelvetiae*

Jan KOHLMEYER[1], David L. HAWKSWORTH[2] and Brigitte VOLKMANN-KOHLMEYER[1,*]

Among marine fungi, the submerged lichens are a small and rarely investigated group. The two species examined have been known for a long time; *Mastodia tessellata* (syn. *Turgidosculum complicatulum*) was first described in 1845, and *Collemopsidium pelvetiae* (syn. *Pyrenocollema pelvetiae*) in 1915. Here we clarified the formerly confused nomenclature and provided full descriptions and detailed illustrations, made with a camera lucida. The name *Ulva tessellata* is lectotypified, a neotype is selected for *Dothidella pelvetiae,* and the new combination *Collemopsidium pelvetiae* (basionym *D. pelvetiae*) is made.

Taxonomic novelty: *Collemopsidium pelvetiae* (G. K. Sutherl.) Kohlm., D. Hawksw. & Volkm.-Kohlm.

Rocky seashores harbor a large number of maritime lichens, often in typical band-like zones. Whereas almost 450 species of lichens have been reported from midlittoral to supralittoral rocks around the coasts of the British Isles (FLETCHER 1980), the number of permanently or periodically submerged marine lichens is small. KOHLMEYER & KOHLMEYER (1979) list five species of submarine lichenoid associations, and another has since been recognized: the permanently submerged *Halographis runica*, found on coral slabs and snail shells in Belize and Australia (KOHLMEYER & VOLKMANN-KOHLMEYER 1988, 1992). These have been referred to as “primitive lichens,” *viz*. loose symbioses in which the algal or cyanobacterial partners may occur also in a free-living state. In these cases, the fungal partner does not develop a well-differentiated cortical layer, i.e. is not clearly an exhabitant as expected in true lichen associations as now generally defined (HAWKSWORTH 1988, HAWKSWORTH & HONEGGER 1994), and neither is the fungal partner immersed in unmodified algae or cyanobacteria as in mycophycobioses (KOHLMEYER & KOHLMEYER 1979; HAWKSWORTH 1987). Yet, the morphology of the algal or cyanobacterial partner is modified, and the associations show a high degree of specialization involving fungi from relatively derived ascomycete orders, but without the formation of well-differentiated fungal tissues generally considered characteristic of lichens (except in the ascomata and conidiomata); we therefore prefer to refer to these associations as lichens, but “borderline” ones.

KOVAČIK & PEREIRA (2001) and LUD, HUISKES & OTT (2001) thoroughly examined the biology and developmental morphology of one of these “borderline” lichens, *Mastodia tessellata* (formerly listed as *Turgidosculum complicatulum*). Both these groups of workers independently concluded that the association could be interpreted as a lichen, albeit one “... with simple organizational level” (LUD, HUISKES & OTT 2001), but did not fully address the nomenclatural implications of their conclusions. A second “borderline” species, *Collemopsidium pelvetiae* (syn. *Leiophloea pelvetiae, Pyrenocollema pelvetiae*), treated as a “primitive lichen” by KOHLMEYER & KOHLMEYER (1979), has also received scant attention both morphologically and nomenclaturally. In this contribution, we investigate the nomenclature and present descriptions and detailed camera-lucida line drawings of both *C. pelvetiae* and *M. tessellata*.

Taxonomy

Mastodia tessellata (Hook. f. et Harv.) Hook. f. et Harv., in Hooker, Flora Antarctica, vol. 1, part II, Botany of Fuegia etc. [The Botany, The Antarctic Voyage of H. M. Discovery Ships Erebus and Terror in the Years 1839-1843, London], p. 499, 1847 **Figs. 1-3**
(*Mastodiaceae* – family of uncertain position)

≡ *Ulva tessellata* Hook. f. et Harv., J. Bot. (Lond.) 4: 297, 1845 (as *U. tesellata*).
≡ *Prasiola tessellata* (Hook. f. et Harv.) Kütz., Species Algarum, p. 473, Leipzig, 1849.
≡ *Laestadia tessellata* (Hook.f. et Harv.) Har., Algues, p. 29 *in* Mission Scientifique du Cap Horn, 1882-1883, Vol. 5, Botanique, 1889.
= *Leptogiopsis complicatula* Nyl., Flora (Jena) 67: 211, 1884.

