

On the genus *Pyxidiophora* sensu lato (Pyrenomycetes) 1980

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The genera *Treleasia* Speg., *Mycorhynchus* sacc., *Copranophilus* Speg., *Ascolanathanus* Caill., and *Acariniola* Maj. & Wiśn. are considered congeneric with the earlier monotypic *Pyxidiophora* Bref. & Tav. *Mycorhynchidium* Mall. & Cain is transferred from the Hypocreaceae to the family Pyxidiophoraceae G. Arnold emend. Lundq., which will thus contain two accepted genera. The nomenclature of *P. asterophora* (Tul.) Lindau, the type species of *Pyxidiophora*, is analysed, and the specific name is lectotypified. The following combinations are new: *Pyxidiophora arvernensis* (Bret. & Faur.), *P. bainemensis* (Bret. & Faur.), *P. caulicola* (Hawksw. & Webst.), *P. fusco-olivacea* (G. Arnold), *P. grovei* (Hawksw. & Webst.), *P. marchalii* (Sacc. & March.), *P. microspora* (Hawksw. & Webst.), *P. moseri* (Maj. & Wiśn.), *P. petchii* (Bret. & Faur.), *P. schotterianus* (Bret. & Faur.), *P. spinuliformis* (Speg.), and *P. subbasalipunctata* (Maj. & Wiśn.). *Ascolanathanus trisporus* Caill. is considered a synonym of *P. spinuliformis*. *P. badiorostris* Lundq., on cow dung from Sweden, is new to science, and *P. arvernensis* and *P. grovei* are reported as new to northern Europe. A *Chalara* state has been found in the two latter species.

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A recent study on the pyrenomycete genus *Mycorhynchus* Sacc. by Hawksworth & Webster (1977) has inspired me to present the Swedish records of three species, material that has been filed in my herbarium since long. The known species of the genus are seldom collected and investigated because of their rarity, smallness, and the short duration of their fruit-bodies. Most of them have been described as new by Breton & Faurel (1968) and by Hawksworth & Webster (1977). These authors also discuss the generic taxonomy and came to the conclusion that *Treleasia* Speg., *Rhynchonectria* Höhn. (≡ *Eleutherospaera* Grove), and *Ascolanathanus* Caill. are related to *Mycorhynchus*, and that *Copranophilus* Speg. should be taken as a synonym of it.

I soon became aware that also the forgotten *Pyxidiophora* Bref. & Tav., a genus not treated by the above-mentioned authors, had to be taken into consideration; it seemed hardly distinct from *Mycorhynchus* and the generic name is older than any of those relevant here. I shall comment upon these genera, but first it is necessary to discuss the nomenclature of the type species of *Pyxidiophora* and its supposed con-

nection to *Artotrogus asterophorus* Fr. and *Asterophora* Ditm. ex Fr.

The nomenclature of *Pyxidiophora asterophora*

The monotypic genus *Pyxidiophora* was established by Brefeld & von Tavel (1891 p. 188) for a pyrenomycete and its phialidic conidial state parasitizing the parasitic agaric *Asterophora lycoperdoides* (Bull. ex Mérat) S. F. Gray (≡ *Nyctalis lyc.*). They called this pyrenomycete *P. nyctalidis*, but were not the first to describe it. The Tulasne brothers, to whom they referred, gave in 1865 an excellent description and illustration of it under the name *Hypomyces asterophorus* Tul. (Fig. 1). However, the Tulasnes believed that the star-like chlamydospores that are so abundant on the pileus of *Asterophora* belong to the pyrenomycete, which thus was supposed to possess two conidial states.

The Tulasnes never intended to describe a new species. They referred to their first publication

on the subject (Tulasne & Tulasne 1860), where the parasite is called "*Hypomyces asterophorus* (Fr.) Tul.", and to a species named *Artotrogus asterophorus* Fr. by Fries (1849 p. 497). *Artotrogus* Mont. was originally a monotypic genus erected for *A. hydnosporus* Mont. (Berkeley 1845), an oomycete belonging to *Pythium* and found on various dicotyledonous plants. Butler (1907 p. 100) and Middleton (1943 p. 127) have surveyed the intricate story of the discovery of this organism. The echinulate oogonia of *A. hydnosporus* apparently made Fries believe in a relationship between this species regarded as a parasite and *A. asterophorus*, after he had abandoned his earlier conviction (1829 p. 205, 1838 p. 371) that the chlamydo-spores were part of the agaric (or gasteromycecete or whatever he considered it to be).

