Naeviella (Rehm) Clem., a resurrected genus of Inoperculate Discomycetes, and some remarks on ascospore symmetry

J. A. Nannfeldt

Institute of Systematic Botany, University of Uppsala,
P. O. Box 541, S-751 21 Uppsala, Sweden

Summary. — The generic name *Naeviella* (Rehm) Clem. (type species: *Naevia paradoxa* Rehm) is resurrected. The genus (comprising also *N. volkartiana* (Rehm) Nannf. n. c. and two taxa left unnamed) is shown to belong to the *Hysteropezizella* complex. Most distinctive are the nonseptate and pigmented ascospores provided with a minute germ-pore topping a lateral conical protuberance. Further marks are the iodine-negative asci and the paraphyses, whose clavate to subglobular tips are enclosed in a thick, brown, externally encrusted slime cap. The symmetry conditions of ascospores are also discussed as well as their phylogenetic value in characterizing genera and higher taxa.

Introduction

Naevia paradoxa Rehm (1881) — inhabiting *Juncus trifidus* — bears for good reasons its specific epithet. It has successively been transferred to four other genera, viz. *Phragmonaevia* Rehm, *Diplonaevia* Sacc., *Hysteropezizella* v. Höhn., and *Eupropolella* v. Höhn. (and a very close ally to a fifth genus, *Phaeophacidium* P. Henn. & Lindau) but has remained an alien element in all of them. A new genus, *Naeviella* (Rehm) Clem., has also been based on it. As will be shown below, not even the latest transfer, that to *Eupropolella* (Défago, 1968), is satisfactory.

The singular features that attracted Rehm's attention were the brown epithecium formed by the pyriform to subglobose tips of the paraphyses and the negative iodine reaction of the asci. A still stranger but not commented feature was observed by Défago: ... "les spores deviennent quelquefois brunâtres dans l'asque ...; à ce stade, on remarque une proéminence dans le premier tiers inférieur (pore germinatif ?)".

The genus *Eupropolella* v. Höhnel (1917), based on *Pseudopeziza vaccinii* Rehm, has been studied in detail by Müller (1957; 1977), Müller et al. (1958), and B. Eriksson (1970). A few closely allied species growing on some members of Ericaceae and *Diapensia lapponica* L. are referred to it, the crucial features being: apothecia subcuticular, flat-bottomed; perihymenial zone of excipulum thin, a few-layered hyaline to brownish "textura porrecta"; excipulum not surpassing hymenium; paraphyses apically slightly enlarged and brownish; ascus tips J+; spores subcylindrical to subclavate and mostly slightly curved, eventually 3-septate and brownish. According to KURKELA (1974) *E. vaccinii* is associated with a snow-blight on *Vaccinium vitis-idaea* L. and *Arctostaphylos uva-ursi* (L.) SPRENG. and is most probably also the cause of the blight.

Judged by the descriptions two recent additions to *Europolella*, viz. *E. britannica* GREENHALGH & MORGAN-JONES (MORGAN-JONES 1972), on *Prunus laurocerasus* L., and *E. arundinariae* (CASH) DENNIS (1975), on *Arundinaria sp.*, must be misplaced but no better position can be suggested for them. Furthermore, description and drawings of *E. celata* GRADDON (1977), on *Carex flacca* SCHREB., are strongly suggestive of *Naevia olivacea* MOUT., a species which in my opinion belongs to a still undescribed genus in the vicinity of *Naeviella*.

Besides *N. paradoxa*, DÉFAGO (l. c.) transferred to *Eupropolella* a closely allied fungus on *Carex curvula*, originally described as *Phragmonaevia paradoxa* var. *volkartiana* REHM (1904) and then raised to specific rank by v. HÖHNEL (1918a, as *Phaeophacidium*). She added two fungi on other hosts and included them in the latter species, viz. one on *Luzula lutea* and *L. silvestris*, the other on *Eriophorum brachyantherum*. They agree all with the descriptions of *Eupropolella* in a number of characters but deviate in others.

N. paradoxa and its allies represent clearly a distinct line of evolution and a genus of its own, which due to the present Code of Botanical Nomenclature inevitably leads to the resurrection of the genus *Naeviella* (REHM) CLEMENTS (1909; cp. HEIN, 1976), in spite of the fact that they do not possess 1-septate spores as stated in the generic diagnosis.

By the way it should be noted that there is a fungus on *Luzula*, viz. *Naevia paradoxoides* REHM (1888: 143), that its author at first considered to be so close to *N. paradoxa* that he described it as f. *luzulae* REHM (1885). However, DÉFAGO (1968 as "*paraxoides*") showed that it is widely different and certainly of another affinity. The proposed transfer to *Drepanopeziza* is to be sure unjustified, but no satisfactory alternative can be given here.

Remarks on ascospore symmetry

Before *Eupropolella* and *Naeviella* are compared it seems useful to say a few words about symmetry conditions in ascospores. So far most authors (except e. g. KORF, 1973 and DENNIS, 1978) have paid little attention to this aspect.

Ascospores are mostly straight, circular in cross-section, possess consequently an indefinite number of planes of symmetry in relation to their longitudinal axis and are then termed radial symmetrical. If they instead are flattened with elliptical cross-section, they get only two longitudinal planes of symmetry, at right angles to each other and one passing through the major axis of the ellipse, the other through the minor axis. In accordance with common usage in zoology such spores will here be designated as biradial symmetrical. The term bilateral symmetrical will be restricted to inequilateral or curved spores that possess a single plane of symmetry. If e. g. the curvature is spiralling, such spores become asymmetrical.

Conspicuously flattened or curved spores have of course been duly registered in specific and generic descriptions, but more general conclusions have only rarely been drawn from such observations. An exception is the so-called allantoid spore, which not only characterizes one of the main groups (Allantosporae) in SACCARDO's sporological system but even led v. HÖHNEL (1918b) to establish the family Allantosphaeriaceae among the true (or unitunicate) Pyrenomycetes. This action has certainly not enhanced the trust in such characters by critical students, for "allantospory" has obviously evolved independently and repeatedly in different groups (cp. e. g. MUNK, 1953).

Nevertheless, I have become convinced that the change from radial symmetry to biradial or bilateral means a step of high taxonomic and phylogenetic importance, a step from a more unspecialized and "primitive" stage to a more specialized and "advanced". But this character must of course — like all other characters — be used with utmost caution and its value judged from case to case.

