ON ANTHOSTOMELLA SACC., ENTOSORDARIA (SACC.) HÖHN. AND SOME RELATED GENERA (PYRENOMYCETES).

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Entosordaria, originally a subgenus of Anthostomella SACC. (1882, p. 286), was raised to generic rank by Höhnel (1920, p. 166). These two genera have always been considered closely related and are in current classification placed in Xylariaceae (Tul.) Lindau emend. MILLER (1928, p. 335). This family was originally based mainly on stromatic characters but has gradually become defined by hymenial characters and now also includes genera with very inconspicuos stromata, e.g., Anthostomella SACC. and Anthostoma NITS. Its distinctive characters are a) the typical hymenium of branched paraphyses and cylindrical, short-stalked asci, b) the apical apparatus of the asci, the "crown" with a perforate plug or ring, always containing amyloid substance(s) staining blue with iodine1 and c) the uniseriate, ±inequilateral, in most cases unicellular, brown-walled spores which as a rule show a longitudinal germ slit. The tendencies to form d) stromata (often large and highly specialized) and e) superficial hyphomycetous conidial states are also worth mentioning. As the

¹ Nannfeldt (oral comm.) and Munk (1957, p. 132) observed that one species, viz. Hypoxylon serpens (Pers. ex Fr.) Fr., does not always show this reaction. Munk (l.c.) studied three collections of this species. In one the asci showed "a distinct blackish blue reaction", in a second "a faint purplish brown I-reaction" and in a third collection the asci were "perfectly non-amyloid". I have examined several samples of H. serpens and found Nannfeldt's and Munk's observations to be correct, but, in fact, it is easy to get all plugs to stain blue, viz. if the mounts are treated first with NaOH and then with HNO3. This technique was used routinary by Minks already in 1881 and in some cases (e.g., Patellaria rubi Lib. = Pezicula rubi (Lib.) Niessl, pp. 63-64) the asci did not stain blue if only iodine was added. Other examples of the same phenomenon are to be found in Santesson (1952, pp. 89-90) and Malme (1929, pp. 27, 29, 31, etc.; in this case not asci, but "nucleus ... J vinose rubens (KOH, HNO3 et J tractatus coeruloscens)"). All these authors are lichenologists. The mycologists seem to have over-looked this technique.

hymenial characters are very uniform in this family they are of minor significance for the delimitation of the genera, which therefore have been based largely on stromatical characters. Consequently the limits between the genera are in some cases very diffuse. Thus, ARX & MÜLLER (1954, p. 313) included Anthostomella in Anthostoma as they considered the differences between the stromata of these genera too insignificant for maintaining them both. These genera are discussed first in my paper. The segregate Entosordaria has turned out to differ from Anthostomella in several taxonomically important respects and has even to be removed from Xylariaceae. This and some possibly related genera are treated in the latter part of this paper.

The genera Anthostoma and Anthostomella are from the beginning far from homogeneous and are still insufficiently known. Anthostoma is adscribed inconsiderable stroma and perithecia immersed in the substrate (wood) and Anthostomella clypeiform or no stroma and immersed perithecia. The selection of type species in these schematical genera involves important nomenclatural consequences.

CLEMENTS & SHEAR (1931, p. 261) selected as the type of Anthostoma, A. decipiens, the first species of the ten in Nitschke's new genus (1867, p. 111). In a later paper Shear (1938, p. 582) proposed to change it to A. melanotes (B. & BR.) SACC. "as this would place the application of the [generic] name in accord with prevailing usage". Unfortunately, it is impossible to follow the last suggestion as all facts are in favour of A. decipiens. The species placed last by NITSCHKE, A. turgidum (Pers. ex Fr.) Nits., alone forms the subgenus Lopadostoma Nits., while the rest form the subgenus Anthostoma (sic!) Nits. This was divided into two groups, one with "ostiola crassa, radiatim exarata" and one with "ostiola exigua, integra". The generic name alludes clearly to the ostiola of the first group (A. decipiens and A. hiascens). As A. decipiens was the better known species to Nitschke and, by the way, also to later mycologists, the choice is easy between it and A. hiascens. The spores of A. decipiens are devoid of germ slit (Vincens 1918, p. 108) and the apical apparatus of the ascus is nonamyloid. As suggested already by Shear (1938, p. 581) these two species should be placed in Diatrypaceae (Munk (1957, pp. 117-119), who included Diatrypaceae in Xylariaceae, referred Anthostoma to his tribus Diatrypeae with hesitation). For the other species in the subg. Anthostoma a generic name remains to be found, which certainly will necessitate a lot of work, advisably spent when this group of fungi is monographed.