The status of the name *Pxidiophora nyctalidis* depends on the typification of *A. asterophorus* and on Art. 59 of the Botanical Code of Nomenclature (Stafleu et al. 1978). Fries (1849) gave no specific diagnosis of his species, only the following references: "Asteroph. Dittm. p.p. Cord. IV. f. 24". The *Asterophora* story was given an ample account by Buller (1924) and Corner (1966), and shall not be repeated here. There has also been some discussion whether Ditmar's genus is anamorphic or teleomorphic. The generic name was validated by Fries in 1821 (not in 1829, as is generally thought), and although no species was mentioned at the time, the genus was monotypic by direct and indirect citation of pre-starting point authors, who mentioned one species only, *Agaricus lycoperdoides* Bull. All these authors described lamellae, i.e. "organs which bear basidia" (Art. 59.1), which makes *Asterophora* a teleomorphic genus. However, this conclusion has been questioned, and the two conflicting views were presented by, i.a., Donk (1964) and Singer (1975 p. 224), respectively. Examples of how the two interpretations affect the nomenclature of *A. asterophorus* are given below.

Artotrogus asterophorus Fr.

The first alternative is Singer's view, viz. that *Asterophora* is a teleomorphic genus. When Fries changed his mind in 1849 about the nature of the chlamydo-spores he was undoubtedly influenced by Corda (1840), whom he cited. Corda

restricted *Asterophora* to the imperfect state, claiming his new species *Ast. agaricicola* to be a parasite on the agaric. He also gave the following citation: "(*Asterophora agaricoides* Fries l.c. [Syst. Mycol.] III. p. 205 *A. lycoperdoides* Dittmar l.c. Taf. 26? Nees Syst. II. Fig. 114?)". But none of these references are relevant for the typification of *Ast. agaricicola* as Corda never used parentheses for what he considered true synonyms of other species dealt with in the same work, and, besides, he questioned two of the references. Fries's citation of Corda binds *Art. asterophorus* to *Ast. agaricicola*, the only species included in the genus by this author, and his pro parte reference to Ditmar's *Asterophora* points naturally also to the chlamydo-spore state.

However, Corda's account is incorrect according to Article 59, as he adopted the name of a perfect state genus for an imperfect fungus, which makes *Ast. agaricicola* a validly published but illegitimate name. Fries was thus entitled to make a new name for the chlamydo-spore state, and *Art. asterophorus* must be typified by Corda's material, if such exists. From this follows, too, that all combinations based on Fries's epithet are referable to the anamorph only. It should be added that *Artotrogus*, although being a name of a teleomorphic genus, does not threaten *Art. asterophorus* as a legitimate name of an imperfect fungus, because pleomorphic oomycetes are not covered by Article 59.

If we now try the second alternative, that *Asterophora* is the name of an imperfect state genus, Article 59 is not applicable. *Ast. agaricicola* is then a legitimate but incorrect name being a younger taxonomic synonym of *Ast. lycoperdoides*. The names *Art. asterophorus* and *Ast. agaricicola* are accordingly no longer connected to each other because Fries's reference to Ditmar now takes precedence. *Art. asterophorus* becomes a superfluous name for *Ast. lycoperdoides*, and all combinations with the epithet also become illegitimate.

The conclusion of this analysis is that whichever application we give to *Asterophora*, *Art. asterophorus* is the name of an imperfect fungus. Thus a full study of the nomenclature of *Asterophora* is irrelevant here, since it has no bearing on the typification of *Hypomyces asterophorus* or *Pxidiophora nyctalidis*. Nor have I had reason to search for the correct name of the chla-

mydosporic state. Finally, it should be mentioned that the name *Nyctalis asterophora* Fr. (Fries 1838), a superfluous name for *Ast. lycoperdoides*, has no nomenclatural connection to *Art. asterophorus* Fr. (Fries 1849).