The biradial-symmetrical spores of Boliniaceae (i. e. *Camarops* KARST. s. lat.) in contrast to the bilateral-symmetrical spores of Xylariaceae and Diatrypaceae became thus one of the fundamental differences between Boliniaceae and the other two families (NANNFELDT, 1972). In Xylariaceae, the sporal bilaterality includes also a special structure, the longitudinal germ slit, with the special complication that in several species the slit is not exactly longitudinal but oblique or even spiralling (cp. e. g. ROGERS, 1979), which renders the spore asymmetrical.

Another sporal feature that should be given due attention in future is heteropolarity (= bipolar asymmetry) in relation to the longitudinal axis, i. e. a morphological difference between the two ends of the spore, viz. the "upper" end (directed towards the ascus tip), and the "lower" end (directed towards the base). INGOLD (1951) observed that in many species the upper end is relatively broad and blunt, the lower end narrow and pointed and that — as it seems — the reverse never occurs. His explanation is that heteropolar spores (with the maximum width towards the upper end) will get greater initial velocity and consequently greater range when shot through a narrow, strongly stretched pore. But when the pore is wide or the spore itself very small, the advantage would be inconsiderable, if any. In fact, all Operculate Discomycetes and all "Allantosporae" have bipolar-symmetrical spores.

Very little is known, indeed, how the "ascus gun" actually works in the various groups. ROGERS (1979) has recently given convincing reasons that the apical ring-shaped thickenings (characteristic of the asci in several groups) cannot act as sphincters through which the spores have to pass. Leaving this and all teleological speculations aside, we note nonetheless that heteropolar spores (almost ?) invariably are orientated in one way only.

Sporal heteropolarity can also take various other expressions e. g. by germ-pores or eccentric septation. Also in this respect Boliniaceae, Diatrypaceae, and Xylariaceae differ from each other. Besides a slight difference in shape between the two halves, *Camarops*-spores are provided with a minute germ-pore in one (mostly the lower) end, whereas the small and flattened "allantoid" spores of the Diatrypaceae show no sign of heteropolarity. It is well known that a few species of the Xylariaceae possess spores with a small cellular basal appendix and that non-cellular ("secondary") appendices may occur in either or both ends. In an increasing number of cases, immature spores have been found to possess cellular appendices that completely disappear before maturity. This and other phenomena are strongly indicative "that the ancestors of the Xylariaceae had two-celled ascospores" (ROGERS, 1979) and showed sporal heteropolarity.

Among the true (= unitunicate) Pyrenomycetes, sporal heteropolarity seems to be widespread. Thus, in the Sordariales or Sordariaceae s. lat. (i. e. incl. Lasiosphaeriaceae) with their extremely diversified spores (cp. e. g. MUNK, 1953, 1957; CARROLL & MUNK, 1964; LUNDQVIST, 1972) only few (if any) species are devoid of any trace of heteropolarity. In the Diaporthaceae much less signs of heteropolarity can be traced but a number of species have spores with a single septum near the lower end.

In the bitunicate Pyrenomycetes (= Loculoascomycetes) straight (or almost straight) heteropolar and radial-symmetrical spores seem to predominate. An exception is e. g. *Clathrospora* RABENH., a good segregate from the large and well-known genus *Pleospora* RABENH., deviating by flattened and often distinctly inequilateral spores (cp. e. g. O. ERIKSSON, 1967).

In the Laboulbeniomycetes the spores are very uniform: hyaline and more or less fusiform with a single eccentric septum and a sheath that is noticeably more thickened at the lower end (BENJAMIN, 1973), thus decidedly heteropolar. Sometimes the spores seem to be inequilateral or even slightly curved.

As well known, Discomycete spores show much less variation than Pyrenomycete spores, and especially small is the variation within the Operculates. Their spores are always unicellular (though plurinucleate in some groups), globose to broadly elongate and not heteropolar (KORF, 1973). As a rule they are radial-symmetrical except in the Sarcoscyphaceae s. lat. (i. e. incl. Sarcosomataceae), where they have a strong tendency to inequilaterality. The monotypical genus *Selenaspora* HEIM & LEGAL with "lunate" spores should thus perhaps be transferred to Sarcoscyphaceae (cp. KORF, 1973). On the contrary, the lack of sporal inequilaterality in the monotypical(?) *Nannfeldtiella* ECKBLAD (1968) is in my opinion an additional hint that it is misplaced in the Sarcoscyphaceae. My first impression of the then undescribed fungus was that of a close ally to *Discina* FR., and KORF (1973) came to the same conclusion. HARMAJA (1979) found it definitely out of place in the Sarcoscyphaceae. I am very sceptical to his proposal to refer *Nannfeldtiella* to the (heterogeneous) Pyronemataceae and to incorporate it into the so far monotypical genus *Pseudombrophila* BOUD.

The spores of the Inoperculates are considerably more varied. In contrast to those of the Pyrenomycetes they have only rarely thick and/or pigmented walls. Lateral germ-pores rendering the spores bilateral-symmetrical are only exceptionally found (see below). terminal pores and germ-slits not at all. The spores range in shape from globular to acicular and are mostly — at least approximately and apparently — radial-symmetrical. No distinctly flattened spores are known, but inequilateral to slightly curved and thus bilateral-symmetrical ones are not rare. Heteropolar spores with the upper end thicker than the lower and/or eccentric septation are rather frequent and in some groups even the rule. In different natural groups the frequency of heteropolarity and of deviations from radial symmetry is significantly different as demonstrated in the following examples:

1. Most (perhaps all) true members of the Rhytismataceae [sensu KORF, 1973 (= Hypodermataceae)] have spores with a thicker upper end and — at least morphologically — radial symmetry. ALLITT (1979) has recently shown that in several long- and narrow-spored species the spores (immediately after shedding) have a strong tendency not only to curve but even to coil up into a plane spiral of about two turns. It is open to speculation whether this plane is innate in the spore or depends upon external conditions at the moment of discharge.

2. In the Sclerotiniaceae (sensu KORF, 1973) the rather broad spores show only slight signs of heteropolarity; they are mostly radial-symmetrical but in some species consistently inequilateral.

3. One of the discriminating features of *Encoelia* (FR.) KARST. is the curved, often almost "allantoid" spores.

4. In *Lachnellula* KARST. em. DENNIS [with spores ranging in size from minute (2—4 × 1.5—4 μm) to large (25 × 8 or 80 × 1.5 μm), and in shape from globular to acicular] there seems to be no signs of heteropolarity nor of deviations from radial symmetry.