Lopadostoma was raised to generic rank by Traverso (1906, p. 169) and must evidently be typified by the monotype of Nitschke's subgenus, although Traverso listed L. turgidum (Pers. ex Fr.) Trav. in the second place. Clements & Shear (1931, p. 261) and Shear (1938, p. 583) chose his first species, L. gastrinum (Fr.) Trav., which however is not in accordance with the International Code of Botanical Nomenclature (1961, p. 64: 4a). L. turgidum is a typical member of Xylariaceae possessing spores with distinct germ slit (Vincens 1918, p. 107; Munk 1953, pp. 59-60) visible in oil immersion and apical apparati in shape of obconical, perforated, strongly amyloid plugs.

Anthostomella was described by SACCARDO in 1875a (p. 84) and characterized among the *Phaeosporae* in the following words: "Perithecia epidermide adhaerente et circa ostiolum vix erumpens nigrificata tecta. — Ex. A. limitata SACC., A. tomicoides SACC., A. perfidiosa (DNts.) SACC. — Obs. Genus Clypeosphaeriae analogum, sed sporidia continua, in nonnulis breviter appendiculata." Already in the subsequent paper (SACCARDO 1875b, p. 101) in the same number of the periodical, a few more species were added. Clements & SHEAR (1931, p. 261) chose one of these, A. phaeosticta (BERK.) SACC., as the type species. This proposal must be rejected and the type selected amongst the species mentioned in Saccardo's first paper. Saccardo's adnotation that in some species ("in nonnulis") the spores are appendiculate suggests that he considered nonappendiculate spores as most typical of his genus, and this is definitely proved in 1882, when he divided the genus into two groups, 1 viz. Eu-anthostomella with non-appendiculate spores and Entosordaria with appendiculate spores. Only one of the original three species is non-appendiculate, viz. A. limitata and this becomes necessarily the type. This species has according to Höhnel (1920, p. 178) an amyloid, xylariaceous apical apparatus in the asci. Other species with non-appendiculate spores belonging to this genus are, e.g., A. lugubris (ROB. in DESM.) SACC. and A. punctulata (ROB. in DESM.) ARX & MÜLLER (= A. phaeosticta (Berk.) SACC. acc. to ARX & MÜLLER 1954, p. 316). The majority of the species with appendiculate spores (subg. Entosordaria) are certainly congeneric with those having nonappendiculate spores, and Munk (1953, pp. 57-58) and Dennis (1960, p. 175) conceived the genus in its broader, original extent. We

¹ There is a third subgenus, *Desciscentes*, characterized by Saccardo in the following words: "macula stromatica nigra circa ostiolum nulla, vel saltem non indicata". This subgenus is of no interest in this connection.

have a parallel in the coprophilous genus Hypocopra Fr. The spores are provided with a germ slit and are either appendiculate or nonappendiculate. Chadefaud (1953, p. 513) examined one of the species with appendiculate spores, H. amphisphaerioides (Ell. & Ev.) GRIFF., and found that the appendage (= a dwarf cell) in some spores "ne se réduit pas à un simple apicule: elle est assez grande; sa paroi s'epaissit, et peut mème se pigmenter en brun clair". The same phenomenon is often seen in, e.g., A. ammophila (PHILL. & PLOWR.) SACC. No septum is laid down between the large cell and its appendage, which then turns brown like the rest of the spore. Such spores are similar to those of, e.g., A. lugubris. It is reasonable to conclude that Eu-Anthostomella originates from one or several species with appendiculate spores by loss of the septum, and we should presuppose that this sub-genus may be polyphyletic. Therefore we had better not base a division of Anthostomella merely upon the septation of the ascospores. In some species, e.g., A. foliicola (SACC.) TRAV., there are even two appendages, one at each end. Its young spores are narrowly fusiform. According to Höhnel (1920, p. 177) two or four very faint transverse septa are formed, the central cell grows thicker and larger, and gets a coloured thick wall, whereas the (one or two) end cells remain thin-walled and simulate gelatinous appendages. These observations are not correct. In the young spore a faint transverse septum cuts off the distal third of the spore. The distal cell remains hyaline and very thin-walled. It contains plasma and is coloured by Cotton blue. In the rest of the spore the plasmatic contents become surrounded by a thick and dark wall. In the proximal end an appendage, similar to that in the distal end, can be seen. It is not stained by Cotton blue, and seems to be gelatinous throughout. It is probable that this part of the spore in a younger stage contains plasma, which, however, contracts toward the middle of the spore. This surmise is strengthened by the fact that the apex of the distal cell is devoid of plasma also.