***Hypomyces asterophorus* sensu Tul. — Fig. 1**

We must now clarify whether *Hypomyces asterophorus* (Fr.) Tul. (Tulasne & Tulasne 1860) was published as a new combination or as the name of a new species. Plowright (1882), Lindau (1897), Maire (1911), and Müller & von Arx (1962) took it for granted that the name should be applied to the pyrenomycete and attributed to the Tulasnes, whereas Winter (1885) maintained that a new epithet should be coined, a name change actually made by Brefeld & von Tavel (1891).

We depend again upon Art. 59 (last paragraph), which means that the combination must be rejected and that the epithet *asterophorus* must be adopted for a new species with a new type and be credited to the Tulasnes alone. The inclusion in their description of the chlamydo-sporic state of *Asterophora* is of no importance, as the specific name in its new position is fixed to the teleomorph of the pyrenomycete. This solution had not been possible if *Art. asterophorus* were the name of a teleomorphic species, in which case the type of the name *H. asterophorus* (Fr.) Tul. would have been that of its basionym, and the pyrenomycete, accordingly, would have to be given another name.

***Pyxidiophora nyctalidis* Bref. & Tav. — Fig. 2**

Brefeld & von Tavel (1891) had a clear concept of this fungus. They managed to grow it in culture, and proved that the phialidic anamorph with catenate conidia was beyond doubt associated with the perithecia. Brefeld (1889) had earlier confirmed by cultural work an old experiment by Krombholz (1831) showing the connection between the chlamydo-spores and *Asterophora*. Because of the particular conidial state, the simple structure of the perithecia, and the absence of a stroma, Brefeld & von Tavel classified the pyrenomycete in a genus of its own, a correct step in my opinion, although their descriptio generico-specifica does not quite suffice to modern standards. They also created the

new name *Pyxidiophora nyctalidis* for the pyrenomycete, and deliberately excluded the chlamydo-sporic state. This was logical but redundant according to our present rules, as they cited the Tulasnes, and thus made *P. nyctalidis* a superfluous name for *Hypomyces asterophorus* Tul. (Art. 63).

It is possible, however, that the solution given here will not be final. Art. 59 is now debated more than ever and there is a two-alternative proposal by an I.M.A. Subcommittee (Warmelo 1979) to change the Article to the effect that any combination of names between imperfect and perfect states shall be considered validly published and legitimate. According to one model there would be, however, possibilities for exceptions when new forms are introduced with "wrong" citations. Pertinent references and indications of comb. nov. or nom. nov. would be regarded as formal errors. This model does not change the situation of *H. asterophorus* as presented here.

But the other alternative allows no such exceptions, and the typifications of all binomials published as combinations shall strictly follow Art. 55. If this version will be sanctioned by the XIII International Botanical Congress 1981, the name *P. nyctalidis* will become the correct name of the pyrenomycete, as Brefeld & von Tavel explicitly excluded the chlamydo-sporic state.