Taxonomy

Eupropolella vs. Naeviella

The anatomy of the excipulum — generally of paramount importance in Discomycete taxonomy — leaves us often in the lurch, especially in taxa with minute, immersed and erumpent apothecia. The simple structure of their thin excipulum seems to be a sign rather of reduction than of primitiveness as supposed by DÉFAGO for *Eupropolella*. Moreover, the pressure against the tissue of the host may distort the excipulum and make its interpretation difficult. A number of needle-inhabiting species, marked by small, immersed and erumpent apothecia "of exceptionally simple structure, ... with scarcely any marginal excipular tissue", were combined by KORF (1962) into the new family Hemiphacidiaceae. In my opinion they should consequently be interpreted as extremely reduced members of Dermateaceae (sensu meo) and their closest relatives sought among the Mollisioideae and the Naevioideae. In such cases we are left to rely upon characters from hymenium, paraphyses, asci, and spores and to study them more carefully than before. Most important taxonomic results can thus be expected from the precise studies of the paraphyses in the Dermateaceae by HEIN (1981, and pers. comm.).

The subcuticular apothecia of *Eupropolella* form at their base a central cushion penetrating deeper into the host (MÜLLER et al., 1958, fig. 6) and are surrounded by a fringe of fungal tissues between cuticle and epidermis, which sometimes even connects adjacent fruitbodies. The apothecia emerge by splitting the cuticle into triangular flaps.

The intra- and subepidermal apothecia of *Naeviella* are very slow in development but emerge much prior to the maturation of the first spores. In *Juncus trifidus* and *Carex curvula* they mostly become exposed through three or four radiating slits producing triangular flaps, rarely through a single longitudinal slit in the cover. In *Luzula* and *Eriophorum* a circular or elliptical, laterally and broadly hinged lid is formed in about the same way as in *Hysteropezizella diminuens* (KARST.) NANNF. The development of the hymenium is successive; asci in various stages occur side by side, and areas with young and full-grown paraphyses can be found in one and the same fruitbody (Pl. 3, fig. D).

Neither in *Eupropolella* nor in *Naeviella* does the excipulum surpass the hymenium, and in both the perihymenial part of the excipulum is thin and soft. In *Eupropolella* the elongated external cells have almost hyaline walls. In *Naeviella*, where the perihymenial excipulum is better developed, the cell-walls are more or less brown.

According to DÉFAGO, the paraphyses of *Eupropolella* are: "segmentées, dichotomes, s'élargissent dans la partie apicale, en clavules souvent brunes". MÜLLER et al. (1958, fig. 4n) depict those of *E. arctostaphyli* with erect straight tips about as in *N. paradoxa*. Older descriptions are more realistic though incorrect in one respect, e. g.: "Paraphyses ... apice clavula fuscescente, cuneato-incrassata aut non determinata instructae, crassit. 3—5 mmm." (KARSTEN, 1871: *Trochila phacidioides* "(FR.)" KARST. = *E. vaccinii*), and "Paraphysen fädig, oben gabelig und unregelmässig, — 5 μ breit, braungrün" (REHM 1888: *Sphaeropezia vaccinii*). In fact, the tips in *E. vaccinii* (Pl. 3, fig. B; cp. also MORGAN-JONES, 1972, fig. 1) are throughout thin- and hyaline-walled and for the uppermost ca. 20 μm irregularly enlarged, torulose, crooked and/or often branched with divergent branchlets. The interlacing tips are embedded in a brownish slime.

As already noted, the paraphyses of *N. paradoxa* and its congeners (Pl. 2, figs. C—E; pl. 3, fig. D) are very peculiar. They are mostly simple, i. e. only rarely dichotomously divided into slightly divergent branchlets, relatively stout from the beginning, cylindrical and very slightly widened towards the tips, but for the uppermost 15—20 μm, where they become distinctly clavate (maximum breadth ca. 6 μm) with pyriform to subglobular tips. The clavula, often delimited by a distinct septum, becomes enclosed in a 1—2 μm thick cap of brownish rather stiff slime, which eventually is covered by an opaque brown granular crust. In crush mounts this cap may break off by pressure, revealing the still hyaline and hardly thickened cell wall. It can then be seen that the clavula is filled by dense homogeneous contents. The paraphyses surpass the asci by ca. 15 μm and form a distinct dark "epithecium".

In *Eupropolella* the ascus-wall is rather thin and shows an apical apparatus in the shape of a minute perforated plate (ca. 2×0.5 μm), which in iodine stains intensely blackish blue.

In *Naeviella* the asci have firm, relatively thick and strongly refractive walls without any discernible apical apparatus and are inert to iodine, even after treatment with KOH.

The spores of *Eupropolella* (Pl. 3, fig. A) are more or less curved, often suballantoid, show very slight heteropolarity, and become eventually distinctly 3-septate, brownish and rough. The colour is, however, not due to pigmentation of the wall but to a crust covering the hyaline and rather thin wall of the spores. This crust, which seems to be formed by confluent granules, appears already when the spores are still unseptate and is first visible on the (more) convex side and remains thickest and darkest there. Within the Inoperculates only two similar cases are known to me, viz. *Micropeziza verrucosa* (MÜLL.) NANNF. and "*Niptera*" *arctica* REHM (NANNFELDT 1976b), but otherwise these taxa do not resemble *Eupropolella*.

The spores of *Naeviella* are straight and smooth (granular coat absent), show no signs of heteropolarity and get distinctly pigmented walls with age. Immature spores have one large drop or several droplets towards each end and an equatorial band of dense homogeneous cytoplasm. This band may be rather narrow and is then easily mistaken for a septum. REHM (1888) described the spores as eventually 2-celled and MINKS (1882) as sometimes even 4-celled. REHM had no other stains than iodine to rely upon. This is the reason why he "eine Spore als septiert auffasste, sobald der Zellinhalt in Portionen geteilt war, auch wenn sich keine deutliche Wand entwickelt hatte" (NANNFELDT, 1932). I have never seen a trace of a septum either in sections stained by Iron Haematoxyline plus Light Green or in crush mounts in Lactic Blue.

In general, pigmented spore walls are rare within the non-lichenized Inoperculate Discomycetes, but common within the true (= unitunicate) Pyrenomycetes and the Bitunicates. The dark-walled Pyrenomycete spores are often provided with germ-pores (or slits), whose number, shape and location nowadays play an important rôle in taxonomy.