Concerning the origin of this genus we are confined to the same possibilities as for Hypocopra. Chadefaud (l.c.) believed that the ascospores of the ancestors of Hypocopra and all other genera of Xylariaceae: "1. soit bicellulaires, à cellule postérieure plus petite que l'autre, donc comparables (simple analogie?) à celles, par example, des Gnomonia. 2. soit porvues d'une queue postárieure formée d'une ou plusieurs cellules, comme celles des Lasiosordariacèes (g. Bombardia et Pleurage) ...". Of these hypotheses the Sv. Bot. Tidskr., 60 (1966): 2

second seems to be the most plausible as it would (l.c.) "permettrait d'envisager une parenté des Xylariacées avec les Lasiosordariacées, et sans doute aussi les Sordariacèes vraies".

Entosordaria was raised to generic rank by Höhnel (1920, р. 166, cf. also р. 176), who expressly designated E. perfidiosa (Denot.) Höhn. as the type. Entosordaria sensu Höhnel is "eine eigene, von Euanthostomella Sacc. verschiedene Gattung mit zweizelligen Sporen mit einer grossen braunen und einer kleinen hyalinen oder fast hyalinen Zelle". Besides the type species Höhnel referred 21 species to this genus, in most cases without having seen any material of them. He pointed out that Entosordaria might be heterogeneous, as the asci were amyloid in some species but not in others. In this sense Entosordaria has been accepted by most mycologists, e.g., Petrak (1924, p. 74), Arx & Müller (1954, p. 308) and Schrantz (1960, p. 365).

There seems to be only one species in Entosordaria with nonamyloid asci, and this happens to be the type species, E. perfidiosa. It differs most markedly from the rest of the species in other characters too, why Entosordaria at least for the moment must be considered monotypical (as mentioned above most of the species in this genus, perhaps all except E. perfidiosa, can be referred to Anthostomella). Already Petrak (1924, p. 75) stated that "E. perfidiosa ... wächst auf Rinde, hat mehr oder weniger hervorbrechende, relativ grosse Perithecien und weicht dadurch vom gewöhnlicher Anthostomella-Typus ab". The most striking differences are, however, to be found in the ascospores. Thus, in Anthostomella there is a lateral, typical xylariaceous germ slit in the brown-walled cell of the spores. Such a slit is not found in Entosordaria, but if the non-appendiculate end of a spore is examined a unique germ apparatus of radiating slits can be seen. Commonly it has the shape of a "K" (Fig. 1 f) but sometimes of an "X", an "I" or "⊢". The germ slits can in general be studied only for a short moment, because the spores take a perpendicular position almost only when rolling in the medium. The spores are somewhat flattened dorsi-ventrally (in Anthostomella, laterally; this can be stated on account of the spores in both genera are commonly somewhat inequilateral) and when studied in lateral view, the germ slits are easy to see (Fig. 1c).

As neither the ascospores nor the asci are xylarioid in *Entosordaria*, we had better not refer this genus to *Xylariaceae*, which as defined above (p. 315) certainly is a homogeneous family. For the moment it is better placed in *Amphisphaeriaceae* sensu Müller & Arx (1962,

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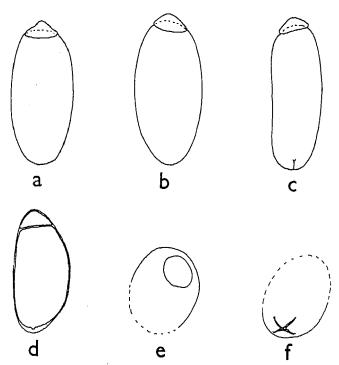