A comparison between *Pyxidiophora* and *Mycorhynchus*

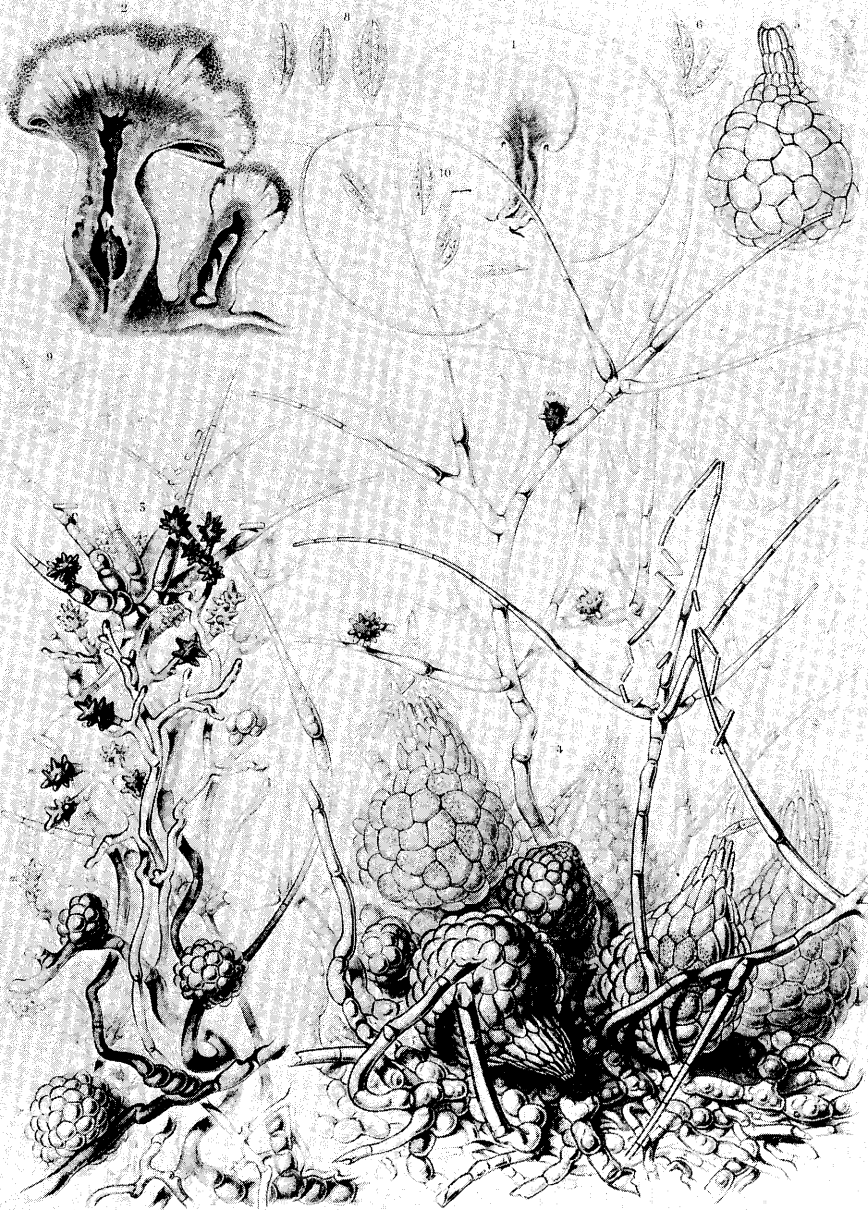
It is evident already from earlier descriptions that these two genera are morphologically strikingly similar. Characters in common are the small, light-coloured, long-necked perithecia, the peridial structure with \pm isodiametric cells below and elongate cells in the neck, the absence of paraphyses, the deliquescence of the asci, the low number of spores per ascus (2–6), and the hyaline, septate, \pm fusiform spores usually arranged in a parallel manner. None of the authors who have studied these genera has thought of comparing them with each other, except perhaps Arnold (1972 a), who placed them in his new family Pyxidiophoraceae, but without further comment. It is possible that the parasitic habit and the presence of a conidial state in *Pyxidiophora asterophora* was considered features alien to *Mycorhynchus*.

The spores

The Tulasnes' and Brefeld's drawings of the

F. R. & C. Tul. SEL. FING. CARPOL. I. III

Tab. IX



HYPOMYCES astrophorus Tul.

