

Revision of marine species of *Didymosphaeria* (Ascomycotina)

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Revision of marine species of *Didymosphaeria* (Ascomycotina). *Mycological Research* 94 (5): 685–690 (1990).

The four marine species of *Didymosphaeria* have been re-examined and the names of three of them transferred to new genera (*Bicrouania*, *Lineolata*, *Verruculina*). A new genus and species from wood of *Rhizophora mangle* in Belize is described as *Coronopapilla avellina*. The following new combinations are proposed: *B. maritima* (syn. *Sphaeria maritima* Crouan & Crouan), *L. rhizophorae* (syn. *Didymosphaeria rhizophorae* Kohlm. & E. Kohlm.), and *V. enalia* (syn. *Didymosphaeria enalia* Kohlm.). Ascomata of *B. maritima* contain hymenial photobionts. A key to the marine *Didymosphaeria*-like fungi is provided.

Key words: Marine fungi, Ascomycetes, *Didymosphaeria*, Taxonomic revision.

The last comprehensive treatise on the higher marine fungi (Kohlmeyer & Kohlmeyer, 1979) included four species of *Didymosphaeria*, namely *D. danica* (Berl.) Wilson & Knoyle, *D. enalia* Kohlm., *D. maritima* (Crouan & Crouan) Sacc. and *D. rhizophorae* Kohlm. & E. Kohlm. A fifth one, *D. lignomaris* Strongm. & Miller, was recently described (Strongman *et al.*, 1985). Schatz (1984) recognized that *D. danica* was not properly placed in *Didymosphaeria* and proposed a new monotypic genus, *Lautitia*. New monographs on different groups of ascomycetes by Eriksson (1981), Hawksworth (1985) and Barr (1987) also included discussions on *Didymosphaeria* and related genera, and allowed us to re-examine the position of the marine representatives of this genus. The type species, *D. fulvis* (Berk. & Br.) Rehm, is compared with four known and one new species of marine Ascomycetes.

Didymosphaeria fulvis was described and illustrated in detail by Scheinpflug (1958) who used a broad concept in the circumscription of the genus, whereas recent authors applied a narrower concept. *Didymosphaeria* appears to be mainly confined to herbaceous stems and can be characterized as having immersed clypeate ascomata; a two-layered peridium, cellular on the inside, pseudostromatous and filamentous on the outside; trabeculate pseudoparaphyses; thin-walled asci with a short stipe, without ocular chamber or ring structures; brown, smooth ascospores, one-septate in the middle (Scheinpflug, 1958; Eriksson, 1981; Hawksworth, 1985; Barr, 1987).

Bicrouania Kohlm. & Volkm.-Kohlm., gen. nov.

Etym.: From the Latin *bi-* = two, and 'Crouan' honouring the brothers Hippolyte-Marie and Pierre-Louis Crouan who described many higher and lower plants and fungi, among them the first marine fungi (Kohlmeyer, 1974).

Genus Melanommatium, Melanommatacearum. *Ascomata* subglobosa ad ellipsoidea, superficialia, erumpentia vel rariter immersa, ostiolata, periphysata, breve papillata vel epapillata, subcarbonacea, fuliginea, aspera, gregaria. *Peridium* extra atro-brunneum, prope ventrum hyalinum, in pseudoparaphysibus transiens, cellulis irregularibus, oclusis materia atra, cellulas hospitis includens, texturam epidermoideam formans. *Hamathecium* pseudoparaphysioideum, trabeculatum. *Asci* octospori, cylindrici, breve pedunculati, non-amyloidei, sine oculo vel apparato apicali, pachydermi, fissitunicati, e textura ascogena basale exorientes, algis hymenialibus in tholo loculi. *Ascospores* monostichae, ellipsoideae, uni-septatae, in medio constrictae, porphyreae, aterrimae circa septum, pachydermae, laeves. Substratum: Herbae litorales.

Typus generis: *Bicrouania maritima* (Crouan & Crouan) Kohlm. & Volkm.-Kohlm.

Bicrouania maritima (Crouan & Crouan) Kohlm. & Volkm.-Kohlm., comb. nov.

Sphaeria maritima Crouan & Crouan, *Florule du Finistère*: 27, Paris & Brest 1867, non *Sphaeria maritima* Cooke & Plowright, *Grevillea* 5:120 (1877).