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[1] Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, North Carolina 28557, USA
[2] The Yellow House, Calle Aguila 12, Colonia la Maliciosa, Mataelpino, Madrid 28492, Spain. Email: myconova@terra.es
[*] Corresponding author: Email: bjkohlm@email.unc.edu

Fig. 1: *Prasiola borealis* with black ascomata and conidiomata of *Mastodia tessellata*. Bar line = 1.5 mm. From syntype of *Guignardia alaskana*, Setchell No. 5138 (FH)

- ≡ *Turgidosculum complicatulum* (Nyl.) Kohlm. et E. Kohlm., Marine Mycology. The Higher Fungi, p. 361, Academic Press, New York 1979.
- ≡ KOHLMEYER*a complicatula* (Nyl.) S. Schatz, Mycologia 72:114, 1980.

= *Physalospora prasiolae* Har., Journal Botanique de Paris 1:233, 1887 (*nomen nudum).*

= *Laestadia prasiolae* G. Winter, Hedwigia 26:16, 1887.
- ≡ *Guignardia prasiolae* (G. Winter) Lemmermann, Abhandlungen des Naturwissenschaftlichen Vereins Bremen 17: 199, 1901 [Note: *Guignardia prasiolae* (G. Winter) M. Reed 1902, superfluous new combination].
- ≡ *Plagiostoma prasiolae* (G. Winter) Clauzade, Diederich et Cl. Roux, Bulletin de la Société Linnéenne de Provence, Numéro spécial 1:47, 1989 (*combinatio invalida*).

= ? *Dermatomeris georgica* Reinsch, p. 425, in Internationale Polarforschung, Die deutschen Expeditionen und ihre Ergebnisse, Vol. II, 1890.

= *Guignardia alaskana* M. Reed, University of California, Berkeley, Publications, Botany 1:161, 1902.
- ≡ *Laestadia alaskana* (M. Reed) Sacc. et D. Sacc., in Saccardo, Sylloge Fungorum17: 576, 1905.

= ? *Mastodia mawsonii* Dodge, British and New Zealand Antarctic Research Expedition Report, Botany, 7: 57 (1948).

Thallus irregularly lobed; ascomata and spermogonia distributed throughout (Fig. 1). *Mycelium* forming a dense network of textura intricata around algal cells. *Ascomata* 240–300 x 200–450 μm, subglobose, immersed, epapillate, ostiolate, coriaceous, dark brown above, sides and base with irregular dark areas, solitary or gregarious (Figs. 1 & 2). *Papillae* absent; ostiole schizogenous, circa 20 μm diam., periphysate, occluded by gelatinous, somewhat striate, turgescent material. *Paraphyses* absent in mature ascomata, but locule filled with gelatinous, faintly striate matrix; short periphysoids arise at the dome of the locule (Fig. 2). Asci (25) 30–46 (57) x (7) 9–15 μm, eight-spored, clavate to subcylindrical, short pedunculate, unitunicate, thick-walled in young asci, deliquescing at maturity, originating all along the inner wall of the ascoma, up to the ostiolar canal, enclosed by gelatinous matrix (Fig. 2). *Ascospores* (8.5) 11–17.5 (18.5) x 3–5 μm, elongate-ellipsoidal to cylindrical, rarely fusiform, ends rounded, one-celled, hyaline, at maturity accumulating in the centrum. *Conidiomata* (spermogonia) 160–240 x 170–280 μm, subglobose to lentiform, immersed, forming irregular chambers, epapillate, ostiolate, coriaceous, dark brown above and at the bottom, sides hyaline, solitary or gregarious (Fig. 3). *Peridium* 12–24 μm thick, cells forming a textura angularis. *Conidiogenous* cells circa 10 x 1.5 μm, cylindrical, lining the walls and lobes of the conidiomatal locule (Fig. 3). *Conidia* (spermatia) 2 x 1 μm, subglobose to ellipsoidal, one-celled, hyaline.

Algal Partners: *Prasiola borealis,* and *P. crispa* ssp. *antarctica*.