As far as I am aware, the presence of germ-pores in Discomycetes was first observed by DÉFAGO on *N. paradoxa* but fully established by L. & K. HOLM (1976) on *Naevia monilispora* STARB., type species of the genus *Phaeonaevia*.

In *Naeviella* the location of the minute lateral germ-pore (ca. 0.5 µm in diam.; pl. 1, figs. C—E) varies from (mostly) subequatorial to subterminal (seen only once!). The pore is more differentiated than in *Phaeonaevia* as it tops a distinct (ca. 1 µm high and at the base ca. 2 µm broad) conical protuberance. Both protuberance and pore apparently develop rather late.

The agglutination of mature spores within the ascus mentioned by DÉFAGO (1968) is certainly not normal but due to disturbed development (drought?).

The two recognized species in *Naeviella* differ in the size and shape of the spores, which are oblong to subfusiform, 10—12(13)× 3.5—4.5 µm in *N. paradoxa*, and ellipsoid, 7—9(10)×3—4 µm in *N. volkartiana*. Spores of specimens inhabiting *Eriophorum* and *Luzula* can hardly be distinguished from those of *N. volkartiana*. Von HÖHNEL (1918a) stated that the spores of *N. volkartiana* become "zuletzt dunkelviolett" but this cannot be confirmed for when observed in water, KOH and lactophenol (with and without iodine) they appear dirty greyish brown at the most (NANNFELDT, 1932).

By the way it should be emphasized that no germ-pore is found in the intensely brown spore wall of the type (and only?) material (S!) of *Phaeophacidium escalloniae* P. HENN. & LINDAU (the generic type), whose spore colour is also reported to be violet by v. HÖHNEL.

The above comparisons inevitably lead to the conclusion that *Eupropolella* and *Naeviella* in fact belong to widely different evolutionary lines. In *Eupropolella* the shape of the paraphyses and the curved, 3-septate spores covered by a granular crust are most unusual features. I cannot support the relationship to *Durella* TUL. (= *Xylogramma* WALLR.) as suggested by MÜLLER et al. (1958) and to some extent endorsed by DENNIS (1975) nor to *Laetinaevia* NANNF. as intimated by KORF (1973) or to any other group whatsoever.

The germ-pore in spores of *Naeviella* is certainly a most unusual character but otherwise the genus does not deviate from the pattern of variation exhibited by the Mollisioideae (sensu meo), especially the *Hysteropezizella* complex. According to the results presented by HEIN (1981) it seems possible to interpret the paraphyses of *Naeviella* as the result of an excessive production of "Paraphysenauflagerungen" characteristic of *Hysteropezizella* s. l. (HEIN, in litt., 30. IX. 1981).

The question remains open whether the germ-pore indicates some affinity to *Phaeonaevia* and, more generally, whether the presence of germ-pores within the Inoperculate Discomycetes may be of indicative value in phylogenetical speculations. The discovery of a third case strongly points in this direction, as this case definitely falls within the Mollisioideae too.

The unexpected new situation is the result of an examination of *Sarcotrochila alpina* (FUCKEL) v. HÖHNEL, contributed by Dr. B. HEIN, who generously gave permission to make use of his observations. At a certain stage of development the slightly pigmented wall of the initially fusiform spores becomes firmer. Later, the spores become plumper, especially in the upper half, and in most spores a (sub)median septum is formed. Further steps in the development seem to take place outside the ascus. As a rule the lower cell changes little only, but I have seen at least one with a median septum. The upper cells enlarges a little, its wall becomes markedly thicker and darker, and a lateral protuberance grows out, which resembles that of *N. paradoxa* in size and shape or is slightly more tubular. Only single spores with uniformly thicker and darker walls have been observed. As far as I am aware, such 2-celled spores are unique in the Discomycetes, but in some true (= unitunicate) Pyrenomycetes, e. g. Xylariaceae (cp. above) and Sordariaceae s. l. parallels may be found.

Paraphyses and margo of the apothecia of *S. alpina* agree rather well with those of *Phaeonaevia*, and this makes it highly probable that at least part of the Hemiphacidiaceae [to which *Sarcotrochila* is referred by KORF (1962, 1973)] had better be regarded as extremely reduced members of the Dermateaceae most closely related to the Mollisioideae and the Naevioideae.

Most Mollisioideae possess iodine-positive ascus-plugs but there are also some members with iodine-negative reaction, and in several taxa the whole apical apparatus is strongly reduced (NANNFELDT 1976a; 1976b), e. g. *Mollisia ligni* (DESM.) KARST., *M. ericae* ROLL. (= *Belonopsis ericae* AEBI, 1972) and a group of closely allied species that are generally referred to *Pyrenopeziza* FUCK. (NANNFELDT, 1932; HÜTTER, 1958).

Negative iodine reaction serves as a cardinal character in *Neotapesia* MÜLLER & HÜTTER (1963; MÜLLER, 1977; with 4 spp.) and in *Cashiella* PETR. (MÜLLER, 1977; with 2 spp.). On the other hand in *Scutomollisia* NANNFELDT (1976b) both two iodine-negative and two iodine-positive taxa occur in the same otherwise uniform genus.

The genus *Naeviella* as delimited here is consistently iodine-negative. In a forthcoming paper I intend to show that about a dozen species — amongst them *Propolis holoschoeni* de NOT. (= *Hysterostegiella holoschoeni* DÉFAGO), *Mollisia advena* KARST. and *Naevia olivacea* MOUT. — inhabiting gramineous, cyperaceous and juncaceous host plants, should be combined into another natural genus, J⁻ but devoid of germ-pores.

Generic limits of Naeviella

Naeviella (REHM) CLEM., Gen. fung., 63. 1909

Bas.: *Phragmonaevia* (sect.) II. *Naeviella* REHM in Rabenh., Krypt.-Fl., ed. 2, 1: 3: 164 (1888) p. p.

Typus (generis): *Naevia paradoxa* REHM (illegitimately exchanged for *Phragmonaevia fuckelii* REHM by CLEM. & SHEAR, Gen. fung., 311. 1931).

Mollisioideae. — Apothecia small (up to 0.3 mm in diam.), dark, immersed and erumpent, slowly growing. Excipulum of a few, rather indistinct layers of ± compressed, brown-walled cell-rows (as in *Hysteropezizella*) and with free enlarged tips, ± simulating paraphysal heads. Hymenium developing successively, with young and mature elements intermingled, eventually flat, not or only slightly surpassed by the excipulum. Paraphyses stout, mostly unbranched, terminating in a pyriform to broadly clavate or even subglobular head, enclosed in a thick cap of rather stiff slime, eventually covered by an opaque brown granular crust, surpassing the asci and forming a distinct dark "epithecium". Asci clavate with rather thick, light-refractive walls and rounded tips, J⁻, no visible apical apparatus. Spores broadly ellipsoid to subfusiform, with smooth, hyaline, ultimately brownish wall, unseptate, eventually with a lateral, broadly conical protuberance topped by a distinct minute germ-pore. No conidial state known. Habitat: dead leaves and culms of Cyperaceae and Juncaceae.