A genus of Melanommatales, Melanommataceae, with one obligately marine species. *Ascomata* subglobose to ellipsoidal, superficial, erumpent or rarely immersed, ostiolate, periphysate, short papillate or epapillate, subcarbonaceous, blackish-brown, rough, gregarious (Fig. 1A). *Peridium* dark brown at the outside, hyaline near the venter and merging into pseudoparaphyses, cells irregular, occluded by dark deposits, enclosing some cells of the host, forming a *textura epidermoidea*. *Hamathecium* pseudoparaphysoid, trabeculate. *Asci* eight-spored, cylindrical, short pedunculate, non-amyloid, without ocular chamber or apical apparatus, thick-walled (Fig. 1B), fissitunicate, maturing successively at the bottom of the locule; with hymenial one-celled photobionts in the dome of the locule (Fig. 1A, D). *Ascospores* monostichous, ellipsoidal,

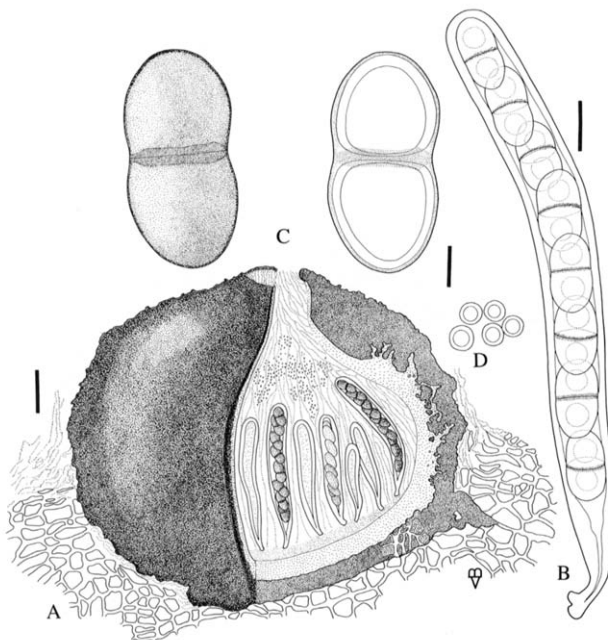
one-septate in the middle, constricted at the septum, reddish-brown, darkest around the septum, thick-walled, smooth (Fig. 1 C).

Material examined: *Sphaeria maritima* on *Halimione portulacoides* (L.) Aellen, Holotype in CO, Isotypes in IMS (J.K. 3097) and IMI (330806), type locality not mentioned, but probably Brittany, France; partly illustrated and described by Kohlmeyer & Kohlmeyer (1979).

The type species of *Bicrouania*, *B. maritima*, is distinguished from *Didymosphaeria* mostly by superficial ascomata lacking a

clypeus (Fig. 1 A), thick-walled asci (Fig. 1 B) and hymenial algae (Fig. 1 A, D; Table 1). Such photobionts, enclosed in the locule of ascomata, occur among terrestrial lichenized fungi, for instance in the genera *Endocarpon* and *Staurothele* (Ahmadjian & Heikkilä, 1970), but this is the first case of a marine ascomycete containing hymenial photobionts. *Bicrouania maritima* does not form a typical lichen thallus, but appears to be loosely associated with one-celled algae in a primitive lichenoid symbiosis, as they occur among other submerged marine ascomycetes (Kohlmeyer & Volkmann-Kohlmeyer, 1988).

Fig. 1. *Bicrouania maritima*, J.K. 3097. A, Ascoma on *Halimione portulacoides*, partly shown in longitudinal section, hymenial algae in the dome of the locule; B, ascus; C, ascospores, the right one in optical section showing the double wall; D, cells of the phycobiont. Scale for A = 50 µm, for B = 15 µm, for C and D = 5 µm.



Coronopapilla Kohlm. & Volkm.-Kohlm., gen. nov.

Etym.: From the Latin, *corona* = crown and *papilla* = papilla, in reference to the crown-like papilla of the ascomata.

Genus *Melanommatalium*, *Didymosphaeriacearum*. *Ascomata* subglobosa, immersa, ostiolata, periphysata, papillata, clypeata, coriacea, supernigra, subter dilute colorata, singularia vel gregaria. *Papilla* conica, coronacea, ad apicem in sectiones carbonaceas findens, emersa. *Peridium* hyalinum, uniforme, texturam angularem formans. *Hamathecium* pseudoparaphysoideum, trabeculatum, in matrice gelatinosa inclusum. *Asci* octospori, cylindrici, elongate pedunculati, non-amyloidei, endoascus cum oculo, pachydermi, fissitunicati, e textura ascogena basale exorientes. *Ascosporeae* monostichae, ellipsoideae, uni- ad triseptatae, brunneae, pachydermae, pariete bistratose. Substratum: Lignum marinum.