Distribution and Ecology: Pacific Ocean (Canada [British Columbia]), Chile [Tierra del Fuego], Falkland Islands, U.S.A. [Alaska], Russia [Siberia]); New Zealand (South Island); Antarctica and neighbouring islands. Although essentially maritime, occurring on rocks near the shore that may often be affected by sea spray, the species can occur several hundred metres from the coast, at least on Deception Island (APTROOT & VAN DER KNAAP 1993), and up to 500 m in altitude in northern Victoria Land (MURRAY 1963). Dependence on salt appears to be reduced in the lichenized state. It is ornithocoprophilous and often occurs in association with *Buellia* and *Caloplaca* species (ØVSTEDAL & SMITH 2001).

Material examined: *Ulva tessellata*: France, Kerguelen Islands, Christmas Harbour, June 1840, No. 657 (BM ex K – ***parte fungus, lectotypus hic designatus***), No. 655 (BM *ex* K). – *Leptogiopsis complicatula*: Fretum Behringii, Konyambay, leg. E. Almquist (Exped. Vega), Nos. 41010-41012. Syntypes (H-NYL). – *Guignardia alaskana*: U.S.A. (Alaska), 1899, leg. W. A. Setchell, Nos. 4021, 5138. Syntypes (BPI, FH, NY). – *Laestadia prasiolae*: Chile, Cape Horn, 1883-84, leg. Hariot, (Expéd. De la Comanche). Syntypes (FH, K). – *Mastodia mawsonii*: type not located (CASTELLO & NIMIS 1995).

Note: Until recently, the association between *Prasiola* and *Mastodia tessellata* was unclear. KOHLMEYER & KOHLMEYER (1979) classified it as a mycophycobiosis or possibly a case of parasitism. LUD, HUISKES & OTT (2001) studied the initial developmental stages and observed the accumulation of hyphae and algal cells, enclosed in a compact layer of mucilage. The final thallus has no differentiated cortex and consists of gelatinized hyphae, separating tetrads or pairs of algal cells, arranged in bands. The association does not form any secondary lichen substances. BRODO (1976) considered that the massive changes in morphology and the ecological success of the association pointed to it being best regarded as a lichen, as have most later authors (e.g. KOVAČIK & PEREIRA 2001); LUD,

Fig. 2: *Mastodia tessellata*. Longitudinal section through ascoma, large algal cells dispersed singly or in small groups throughout the fungal network; asci along the entire wall of the locule, enclosed in a gelatinous matrix; short periphyses in the ostiole, periphysoids at the dome of the locule. Bar line = 25 µm. From syntype of *Laestadia prasiolae* (K)