The distributions of all members are evidently restricted to montane to northern climates. The material available is still insufficient for infrageneric taxonomy. Best know is *N. paradoxa* (14 collections examined, all on *Juncus trifidus* s. l.). As mentioned above it is distinguished from the three other taxa by distinctly larger spores. Of *N. volkartiana* only the type collection (on *Carex curvula*) was studied (cf. v. Höhnel, 1918a). Défago (1968) refers also three specimens on *Eriophorum brachyantherum*, *Luzula lutea* and *L. silvatica* to the same species, because she found them to agree in hymenial characters. After examining the authentic collections I can not follow her, for the collections disagree in other characters, e. g. by apothecia emerging through a rounded, hinged lid, in the *Luzula* species sometimes through a common elongated lid. Median sections show the apothecia of the *Eriophorum* fungus to be conical and penetrating deep into the host, whereas those of the *Luzula* fungi are flat-bottomed and mainly intraepidermal. In the latter, fungal tissues are also found on the lid, both between cuticle and epidermis and covering the inner side of the lid. As *N. paradoxa* obviously has a very narrow host spectrum, the same can be expected from the fungi on *Eriophorum* and *Luzula*, which might lead to two more taxa.

Material examined

1. *Naeviella paradoxa* (Rehm) Clem., Gen. fung. 174. 1909.

Bas.: *Naevia paradoxa* Rehm, Ascom. n. 419 (1878; n. nud.), Ber. Nat. Ges. Augsburg 26: 102. 1881.

Syn.: *Phragmonaevia paradoxa* Rehm in Rabenh., Krypt.- Fl., ed. 2, 1 (3): 165. 1888.

Diplonaevia paradoxa Sacc., Syll. fung. 8: 666 1889.

Hysteropezizella paradoxa Nannf., N. Acta Reg. Soc. Sci. Upsal. 4: 8: 2: 122 1932.

Eupropolella paradoxa Défago, Sydowia 21: 68. ("1967") 1968.

Typus: *Juncus hostii*: Rehm, Ascom. n. 419 (holotypus; S!).

Matrix: *Juncus trifidus* L. s. lat. (i. e. incl. *J. hostii* Tausch = *J. monanthos* Jacq.). — A report on *J. filiformis* L. (Défago, 1968; Müller, 1977) is due to misidentification of the host.

Exsiccata: Rehm, Ascom. n. 419 (typus).

Illustrations: Pl. 1, fig. A; pl. 2 figs. D, E; pl. 3, figs. C, D. — Défago (1968: fig. 26d).

Distribution:

Alps: Austria: Tirol, Pitztal, Taschach-Gletscher, Rehm; typus; H!, S!, UPS!; Rehm (1912: 151). — Switzerland: Graubünden: 3 finds (GZU!, UPS!, ZT!); Wallis, Aletschwald: 3 finds (ZT!; Défago, 1968; Müller, 1977). — Italy: Trentino Alto Adige, Giogo di Stelvio (= Stilfser Joch) (Rehm, S!).

Scandes: Finland: Lapponia enontekiensis, Kilpisjärvi, Siilaslahti, ca. 500 m s. m., L. & H. Roivainen (H, ZT!; Défago, l. c.). — Norway: Sør-Trøndelag, Oppdal, Mt. N. Falkfangarhøa, ca. 1100 m, K. & L. Holm, 651e (UPS!). — Sweden: Härjedalen, Tännäs, Mt. Hamrafjället, ca. 1000 m, Nannfeldt, 4798c (UPS!); Lule Lappmark, Kvikkjokk, Sarek National Park, Mt. Skaitetjåkko, VESTERGREN (S!, UPS!); Torne Lappmark, Kiruna, Mt. Nissontjårro, ca. 800 m, NANNFELDT, 992a (UPS!).

Arctic: East-Greenland: (Griffenfeld Isl. (= Ũmmánaq), "Umanak Boplads", 68°55′ N, 41°34′ W (cp. SEIDENFADEN (1933), EBERLIN (C!; ROSTRUP, 1888: as *Trochila juncicola*). — This locality should not be confused with the more widely known Umanak in West-Greenland.

2. *Naeviella volkartiana* (REHM) NANNFELDT, comb. nov.

Bas.: *Phragmonaevia paradoxa* (REHM) REHM var. *volkartiana* REHM, Hedwigia 43: 31. 1904.

Syn.: *Phragmonaevia caricum* (AUERSW.) REHM var. *volkartiana* REHM, Ber. Bayr. Bot. Ges. 13: 151. 1912.

Phaeophacidium volkartianum v. HÖHNEL, Sitzb. Akad. Wiss. Wien, Math.-nat. Kl. I: 127: 552. 1918.

Hysteropezizella volkartiana NANNF., N. Acta Reg. Soc. Sci. Upsal. 4: 8: 2: 122. 1932.

Eupropolella volkartiana DÉFAGO, Sydowia 21: 70. 1968.

Typus: *Carex curvula*; REHM, Ascom. n. 1533 (holotypus, S!).

Matrix: *Carex curvula* ALL.

Exsiccata: Jaap, F. sel. 156 (together with *Clathrospora elynae* RABENH., fide v. HÖHNEL, not in the copy in S!). — REHM, Ascom. 1533 (typus).

Illustrations: Pl. 1, figs. B, D, E. — DÉFAGO (1968: figs. 26a—c).

Distribution:

Alps: Switzerland: Graubünden, Piz d'Aela, Lajets, ca. 2600 m, VOLKART (typus; S!); Uri—Wallis, Furkapasshöhe, ca. 2450 m, JAAP (F. sel. 156, fide v. HÖHNEL).

3. *Naeviella* taxon. sp. 1.

Matrix: *Eriophorum brachyantherum* TRAUTV. & MEY. (= *E. callitrix* sensu auctt. scand.).

Illustration: DÉFAGO (1968: fig. 27, left half).