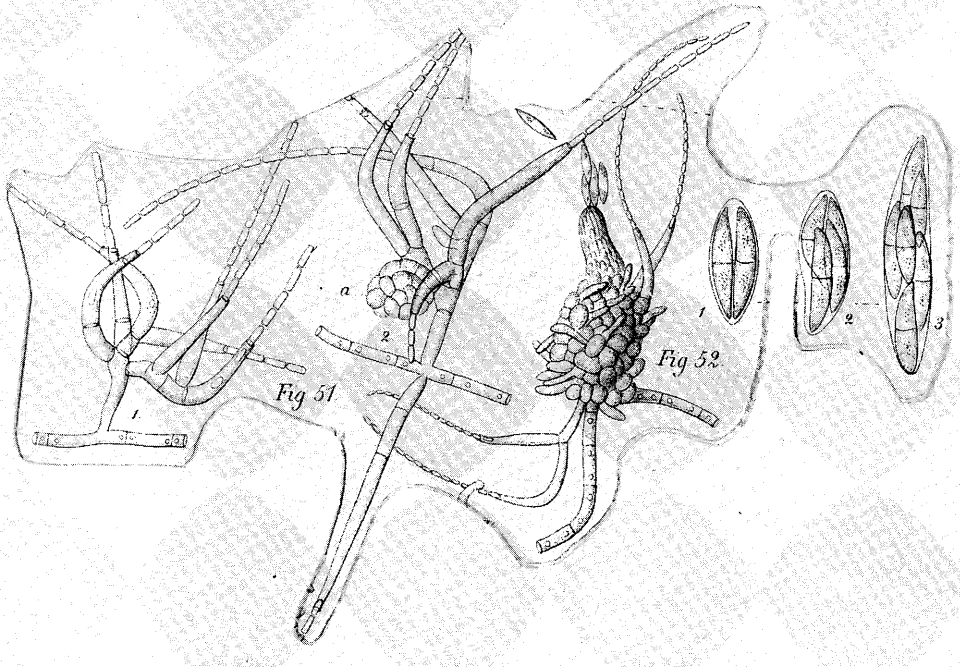


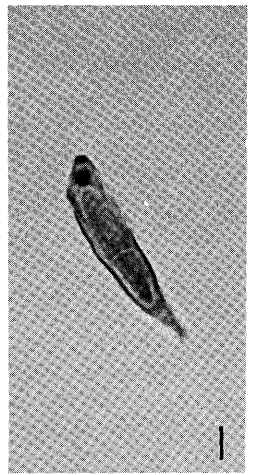
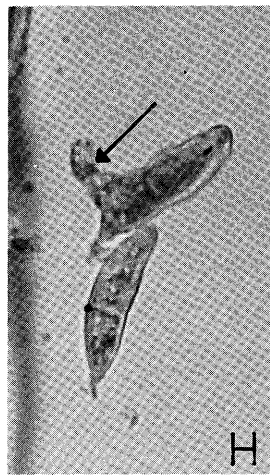
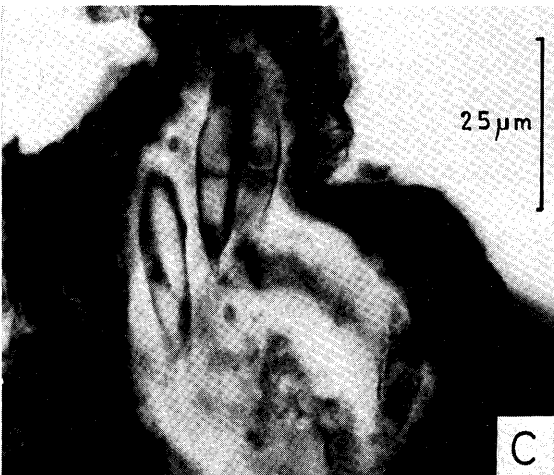
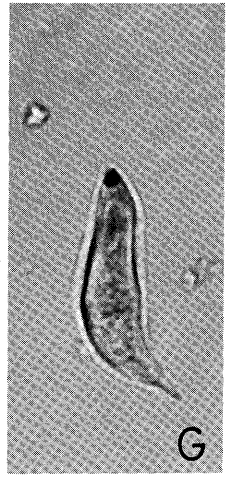
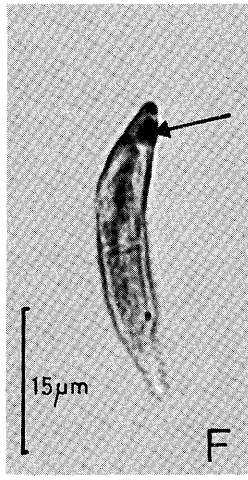
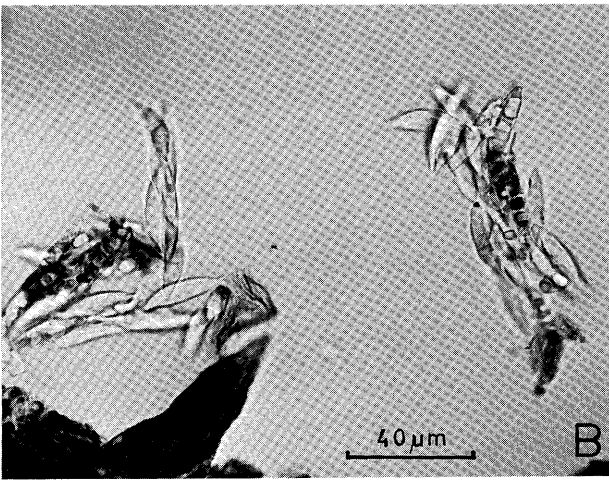
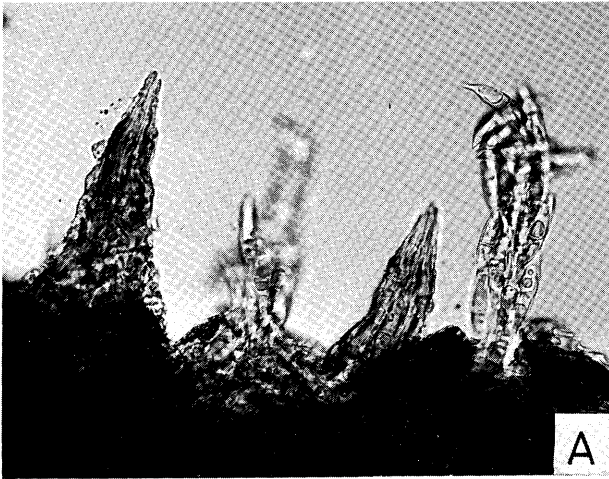
Fig. 2. *Pyxidiophora nyctalidis* (after Brefeld & von Tavel 1891) and its phialidic *Chalara* state; perithecia, asci, and ascospores to the right.