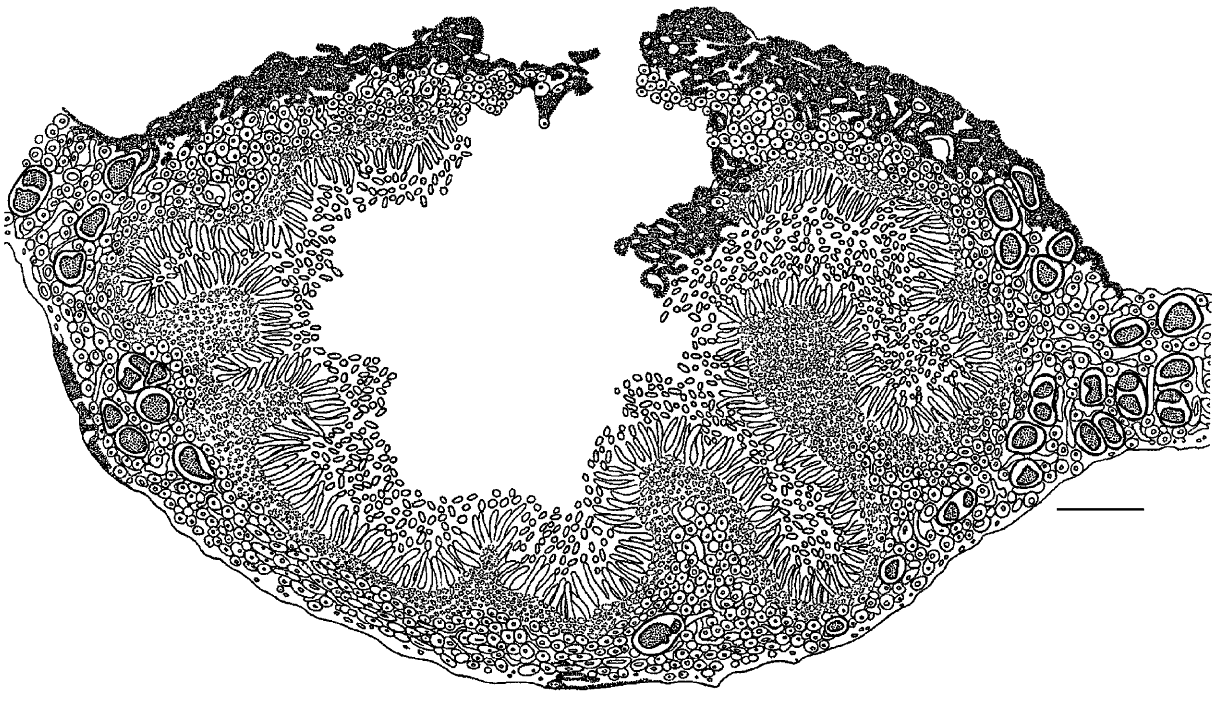

Fig. 3: *Mastodia tessellata*. Longitudinal section through conidioma, large algal cells dispersed singly or in small groups throughout the fungal tissue, conidiogenous cells lining the wall and lobes of the locule. Bar line = 20µm. From syntype of *Laestadia prasiolae* (FH)

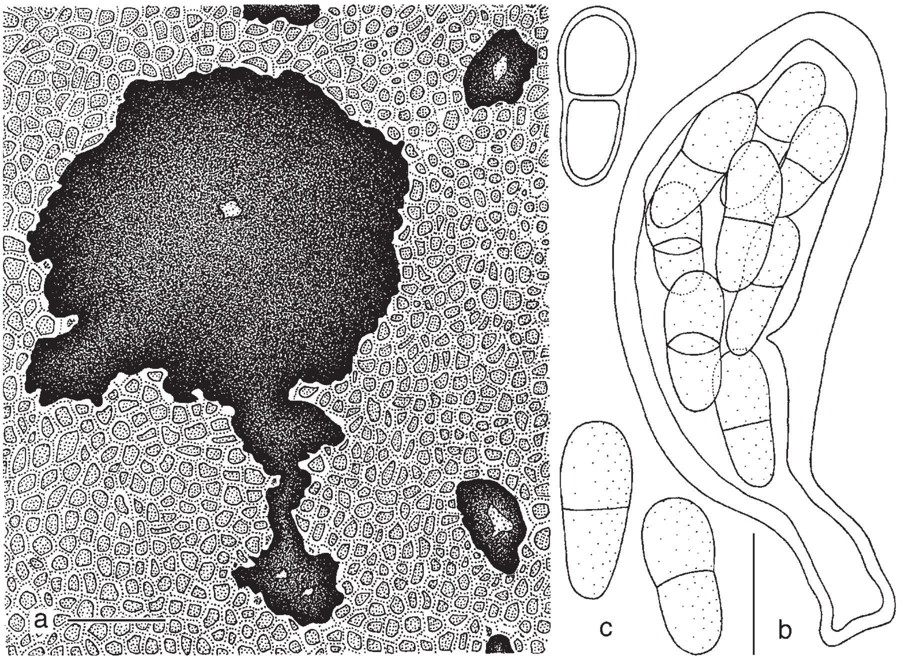

Fig. 4: *Collemopsidium pelvetiae.* **a**. Surface of *Pelvetia canaliculata* with large ascoma and several smaller conidiomata. Bar line = 75 µm. **b**. Ascus. **c**. Ascospores in surface view and optical section (top). Bar line = 10 µm. From holotype of *Plowrightia pelvetiae* (MA)

Huiskes & Ott (2001) classified it as a lichen with a very low level of differentiation.