Specimen seen:

Scandinavia: Finland: Lapponia enontekiensis, Konkamaieno, Konttaniva, ROIVAINEN (ZT!; DÉFAGO l. c., as *Eupropolella volkartiana*).

4. *Naeviella* taxon. sp. 2.

Matrices: *Luzula lutea* (ALL.) LAM. & DC. and *L. silvatica* (HUDS.) GAUD. (= *L. sieberi* TAUSCH).

Illustrations: Pl. 2, figs. A—C. — DÉFAGO (1968: fig. 27, right half).

Specimen seen:

Alps: Switzerland: Wallis, Aletschwaldreservat, *L. lutea* and *L. silvatica* (one find each), MÜLLER (ZT!; DÉFAGO, 1968; MÜLLER, 1977 (as *Eupropolella volkartiana*).

Acknowledgements

My sincere thanks are due to the directors and staffs of C, GZU, H, O, S, and ZT for loans of relevant specimens and to numerous collegues for instructive and illuminating discussion and aid in various ways. Among them I am especially indebted to Drs B. Hein (Berlin), L. Holm, N. Lundqvist, and R. Moberg (Uppsala).

References

Aebi, B. (1972). Untersuchungen über Discomyceten aus der Gruppe *Tapesia-Trichobelonium*. — Nova Hedwigia 23: 49—112.

Allitt, U. (1979). Coiled ascospores in the Hypodermataceae. — Trans. Brit. Myc. Soc. 72: 147—151.

Benjamin, R. K. (1973). Laboulbeniomycetes. — In: Ainsworth, G. C. et al., The Fungi. An advanced treatise 4A: 223—246. New York & London.

Carroll, G. C. & Munk, A. (1964). Studies on lignicolous Sordariaceae. — Mycologia 56: 77—98.

Clements, F. E. (1909). The genera of fungi. — Minneapolis.

— & Shear, C. L. (1931). The genera of fungi. — New York.

Défago, G. (1968). Les *Hysteropezizella* v. Höhnel et leurs formes voisines (Ascomycètes). — Sydowia 21: 1—76 ("1967").

Dennis, R. W. G. (1975). New or interesting British Microfungi, 3. — Kew Bull. 30: 345—365.

— (1978). British Ascomycetes. Revised and enlarged edition. — (J. Cramer) Vaduz.

Eckblad, F.-E. (1968). The genera of the Operculate Discomycetes. A re-evaluation of their taxonomy, phylogeny and nomenclature. — Nytt Mag. Bot. 15: 1—191.

Eriksson, B. (1970). On Ascomycetes on Diapensiales and Ericales in Fennoscandia 1. Discomycetes. — Symb. Bot. Upsalienses 19: 4.

Eriksson, O. (1967). On graminicolous Pyrenomycetes from Fennoscandia 1. Dictyosporous species. — Ark. f. Bot. 2: 6: 7: 339—379.

Graddon, W. D. (1977). Some new Discomycetes on Cyperaceae. — Kew Bull. 31: 511—516.

Harmaja, H. (1979). Studies on vernal species of *Gyromitra* and *Pseudombrophila* (syn. *Nannfeldtiella*). — Ann. Bot. Fenn. 16: 159—162.

Hein, B. (1976). Revision der Gattung *Laetinaevia* Nannf. (Ascomycetes) und Neuordnung der Naevioideae. — Willdenowia Beih. 9.

— (1981). Zum Wert von Paraphysenauflagerungen für die Taxonomie des *Hysteropezizella*-Komplexes (Dermateaceae, Mollisioideae) unter Berücksichtigung von rasterelektronenmikroskopischen Untersuchungen. — Nova Hedwigia 34: 449—474.

Höhnel, F. v. (1917). Mycologische Fragmente. — Ann. Myc. 15: 293—382.

— (1918a). Fragmente zur Mykologie, 22. Mitteilung, Nr. 1092 bis 1153. — Sitz.-ber. Akad. Wiss. Wien, Math.-nat. Kl. I: 127: 549—634.

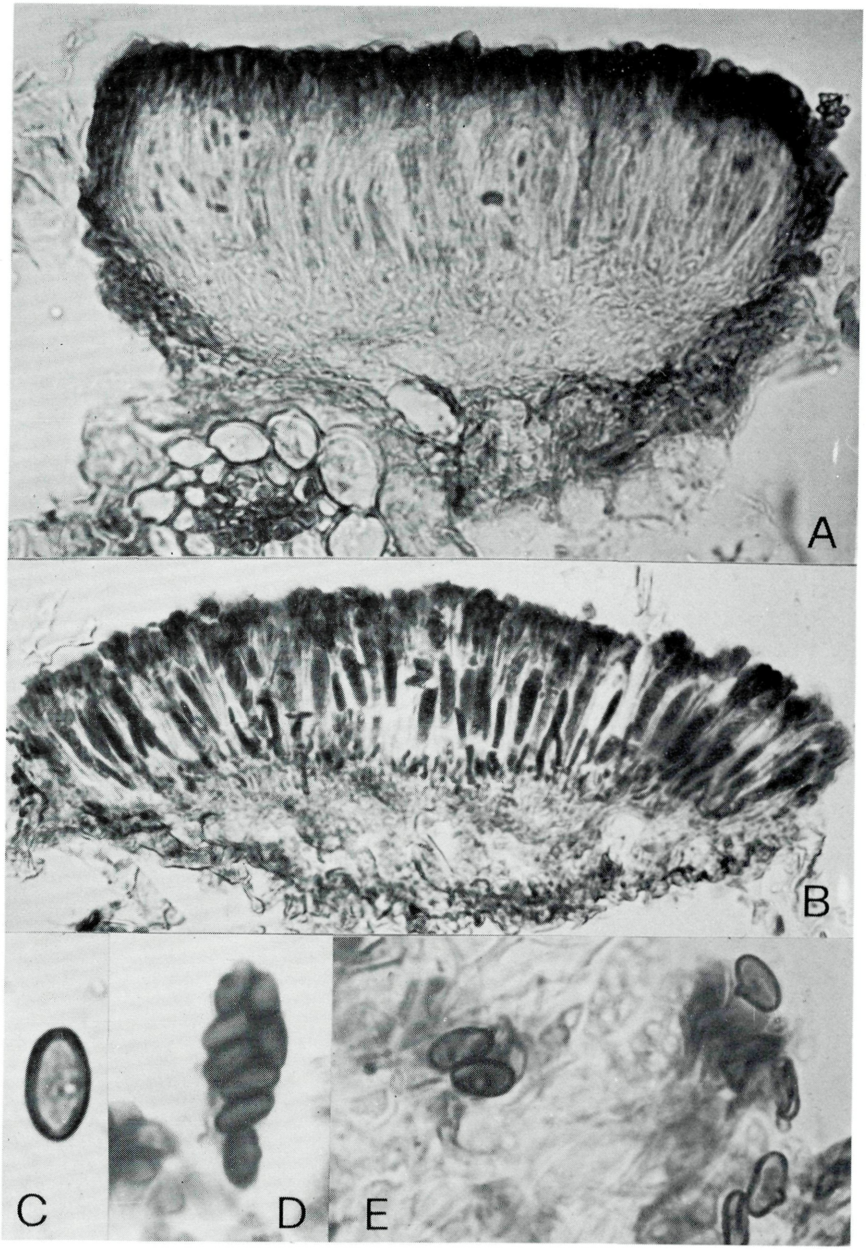
— (1918b). Mycologische Fragmente. — Ann. Myc. 16: 35—174.