Fig. 1. Entosordaria perfidiosa. a-f ascospores. a spore in ventral (or dorsal) view, b in semi-lateral view, c in lateral view, d young spore, e appendiculate end of a spore, f the opposite end with the germ apparatus of radiating slits. — Coll. exam.: "Anthostomella perfidiosa (DeNot.) Sacc. — Riva-Valdobbia: 4 Marzo 1895. — Sulla corteccia dell'Acer Pseudoplatanus. —Ab. Carestia", Herb. Bresadola (S). — Magnification: × 1560.

p. 668), which no doubt is a heterogeneous family, in need of a future study, but for the present very useful as a temporary refuge for some genera not to be included in, but related to Xylariaceae. In most genera the asci are amyloid, e.g., in Cainia ARX & MÜLLER (1955, p. 110), Ceriophora HÖHN. (1919, p. 585) and Chitonospora BOMM., Rouss. & Sacc. (ipse; France, Normandie, Cabourg, 25.VI.1954. leg. L. HOLM, UPS; Coll. orig. not refound in Herb. Sacc., PAD). Cainia and Ceriophora were referred to Amphisphaeriaceae already by Schrantz (1960, p. 367) and MÜLLER & ARX (1962, pp. 689, 703) while Chitonospora hitherto has been placed in Pseudosphaeriales (see, e.g., Dennis 1960, p. 248, pl. XXXVIIIh). The spores of Cainia and Ceriophora are 1-septate while those of Chitonospora are 3-septate. They are remarkable in having longitudinal ridges which are paler than the rest of the wall, due to the occurrence of a low Sv. Bot. Tidskr., 60 (1966): 2

furrow in the wall under each ridge, visible in cross-sections (c. 5 μ thick) of the spores. There are commonly 6 ridges on each spore in Cainia (8 acc. to Arx & Müller 1955, p. 111 and Fig. 2e), 5 in Ceriophora (acc. to Arx & Müller 1955, p. 113: "eine feine Längsstreifung ... aber im Querschnitt rundlich"; the same opinion in Paraguay-Leduc & Chadefaud 1963, p. 211, Figs. 15, 16) and in Chitonospora only 2 ridges (here plenty of oil drops in the plasmatic contents near the ridges).

The genus Amphisphaerella (Sacc.) Kirschst. emend Munk (1953, p. 88) is by most authors placed in Xylariaceae (e.g. Arx & Müller 1954, p. 310, Munk 1957, p. 137 and Dennis 1960, p. 175). The distinct feature of this genus is the equatorial and ± equidistant pores in the ellipsoidal, nonseptate and dark brown ascospores. Thus, the ascospores are not typically xylarioid, nor are the asci (see below), and therefore this genus has to be transferred to Amphisphaeriaceae. There are at least three species in Amphisphaerella: A. dispersella (Nyl.) O. Eriks. comb. nov.¹ (= A. amphisphaerioides (Sacc. & Speg.) Kirschst., the type of the genus), A. vaga (Niessl in Rabenh.) O. Eriks. comb. nov.² and A. xylostei (Pers. ex Fr.) Munk. Among characters separating these species the following may be mentioned:

A. dispersella: on Populus (spp.); asci non-amyloid; ascospores 21-26 × 8-10 μ, with (3-) 4 (-several) pores ("A. amphisphaerioides": 3 pores acc. to Munk 1957, pp. 137-138, 4 pores acc. to Arx & Müller 1954, p. 312).
A. vaga: on Clematis (vitalba); asci non-amyloid; ascospores 10-14 × 6-7.5 μ,

with (3-) 4 pores.

A. xylostei: on Lonicera (spp.); asci with a low but distinct amyloid ring with a very wide opening; ascospores commonly c. $14-18\times6-9~\mu$ (but very variable), with (4-) 5-6 (-several) pores (4 pores acc. to Munk 1953, p. 89, 4 pores acc. to Arx & Müller 1954, p. 313, but in 1955, p. 368, they stated that "sehr häufig nur vier äquatorial angeordnete Keimporen vorhanden sind, dass aber ebenso häufig zwei Keimporenzonen mit einer variablen Zahl von Keimporen auftreten").