species do not show distinctly the elongate spore base characteristic of *Mycorhynchus*, although the former authors described the spores as mucronate at each end. However, it appears from the illustrations by Maire (1911) and Müller & von Arx (1962), which are founded on authentic specimens, that at least the base of the spores is drawn out. Maire's figure also shows an apical outgrowth caused by a thickening of the wall, but there is no indication that the spore wall inflates laterally as in most *Mycorhynchi*. I have examined this material in PC and ZT (see further discussion under *P. asterophora*). In the PC sample numerous loose ascospores and remnants of perithecia were found. The ZT collec-

tion contains intact perithecia and spores. In no case were asci seen.

The spores are $25-29 \times 5-5.5 \mu\text{m}$, \pm fusiform with a pointed base and a more obtuse apex, both formed by a thickening of the wall, and staining with cotton blue; the rest of the spore wall is fairly thick, but not inflated. The shape is more asymmetric than is evident from earlier illustrations; the spores may be flat on one side and rounded on the other, sometimes bent and boomerang-like, even slightly sigmoid, but regular in ventral view. The young spores are one-celled, filled with small oil drops, then transversely septate in the middle late in their development. The protoplast is c. $15 \times 5 \mu\text{m}$,

Fig. 1. *Hypomyces asterophorus* (after Tulasne & Tulasne 1865). Fruit-bodies and chlamydospores of the agaric *Asterophorus lycoperdoides* to the left; perithecia, asci, ascospores, and a phialidic *Chalara* state of *H. asterophorus* to the right. both conidial states are somewhat intermingled on the figure, since the Tulasnes thought them to belong to one and the same species, the pyrenomycete.



usually with rounded ends. Mature spores often contain a couple of large oil drops, and do not usually stain with cotton blue. The most remarkable discovery is that many spores are provided with a brown, apical or subapical spot in the wall of exactly the same kind as in *Mycorhynchus* (see below). In one spore even two spots were observed (Fig. 3).