Typus generis: *Coronopapilla avellina* Kohlm. & Volkm.-Kohlm.

A genus of *Melanommatales*, *Didymosphaeriaceae*, with one obligately marine species. *Ascomata* subglobose, immersed, ostiolate, periphysate, papillate, clypeate, coriaceous, black above, light-coloured below, single or gregarious. *Papilla* conical, crown-like, tearing at the top in carbonaceous sections, emerged. *Peridium* hyaline, uniform, forming a *textura angularis*. *Hamathecium* pseudoparaphysoid, trabeculate, with gelatinous matrix. *Asci* eight-spored, cylindrical, long pedunculate, non-amyloid, endotunica with oculus, thick-walled, fissitunicate, maturing successively at the bottom of the locule. *Ascospores*

Table 1. Comparison of the type species of *Didymosphaeria* (*D. futilis*) with marine taxa presently or formerly assigned to this genus

	Clypeus	Ascomata often superficial or erumpent	Peridium laterally and basally hyaline	Hamathecium with gelatinous matrix	Hymenial photobionts	Asci		Ascospores	
						Long pedunculate	With apical ring	With ocular chamber	Always 1-septate
<i>Didymosphaeria futilis</i>	+	-	+	-	-	-	-	+	-
<i>Didymosphaeria lignomaris</i>	-	+	-	-	-	-	+	+	+
<i>Bicrouania maritima</i>	-	+	-	-	+	-	-	+	-
<i>Coronopapilla avellina</i>	+	-	+	+	-	+	+	-	-
<i>Lineolata rhizophorae</i>	-	+	-	+	-	-	+	+	+
<i>Verruculina enalia</i>	+	+	-	+	-	-	+	+	+

+, Character present; -, Character absent.

monostichous, ellipsoidal, one- to three-septate, brown, thick-walled, wall two-layered.

Coronopapilla avellina Kohlm. & Volkm.-Kohlm., sp. nov.

Etym.: From the Latin, *avellinus* = hazel, nut-brown, in reference to the colour of the ascospores.

Ascomata 600–850 µm alta, 450–650 µm diam, subglobosa, in lignum immersa, ostiolata, papillata, clypeata, coriacea, pallida, singularia vel gregaria. *Papilla* 80–160 µm alta, 245–430 µm diam, conica, nigra, coronacea, ad apicem in 3–5 sectiones carbonaceas findens, clypeo nigro circumdata. *Canalis ostioli* 95–180 µm longus, 70–95 µm diam, periphysatus. *Peridium* 25–45 µm crassum, 8–15 stratis cellularum polygonarum, hyalinarum compositum, texturam angularem formans. *Hamathecium* pseudoparaphysoideum, trabeculatum, ramosum et anastomosans, in matrice gelatinosa inclusum, reticulum formans. *Asci* 350–430 × 28–37 µm, octospori, cylindrici, elongate pedunculati, pachydermi, fissitunicati, non-amyloidei, sine apparatu apicale, sed oculo in endoasco pachydermo, successive e textura ascogena basale exorientes. *Ascospores* 40–54 × 18–22.5 µm (\bar{x} = 47.1 × 19.8 µm; n = 80), monostichae, ellipsoideae, uni- vel tri-septatae, ad septum medium constrictae, avellaneae, muri pachydermi, bistrati. *Substratum*: Lignum radices *Rhizophorae mangle*. *Distributio*: Oceanus Atlanticus (Belize). *Holotype*: J.K. 5144a (IMS), *Isotype*: J.K. 5144b, IMI 330805.