MÜLLER & ARX (1955, p. 368) placed a fungus, described by Luc (1951, pp. 110-115) under the name Phaebotryosphaeria varians, in

² Amphisphaerella vaga (Niessl in Rabenh.) O. Eriks. comb. nov. (basionym: Anthostomella vaga Niessl in Rabenhorst, Fungi europei, no. 3551, 1886; isotypus

in UPS).

¹ Saccardo & Spegazzini described their species in 1877, but the same fungus was described by Nylander already in 1859, and therefore the correct name on the type species now has to be *Amphisphaerella dispersella* (Nyl.) O. Eriks. comb. nov. (basionym: *Sphaeria dispersella* Nylander in Herbarium Musei Fennici, Appendix, p. 112, 1859; synonym: *Rosellinia dispersella* (Nyl.) Karst.; *coll. orig.* in HEL).

Amphisphaerella. The ascospores are, however, not ellipsoidal in this species but rather rhomboidal, and there is also an apical pore in the one end of the spores, besides the three equatorial pores (see Luc op. cit., Fig. 6 D, E). Neither are the figured asci of Amphisphaerella type, and this fungus can hardly belong to this genus.

To sum up, in the homogeneous family Xylariaceae the asci are always provided with an amyloid plug of a typical shape; in Amphisphaeriaceae there are many types of apical apparati, chemically as well as morphologically, and amyloid and non-amyloid asci may even occur in the same genus (Amphisphaerella). In Xylariaceae the ascospores are commonly non-septate, with dark brown walls provided with a longitudinal germ slit; in Amphisphaeriaceae we have the most different types of ascospores, hyaline (Lejosphaerella Höhn.) to dark brown (Cainia), non-septate (Xylochora Arx & Müller 1954, acc. to Müller & Arx 1962, p. 669) to several septate (Chitonospora) and with ridges, germ pores or slits or without such equipments. It is possible that Amphisphaeriaceae will be split up into several families, in some cases perhaps very small ones. We have many parallels to this among the phanerogams.

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Summary.

In this paper the following statements are done:

- 1. Anthostoma Nits. (Type: A. decipiens (DC) Nits.) belongs to Diatrypaceae.
- 2. Lopadostoma (Nits.) Trav. (Type: L. turgidum (Pers. ex Fr.) Trav.), a segregate of Anthostoma, belongs to Xylariaceae.
- 3. Anthostomella Sacc. (Type: A. limitata Sacc.) belongs to Xylariaceae. This genus contains species with non-appendiculate spores as well as species with one or two appendages on the spores.
- 4. Entosordaria (SACC.) Höhn. (Type: E. perfidiosa (DENOT.) Höhn.), a segregate of Anthostomella, is a monotypical genus that belongs to Amphisphaeriaceae. The single species is lignicolous, has Sv. Bot. Tidskr., 60 (1966): 2

non-amyloid asci and appendiculate spores, provided with a unique, apical germ apparatus of commonly 4 radiating slits in the end opposite to the appendage.

- 5. Xylariaceae is a homogeneous family, while Amphisphaeriaceae in this paper serves as a refuge for some genera not to be included in, but related to Xylariaceae. The variation within Amphisphaeriaceae is examplified by
- a) Entosordaria with non-amyloid asci and appendiculate spores with a unique germ apparatus (see above).
- b) Cainia ARX & MÜLLER, Ceriophora HÖHN. and Chitonospora Bomm., Rouss. & Sacc. with amyloid (but not xylarioid) asci and spores with 6 (Cainia), 5 (Ceriophora) or 2 (Chitonospora) ridges and 1 (Cainia and Ceriophora) or 3 (Chitonospora) septa. Of these genera Chitonospora has hitherto been referred to Pseudosphaeriales.
- c) Amphisphaerella (SACC.) KIRSCHST. sensu MUNK with three species, two with non-amyloid asci and one with amyloid (but not xylarioid) asci. In all species the spores are non-septate and provided with equatorial germ pores. The species with amyloid asci is A. xylostei (Pers. ex Fr.) Munk, the others are A. dispersella (NYL.) O. Eriks. comb. nov. (syn. A. amphisphaerioides (SACC. & SPEG.) Kirschst.) and A. vaga (Niessl in Rabenh.) O. Eriks. comb. nov.

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