The nomenclature of the fungus was quite confused, as demonstrated by the long list of synonyms. Johnson & Sparrow (1961) regarded the name *Ulva tessellata* as referring to the alga alone, and so employed the name *Guignardia prasiolae* for the fungal component. However, Eriksson (1981) argued that the name *Mastodia tessellata* “may be” correct but that it should be attributed to ‘Hook.f. *et* Harv.’ , i.e. treated as a new species described in 1847, and not regarded as a combination based on the earlier name *Ulva tessellata* Hook. f. *et* Harv., a name describing an alga only (Hooker & Harvey 1845). Sadly, this view cannot be sustained as Hooker and Harvey (in Hooker 1847) did not exclude the original syntype material and clearly intended to make a new combination based on the name in *Ulva.* Further, in stressing what were actually perithecioid ascomata as the diagnostic characters for *Mastodia,* we consider that already in 1847 the name *Ulva tessellata* was lectotypified by the fungal element. Two syntypes are preserved in BM, having been transferred from the Royal Botanic Gardens Kew (which held J. D. Hooker’s collections) to The Natural History Museum in London when the lichens were moved there in 1968. We select the fungal element in one of these as lectotype to end the long controversy over this name. Of course, if the composite is regarded as a lichen, the current consensus, the scientific name automatically refers to the fungal partner (Art. 13.1(d)) and so it could be argued that there is no choice to be made over the element to which the name applies (see also Hawksworth 2000). Prior to1975, names that were based on discordant elements could be rejected automatically where one element could not be selected as a satisfactory lectotype. However, this rule no longer applies and in the case of mixtures one portion has to be selected as lectotype (Art. 9.12), ideally in a way to preserve current usage (Rec. 9A.5). As both *Mastodia tessellata* and *Turgidosculum complicatum* are in current use, the Recommendation is of little help in this case.

The species epithet is commonly spelled as “tesselata”, but the name is derived from the Latin “*tessellatus*” = tiled, and the spelling has to be corrected in accordance with Art. 60.1. Hooker & Harvey (1845) wrote *Ulva tesellata,* but later corrected the epithet to *tessellata* (Hooker 1847).

Prasiola crispa ssp. *antarctica* can occur also in the nonlichenized form, mostly in or near meltwater streams, whereas the lichenized stage is mainly found on coastal rocks (Kováčik & Pereira 2001, Lud, Huiskes & Ott 2001). The material examined by us had consistently one-celled ascospores. Øvstedal & Smith (2001) reported three-septate ascospores; this observation needs confirmation, but if consistent suggests that a different species could be involved.

Collemopsidium pelvetiae (G. K. Sutherl.) Kohlm., D. Hawksw. & Volkm.-Kohlm., **comb. nov.** **Figs 4-6**

(*Xanthopyreniaceae* – family of uncertain position)

≡ *Dothidella pelvetiae* G. K. Sutherl., Transactions of the British Mycological Society 5: 154, 1915.
≡ *Placostroma pelvetiae* (G. K. Sutherl.) Meyers, Mycologia 49: 480, 1957.
≡ *Leiophloea pelvetiae* (G. K. Sutherl.) Kohlm. *et* E. Kohlm., Marine Mycology: The Higher Fungi, p. 376, Academic Press, New York, 1979.
≡ *Pyrenocollema pelvetiae* (G. K. Sutherl.) D. Hawksw., Botanical Journal of the Linnean Society 96: 10, 1988.
= *Plowrightia pelvetiae* Gonz. Frag., Memorias de la Real Sociedad Española de Historia Natural 11: 110, 1919.