Ascomata 600–850 µm high, 450–650 µm in diam, subglobose, immersed in wood, ostiolate, papillate, clypeate, coriaceous, light-coloured, single or in groups (Figs 2, 3). *Papilla* 80–160 µm high, 245–430 µm diam, conical, black, crown-like, tearing at the top into 3–5 carbonaceous sections surrounded by a shield-like, black clypeus (Fig. 3); ostiolar canal 95–180 µm long, 70–95 µm diam, periphysate. *Peridium* 25–45 µm thick, composed of 8–15 layers of polygonal hyaline cells, forming a *textura angularis* (Fig. 4 C). *Hamathecium* pseudo-paraphysoid, trabeculate, forming a network of anastomosing filaments, embedded in a gelatinous matrix (Fig. 4 B). *Asci* 350–430 × 28–37 µm, 8-spored, cylindrical, long pedunculate, thick-walled, fissitunicate, non-amyloid, without an apical apparatus, with an oculus in the thick-walled endoascus, maturing successively on the ascogenous tissue at the bottom of the locule (Fig. 4 A, E). *Ascospores* 40–54 × 18–22.5 µm (\bar{x} = 47.1 × 19.8 µm; n = 80), arranged monostichously (slightly overlapping) in the ascus, ellipsoidal,

Fig. 2. *Coronopapilla avellina*, J.K. 5144. Coronaceous apices of ascomata breaking through the wood surface of a *Rhizophora mangle* propropoot. Scale = 150 µm.

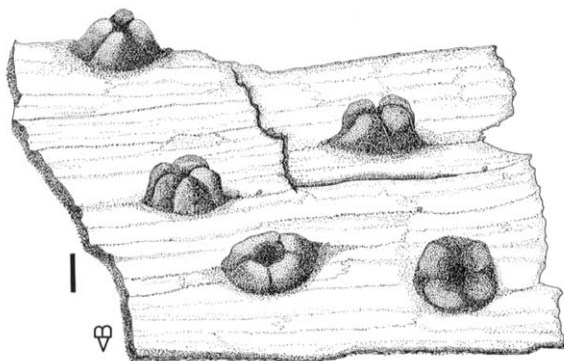
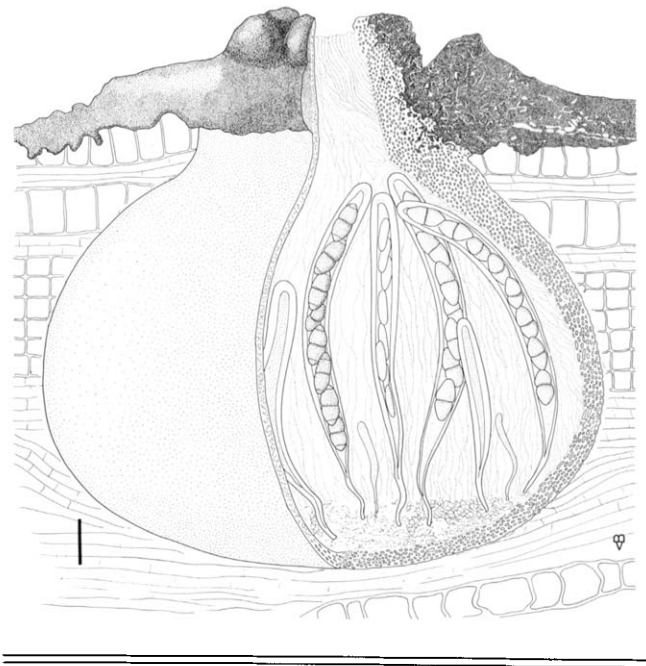


Fig. 3. *Coronopapilla avellina*, J.K. 5144. Clypeate ascoma, partly shown in longitudinal section. Scale = 50 µm.



one- to three-septate, constricted at the central septum, hazel; wall thick, two-layered (Fig. 4 D, E).

Substrate: Wood of propropoot of *Rhizophora mangle*.

Range: Atlantic Ocean (known only from the type locality, Belize).

Material examined: Intertidal dead propropoot of *R. mangle*, among *Bostrychia* sp. Twin Cays, Belize, 16° 50' N, 88° 06' W, 17 Nov. 1984, J.K. 5144a (Holotype, IMS), J.K. 5144b (Isotype, IMI 330805).

Coronopapilla avellina superficially resembles species of *Didymosphaeria*, but is distinguished from *D. futilis* by one- to three-septate ascospores, a hamathecium with gelatinous matrix, and long pedunculate asci with ocular chamber. Differences from the other genera are listed in Table 1.