Holm, L. & K. (1976). New or noteworthy fungi on *Rubus chamaemorus*. — Kew Bull. 31: 567—571.

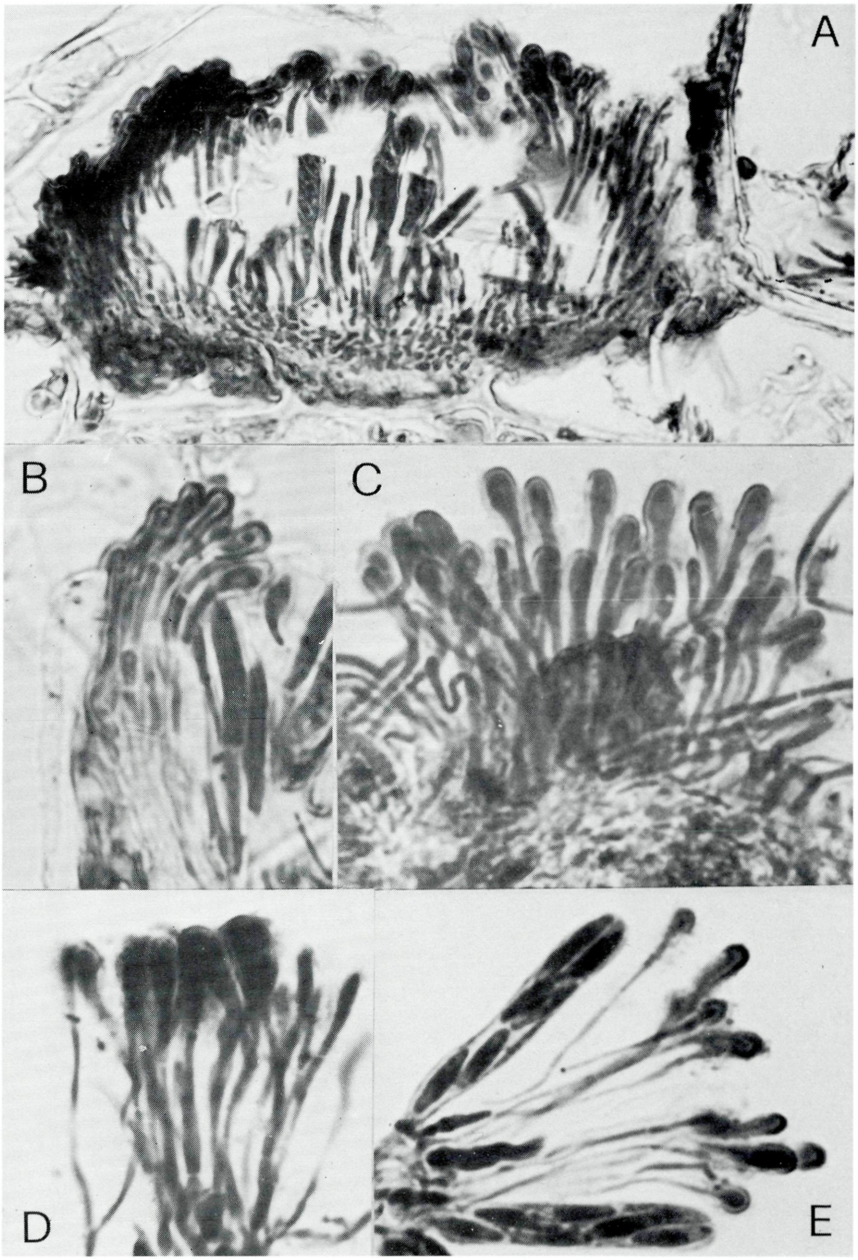
Hütter, R. (1958). Untersuchungen über die Gattung *Pyrenopeziza* Fuck. — Phytopath. Zeitschr. 33: 1—54.

Ingold, C. T. (1951). Ascospore form. — Trans. Brit. Myc. Soc. 37: 19—21.

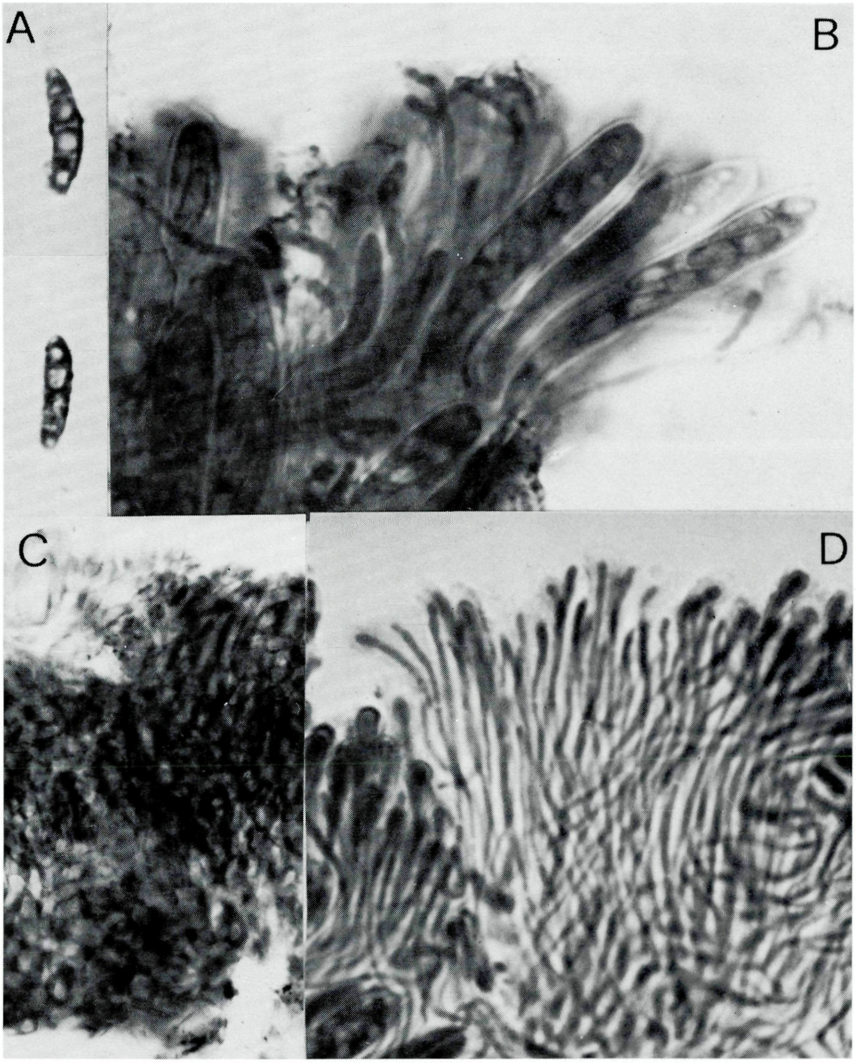
Karsten, P. A. (1871). Mycologia fennica. Pars prima. Discomycetes. — Bidr. känned. Finlands nat. folk 19.