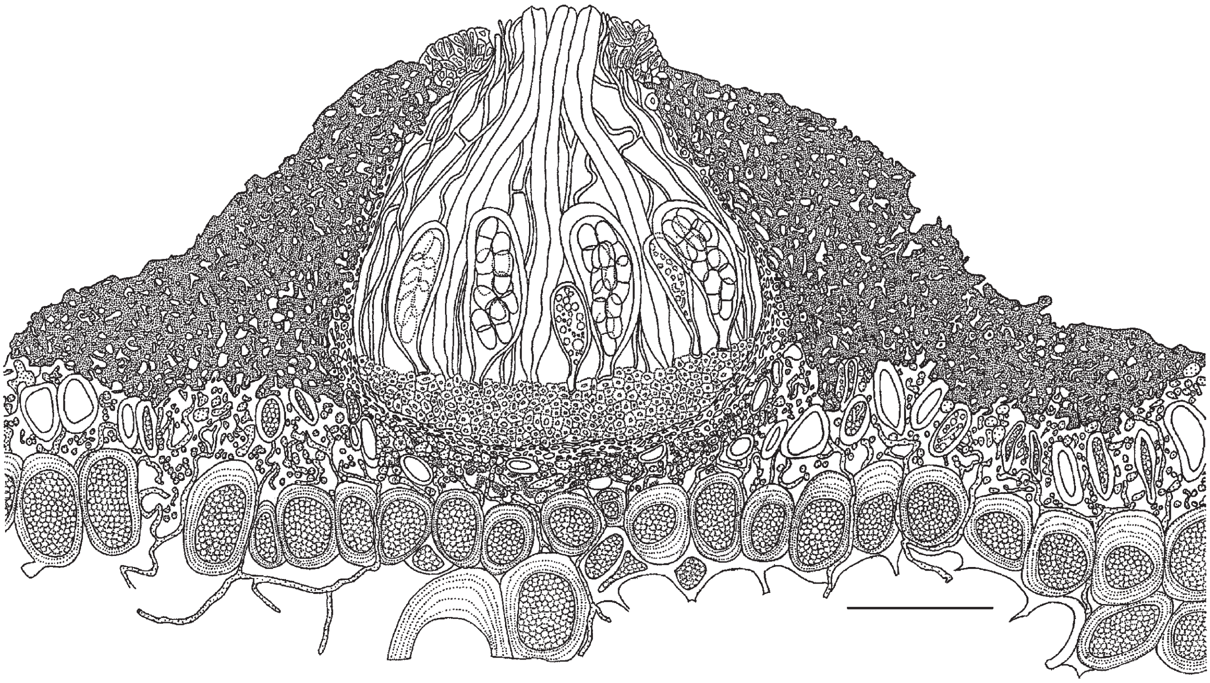

Fig. 5: *Collemopsidium pelvetiae.* Longitudinal section through dark stroma enclosing ascoma on *Pelvetia canaliculata*; between the large cells of *Pelvetia* and stroma is a hyphal network surrounding some cells of the cyanobacterial photobiont; endoasci of discharged asci protrude into the ostiole. Bar line = 40 µm. From the holotype of *Plowrightia pelvetiae* (MA)

Ascomata 60–140 x 120–340 µm, in bi- or trilocular stromata 310–590 µm long, depressed conoidal, superficial, epapillate, ostiolate, carbonaceous, black, gregarious (Figs 4a, 5). *Locules* 45–120 x 65–140 µm, subglobose to pyriform, truncate at maturity. *Ostioles* 15–60 µm diam., without periphyses, developing schizogenously. *Peridium* above and on sides 20–40 µm thick, with irregular thick walled, small luminate cells, black, enclosing some epiphytic cyanobacteria; base 8–12 µm thick, light brown, forming a textura angularis in longitudinal section (Fig. 5). *Pseudoparaphyses* 1–2 µm thick, anastomosing, rarely branching, gelatinizing immature ascomata and surrounding the asci as a tight ball. *Asci* 40–60 x 13–18 µm, eight-spored, clavate, short pedunculate, thick-walled, bitunicate, physoclastic; protruding endoasci fill ostiolar canal after ascospore discharge, developing at the base of the venter (Figs 4b, 5). *Ascospores* 11.5–16 x 5–6.5 µm, biseriate, elongate ovoidal, one-septate, upper cell wider than lower one, hyaline (Fig. 4). *Conidiomata* (spermogonia) 40–110 x 44–68 µm, subglobose, superficial, epapillate, ostiolate, subcarbonaceous, black, gregarious, sometimes connected with ascomata (Figs 4a, 6). *Ostioles* 4–50 µm diam. *Peridium* at top 10–26 µm thick, clypeoid, brown; sides and base 2.5–3.5 µm thick, two or three layers of cells with large lumina, hyaline, forming a textura angularis in longitudinal section (Fig. 6). *Conidiogenous cells* (spermatiophores) 7–9 x 1–1.5 µm, cylindrical to elongate-conical, tapering at apex, forming conidia singly at the tip, lining the walls of the locule up to the ostiole (Fig. 6). *Conidia* (spermatia) 2–2.5 x 1–1.5 µm, bacilliform, hyaline, holoblastic.