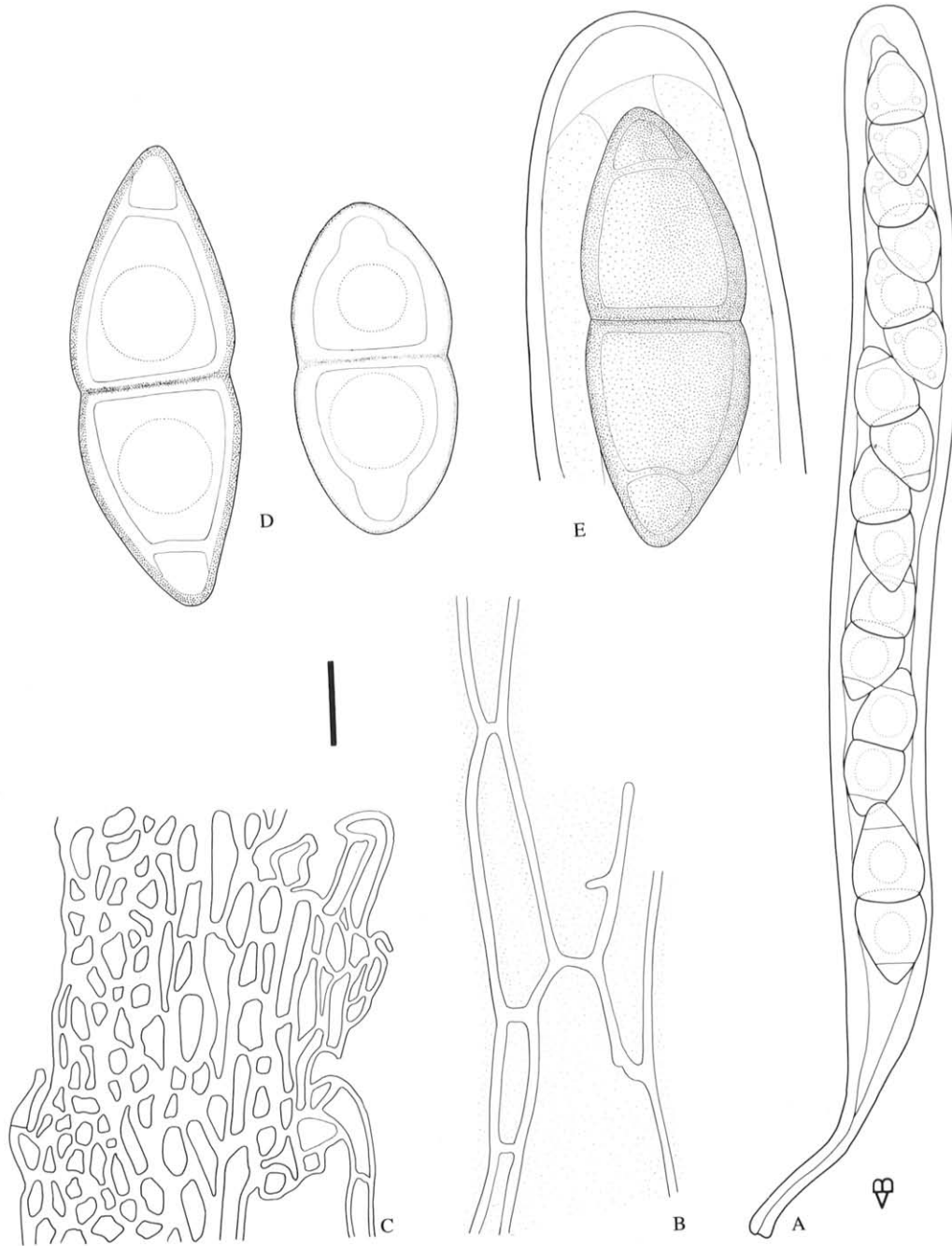
Lineolata Kohlm. & Volkm.-Kohlm., gen. nov.

Etym.: From the Latin, *lineolatus* = marked by fine parallel lines, in reference to the ascospores, ornamented with delicate costae.

Genus *Melanommatalium* incertae sedis. *Ascomata* obpyriformia, fere superficialia ad immersa, ostiolata, periphysata, papillata, subcarbonacea ad subcoriacea, nigra, gregaria. *Peridium* crassum, bistratosum; stratum externum pseudostromaticum, cellulis irregularibus brunneis, fere hyphoideum prope substratum; stratum internum tenue, cellulis hyalinis, compressis, texturam angularem formantibus. *Hamathecium* pseudoparaphysoideum, trabeculatum, in matrice gelatinosa inclusum. *Asci* octospori, cylindrici, breve pedunculati, non-amyloidei, annulo refractivo in endotunica circa oculum, pachydermi, fissitunicati, e textura ascogena basale exorientes. *Ascospores* monostichae, ellipsoideae, uniseptatae, brunneae, tenuiter costatae. *Substratum*: Lignum vel cortex marinus.