It is difficult to find any fundamental differences in spore morphology (or perithecial structure) between *Pyxidiophora* and *Mycorhynchus*. In the latter genus the species are distinguished in the main by different size and form of the perithecia, peridial cells, and spores, form of the protoplast, occurrence of the pigmented spot in the spores, sometimes spore number, and number and position of the sporal septa. Even the pigmentation and the septation may sometimes vary *within* the species, the former feature being particularly capricious. The fact that the spore wall in *P. asterophora* does not gelatinize and swell laterally is probably of no more than specific value. This detail remains to be investigated more thoroughly on living *Mycorhynchus* spp., where in some cases a lateral inflation seems only little marked.

The asci

Both *Pyxidiophora* and *Mycorhynchus* have early deliquescing, \pm ellipsoidal asci with a few spores at about the same level. An apical apparatus is not known in the *Mycorhynchi*, but Müller & von Arx (1962) and Parguey-Leduc (1977, quoting from Durand 1964) have described and illustrated a thickened, refractive apical ring with a narrow pore in *P. asterophora*. No other author seems to have noticed this ring, not even such keen observers as Brefeld and the Tulasnes. Neither have I seen it; in fact, there is not a trace of asci in the material investigated by me, which also includes sectioned perithecia full of spores. Apparently intact asci can be seen only in young, living fungi.

Oddly enough, the ZT collection, which obviously was studied by Brefeld, is the one on which Müller & von Arx discovered the ring. Dr Emil Müller in Zürich has informed me (in litt.) that the two asci on his illustration are the only ones that were found. As far as he can remember there was an apical ring, but not quite as distinct as appears from his drawing.

I have not been able to contact Miss Françoise Durand, who left science some years ago, but Dr Agnès Parguey-Leduc in Paris has kindly commented on the subject (in litt.) and also sent me some excerpts from Durand's unpublished paper (drawings and legends). Durand sectioned young, living perithecia and examined the ascus cytology on material stained with trypan blue and iron hematoxylin-eosin. She states that the apical ring is far from being constant, and when present, it is in the form of "deux masses claires, arrondies, symétriquement disposées et fixées à la paroi ascale". She did not investigate whether it was chitinous or amyloid, but noticed that it stained more or less with trypan blue. According to Dr Parguey-Leduc, the material on Durand's microscopic slides has now totally deteriorated.

It is thus proved that *P. asterophora* at an early stage possesses some kind of non-functional ring. It seems to be indistinct and evanescent, which explains why so few mycologists have seen it. In my opinion the ephemerality of this apical apparatus disqualifies it as a generic character versus *Mycorhynchus*.

Müller & von Arx have also depicted an elongate ascus with five 2-3-seriate spores, and a similar phenomenon was illustrated by Brefeld & von Tavel (1891 Fig. 52: 3). It is possible that with a larger number of spores per ascus the asci may elongate further. When liberated from the asci, the spores adhere to one another in various numbers and combinations (Fig. 3 A, B). In Durand's material the asci are 8-nucleate, but only three spores per ascus developed and they were all arranged at the same level when full-grown.

Fig. 3. *Pyxidiophora asterophora*. A-D: *Pyxidiophora nyctalidis* from Herb. von Tavel (ZT). — E-I: *Hypomyces asterophorus* from Herb. Tulasne (PC, lectotype). Material in lactic blue and water (A). Fig. E taken in phase contrast. — A, B: Perithecia and aggregations of discharged spores. — C: Vertical section of perithecium with spores; note the orientation of the spores with their broad end directed upwards. — D-I: Spores; note the rounded ends of the protoplast in D, E, the pigmented spot in F, G, I (arrow), and the germ hypha in H (arrow). Scales: A = B; D, E, G = F; H, I = C.