Host: *Pelvetia canaliculata.*

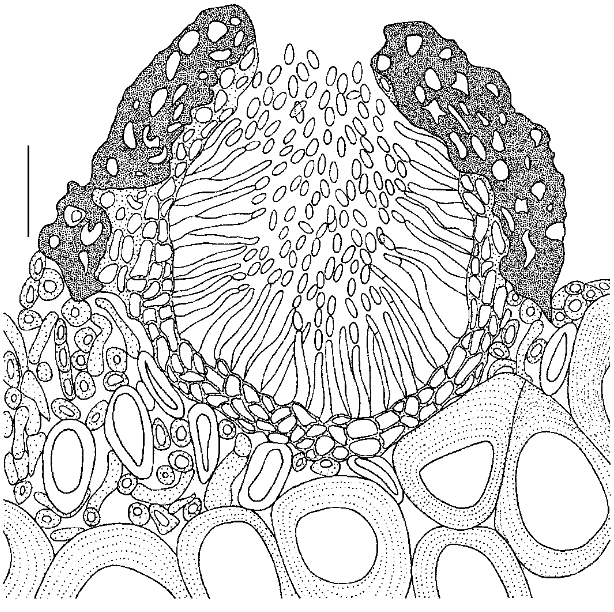

Fig. 6: *Collemopsidium pelvetiae.* Longitudinal section through conidioma on *Pelvetia canaliculata*. Bar line = 10 µm. From holotype of *Plowrightia pelvetiae* (MA)

Distribution: Atlantic Ocean (France, Great Britain [England, Scotland], Spain). The species is known from many sites in sheltered estuaries and sheltered coastal inlets in Devon, south-west England (BENFIELD 2001).

Material examined: *Dothidella pelvetiae*: England, Salcombe, North Sands, South Devon, 19 Sept. 1971, leg. J. & E. KOHLMEYER,

J. K. 2951 (NY – ***neotypus hic designatus***, IMS – isoneotypus); France, Concarneau, Bretagne, 1 and 2 Oct. 1971, leg. J. KOHLMEYER, J. K. 2962-2965 (IMS). – *Plowrightia pelvetiae*: Spain, Ramallosa Lourido, Pontevedra, Aug. 1915, leg. Bescansa, No. 3198. Holotype (MA).

Note: HAWKSWORTH (1988) referred to this association with various species of epiphytic cyanobacteria as an ‘obligately algicolous lichen’. Because no type material of Sutherland’s collections appeared to be in existence (KOHLMEYER 1968), one from south-west England has been selected as neotype (KOHLMEYER 1973). However, KOHLMEYER (1973) cited duplicates of the proposed neotype deposited in NY and IMS, not a single specimen; the collection in NY is here designated as neotype as required by the Code, the one in IMS thus becoming an isoneotype.

This species has been placed in *Pyrenocollema* Reinke along with several other marine, maritime, and semi-aquatic cyanobacterial lichens currently referred to it. We have not examined the original material of the type species, *P. tremelloides* Reinke, but GRUBE & RYAN (2001) found it to be a parasite of *Nostoc.* Those authors took up the generic name *Collemopsidium* Nyl. for the lichenized species formerly placed in *Pyrenocollema,* and their usage is now being followed by other workers (e.g. NORDIN 2002). The marine species of the genus occuring in northwest Europe have also been revised using molecular and morphological criteria (MOHR, EKMAN & HEEGAARD 2004). Five species were accepted, but the present species was not treated as it does not appear to occur in Scandinavia; it is readily separated by the larger ascomata from the other accepted species, as well as in growing on an alga rather than on rock or shells. As the ascomatal structure of *P. pelvetiae* appears to conform to that of the lichenized species referred to *Collemopsidium* by GRUBE & RYAN (2001), it is also appropriate to transfer that species to Nylander’s genus here.

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