Typus generis: *Lineolata rhizophorae* (J. & E. Kohlm.) Kohlm. & Volkm.-Kohlm.

Fig. 4. *Coronopapilla avellina*, J.K. 5144. A, Ascus; B, pseudoparaphyses with gelatinous matrix; C, peridium, outside to the left; D, thick-walled ascospores in optical section; E, apex of ruptured ascus, showing endotunica (with oculus) separated from ectotunica. Scale for A = 25 μ m, for B–E = 10 μ m.



Lineolata rhizophorae (Kohlm. & E. Kohlm.) Kohlm. & Volkm.-Kohlm., comb. nov.

Didymosphaeria rhizophorae Kohlm. & E. Kohlm., *Icones Fungorum Maris*, Fasc. 4 & 5, Tabs 62 and 62a, Figs 1–19, J. Cramer, Weinheim (1967).

A genus of Melanommatales *incertae sedis*, with one obligately marine species. *Ascomata* obpyriform, almost superficial to immersed, ostiolate, periphysate, papillate, subcarbonaceous to subcoriaceous, black, gregarious. *Peridium* thick, two-layered; outer stratum pseudostromatic, composed of irregular elongate or roundish, dark brown cells, mostly

with small lumina, almost hyphoid near the substratum; inner stratum thin, composed of hyaline, polygonal, compressed, thin-walled cells with large lumina, forming a *textura angularis*. *Hamathecium* pseudoparaphysoid, trabeculate, with gelatinous matrix. *Asci* eight-spored, cylindrical, short pedunculate, non-amyloid, with a multi-layered refractive ring in the endotunica around the oculus, thick-walled, fissitunicate, maturing successively at the bottom of the locule. *Ascospores* monostichous, ellipsoidal, one-septate, brown, with delicate costae.

The type species, *L. rhizophorae*, has been described and illustrated in detail by Kohlmeyer & Kohlmeyer (1967, 1979). Transfer to a new genus is required because the generic

concept of *Didymosphaeria* has been changed in recent years. *Lineolata rhizophorae* differs from *D. futilis* by the absence of a clypeus, by almost superficial ascomata, a coloured peridium, a hamathecium with gelatinous matrix, asci with apical ring-like structure around the ocular chamber, and by ornamented ascospores.

Verruculina Kohlm. & Volkm.-Kohlm., gen. nov.

Etym.: From the Latin, *verrucula* = small wart, in reference to the verruculose ascospores.

Genus Melanommatalium, Didymosphaeriacearum. *Ascomata* subglobosa, ampulliformia vel ellipsoidea, partim vel omnino immersa, ostiolata, periphysata, papillata, clypeata, carbonacea, nigra, singularia. *Papilla* brevis, conica, clypeo circumdata, plerumque immersa, canalis ostioli obturbinatus. *Peridium* 6 vel plus stratis cellularum irregularium rotundarum vel applanatarum, atro-brunnearum, texturam angularem formantium; fere hyphoideum vel stromaticum juxta substratum. *Hamathecium* pseudoparaphysoidem, trabeculatum, in matrice gelatinosa inclusum. *Asci* octospori, cylindrici, breve pedunculati, non-amyloidei, sine apparato apicali, cum oculo, pachydermi, fissitunicati, e textura ascogena basale exorientes. *Ascosporae* monostichae, ellipsoideae, uniseptatae, atro-brunneae, verrucosae ad verruculosae. Substratum: Lignum marinum.

Typus generis: *Verruculina enalia* (Kohlm.) Kohlm. & Volkm.-Kohlm.

A genus of Melanommatales, Didymosphaeriaceae, with one obligately marine species. *Ascomata* subglobose, ampulliform or ellipsoidal, partly or completely immersed, ostiolate, periphysate, papillate, clypeate, carbonaceous, black, single. *Papilla* short, conical, surrounded by the clypeus, mostly immersed; ostiolar canal obturbinate. *Peridium* composed of six or more layers of irregular rounded or flattened, dark brown cells, forming a *textura angularis*, with hyphae or stromatic structures embedded in the substrate. *Hamathecium* pseudoparaphysoid, trabeculate, with gelatinous matrix. *Asci* eight-spored, cylindrical, short pedunculate, non-amyloid, without apical apparatuses, with ocular chamber, thick-walled, fissitunicate, developing at the bottom of the locule. *Ascospores* monostichous, ellipsoidal, one-septate, dark brown, verrucose to verruculose. *Substrate*: Marine wood.