Pl. 1. Fig. A. *Naeviella paradoxa* (typus): Apothecium, median section, ca. 625×. — Figs. B—E. *N. volkartiana* (typus): — B. Apothecium, median section, ca. 400×. — C. Spore, ca. 1750×. — D, E. Asci and spores, ca. 1000×



Pl. 2. Figs. A—C. *Naeviella* taxon. sp. 2 (*Luzula lutea*): A. Apothecium, median section, ca. 625×. — B. Margin, ca. 1000×. — C. Paraphyses, ca. 1000×. — Figs. D, E. *N. paradoxa* (VESTERGREN): Paraphyses and asci, ca. 1000×



Pl. 3. Figs. A, B. *Eupropolella vaccinii* (NANNFELDT, 20701): A. Two spores, ca. 1000×. — B. Hymenium, ca. 1000×. — Figs. C, D. *Naeviella paradoxa*: C. (VESTERGREN) Excipulum, ca. 625×. — D. (ROIVAINEN) Hymenium with full-grown and young paraphyses, ca. 1000×

KORF, R. P. (1962). A synopsis of the Hemiphacidiaceae, a family of the Helotiales (Discomycetes) causing needle-blights of conifers. — Mycologia 54: 12—33.

— (1973). Discomycetes and Tuberales. — In: AINSWORTH, C. G. et al., The Fungi. An advanced treatise 4A: 249—319. New York & London.

KURKELA, T. (1974). The association of *Eupropolella vaccinii* (REHM) v. HÖHN. and winter mortality of some ericaceous plants. — Karstenia 14: 97—101.

LUNDQVIST, N. (1972). Nordic Sordariaceae s. lat. — Symb. Bot. Upsalienses 20: 1.

MINKS, A. (1882). Symbolae licheno-mycologicae 2. — (Th. Fischer) Kassel und Berlin.

MORGAN-JONES, G. (1972). A new species of *Eupropolella* v. HÖHNEL. — Canadian J. Bot. 50: 1073—1076.

MÜLLER, E. (1957). Die Gattung *Eupropolella* v. HÖHN. — Sydowia 11: 130—132.

— (1977). Zur Pilzflora des Aletschwaldreservats (Kt. Wallis, Schweiz). — Beitr. Krypt.-Fl. Schweiz. 15: 1.

— et al. (1958). Über einige bemerkenswerte Discomyceten aus den Alpen. — Sydowia 12: 404—430.

— & HÜTTER, R. (1963). Eine neue Discomycetengattung aus den Alpen, *Neotapesia* nov. gen. — Ber. Schweizer. Bot. Ges. 73: 325—331.

MUNK, A., (1953). The system of the Pyrenomycetes ... — Dansk Bot. Ark. 15: 2.

— (1957). Danish Pyrenomycetes ... — Ibid. 17: 1.

NANNFELDT, J. A. (1932). Studien über die Morphologie und Systematik der nicht-lichenisierten Inoperculaten Discomyceten. — N. Acta Reg. Soc. Sci. Upsaliensis 4: 8: 2.

— (1972). *Camarops* KARST. (Sphaeriales-Boliniaceae) with special regard to its European species. — Svensk Bot. Tidskr. 66: 335—376.

— (1976a). Iodine reactions in ascus plugs and their taxonomic significance. — Trans. Brit. Myc. Soc. 67: 283—287.

— (1976b). *Micropeziza* FUCK. and *Scutomollisia* NANNF. nov. gen. (Discomycetes Inoperculati). — Bot. Not. 129: 323—340.

REHM, H. (1881). Ascomyceten. In getrockneten Exemplaren herausgegeben. — Ber. Naturh. Ver. Augsburg 26: 1—132.

— (1885). Ascomyceten fasc. 16. — Hedwigia 24: 7—17.

— (1888). Ascomyceten: Hysteriaceen und Discomyceten. — In: RABENHORST's Kryptogamenflora von Deutschland, Oesterreich und der Schweiz. 2. Aufl. 1: 3 (1886—1896).

— (1904). Ascomycetes exs. fasc. 32. — Hedwigia 43: (31)—(33).

— (1912). Zur Kenntnis der Discomyceten Deutschlands, Deutsch-Österreichs und der Schweiz. — Ber. Bayer. Bot. Ges. 13: 102—206.

ROGERS, J. D. (1979). Xylariaceae: systematic, biological and evolutionary aspects. — Mycologia 71: 1—42.

ROSTRUP, E. (1888). Fungi Groenlandiae ... — Medd. Grønl. 3: 517—590.

SEIDENFADEN, G. (1933). The Vascular Plants of South-East Greenland 60°04′ to 64°30′ N. Lat. — Ibid. 106: 3.

Zeitschrift/Journal: Sydowia

Jahr/Year: 1982

Band/Volume: 35

Autor(en)/Author(s): Nannfeldt J. A.

Artikel/Article: Naeviella (REHM) CLEM., a resurrected genus of Inoperculate Discomycetes, and some remarks on ascospore symmetry. 162-175