Verruculina enalia (Kohlm.) Kohlm. & Volkm.-Kohlm., comb. nov.

Didymosphaeria enalia Kohlm., *Ber. Deutsch. Bot. Ges.* **79**:28, Figs 1, 2, 7–10 (1966).

Like *Lineolata rhizophorae*, *V. enalia* has been illustrated earlier and described in detail (Kohlmeyer & Kohlmeyer, 1967, 1979). Although the new genus is characterized by partly or completely immersed clypeate ascomata, and resembles in this respect *Didymosphaeria futilis*, it differs from the latter by a dark peridium, a gelatinous matrix around the pseudo-paraphyses, by stipitate asci with a distinctive ocular chamber and by coarsely verruculose ascospores.

Didymosphaeria lignomaris Strongman & Miller

This species was collected by Strongman *et al.* (1985) on submerged birch panels on the Atlantic coast of Canada. We have examined the holotype (DAOM 193904), but the condition of the material on permanent slides does not permit judgement of the generic placement of the species. A pure culture (DAOM 193904) kindly supplied by the Biosystematics Research Centre, Agriculture Canada (Ottawa) yielded ascomata on balsa wood and alfalfa straw. These fruiting bodies are superficial, black and without clypeus, the peridium is very broad, forming a *textura angularis*, toward the outside occluded by melanin, and the peridial cells are thin-walled with large lumina. The broad pseudoparaphyses are not trabeculate. These characters indicate that *D. lignomaris* does not belong to *Didymosphaeria* as characterized by Eriksson (1981), Hawksworth (1985) and Barr (1987), but a reclassification is not warranted at this time. Features of the ascomata developed in culture, e.g. position, ascospore size, do not agree completely with those grown under natural conditions (Strongman *et al.*, 1985), and, therefore, new material is required for a decision on the placement of *D. lignomaris*.

CONCLUSION

Because of recent changes in the concept of *Didymosphaeria*, all but one marine species formerly assigned to this genus had to be referred to new genera. As discussed above it is unlikely that the remaining species, *D. lignomaris*, is a *Didymosphaeria*. The following key may help in separating *Didymosphaeria*-like marine Ascomycetes.

Key to the marine Didymosphaeria-like Ascomycotina

- 1. Ascomata completely immersed 2
- 1. Ascomata superficial or only partly immersed 3
- 2. Ascomata clypeate; spores 1–3 septate, without sheath *Coronopapilla avellina*
- 2. Ascomata with pseudoclypeus; spores 1-septate, with a gelatinous deliquescent sheath *Helicascus kanaloanus* Kohlm.
- 3. Ascospores ornamented 4
- 3. Ascospores smooth 7
- 4. Ascospores striate *Lineolata rhizophorae*
- 4. Ascospores verrucose to verruculose 5
- 5. Ascospores with hyaline apices *Caryospora rhizophorae* Kohlm.
- 5. Ascospores brown throughout 6
- 6. Ascospores without distinct dark band around the septum, reddish-brown; a tropical species *Verruculina enalia*
- 6. Ascospores with dark band around the septum, olive-brown; a temperate species *Didymosphaeria lignomaris*
- 7. Ascospores septate below centre, shorter than 22 µm; without photobionts *Kirschsteiniethelia maritima* (Linder) D. Hawksw.
- 7. Ascospores septate in centre, longer than 22 µm; with hymenial photobionts *Bicrouania maritima*

All four genera described in the present paper belong to the Melanommatales, *Coronopapilla* and *Verruculina* are members of the Didymosphaeriaceae, *Bicrouania* of the Melanommataceae, while the familial position of *Lineolata* is uncertain. Three of the type species are restricted to the tropics (*C. avellina*, *L. rhizophorae*, *V. enalia*), whereas *B. maritima* is known only from a temperate location. These four species grow in the intertidal zone and have not been found on permanently submerged substrates. This is in agreement with our observations that most marine Loculoascomycetes are restricted to intertidal habitats (Kohlmeyer & Volkmann-Kohlmeyer, unpubl.).

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