Other characters

The parasitism and the presence of a conidial state in *P. asterophora* are certainly not more than specific characters. The habitat is not exclusive compared to the ecological range in *Mycorhynchus*. *Treleasia sacchari* Speg., which is reported from sugar cane leaves and belongs either in *Pyxidiophora* or *Mycorhynchus*, may be a parasite, too. *M. caulicola* Hawksw. & Webst. and *M. petchii* Bret. & Faur. are saprobes on rotten herbaceous stalks, and *M. brunneo-capitatus* Hawksw. & Webst. on polypores. "*Rhynchonectria longispora*" sensu Grove inhabits, i.a., myxomycete plasmodia, and two or three species are supposed to grow in bark beetle galleries (see discussion under *Acariniola*). The remaining species are coprophilous.

Unfortunately the anamorph was absent from the samples of *P. asterophora* studied by me. According to descriptions and illustrations it is a brownish *Chalara* with lageniform phialides and cylindrical to ellipsoidal, one-celled, hyaline conidia, 7–10×3 μm. Conidial states were thought to be missing in *Mycorhynchus*, but do exist in four other species, and are similar to that of *Pyxidiophora* (see discussion under *Ascolanthanus*, *Copranophilus*, *Pyxidiophora arvernensis*, and *P. grovei*).

Conclusion

The foregoing account shows the difficulty in separating the two genera. Admittedly, *P. asterophora* exhibits a combination of characters not observed in typical *Mycorhynchus* species, but they are not sufficient for a generic distinction.

Other supposedly related genera

The emended circumscription of *Pyxidiophora* demands a renewed scrutiny of other genera considered as related to *Mycorhynchus*. The amplest survey was given by Breton & Faurel (1968), on which some additional comments shall be made.

Treleasia Speg. 1896

Specimens of the type species, *T. sacchari*

Speg., are no longer present in Spegazzini's herbarium (LPS), which has been verified by at least four mycologists. To judge from Spegazzini's original sketch of the species, published by Petrak & Sydow (1935), *Treleasia* stands very close to *Mycorhynchus* in the old sense. The spores are said to be, i.a., fusiform, straight, and uni-septate in the middle. Breton & Faurel rated the sporal differences between the genera highly, stressing the symmetry and acute ends of the *Treleasia* spores in contrast to the asymmetrical, subclaviform spores in *Mycorhynchus*. There is, however, a hitch in this comparison. One has to distinguish between the shape of the protoplast and the form of the whole spore after the swelling of the wall. Several *Pyxidiophorae* have fusiform, more or less symmetrical protoplasts very similar to the spores of *T. sacchari*. The pertinent question is whether Spegazzini's description and drawing are accurate, or if he disregarded or failed to observe a thickened spore wall. With the wide circumscription adopted for *Pyxidiophora* here, *Treleasia* falls within it, and his concept is of little importance. However, if *Pyxidiophora* and *Mycorhynchus* are kept as separate genera, it is hardly possible to tell which one is congeneric with *Treleasia* as long as *T. sacchari* has not been found and restudied. Moreover, Spegazzini's description and figure of 8-spored asci may be a misinterpretation of a discharged spore cluster (Petch 1936).

Rhynchonectria Höhn. 1902

No material is left at K of the monotype, the fungicolous *R. longispora* (Phill. & Plowr.) Höhn. (Petch 1941). The discussion on the relationship between *Rhynchonectria* and *Mycorhynchus* has been totally focussed on interpretations of the *Rhynchonectria* spores, which are said to be, i.a., fusiform, one-septate, and appendaged at both ends. Some authors merge the genera, others keep them apart (e.g. Hawksworth & Webster 1977). Further speculations on the nature of these spores are certainly fruitless until the type species has been found again and examined. Other, neglected characters may be equally important. The long and relatively narrow asci (130–150×20–25 μm) are atypical of *Pyxidiophora* s. lato. I consider *Rhynchonectria* unrelated to this genus.

Ascolanthanus Caill. 1967

The discriminating features of this genus against *Mycorhynchus* are, according to Breton & Fauré (1968 p. 257), a stroma, a conidial state, 3-spored asci, and spores with pigmented girdles and an appendage at both ends. Such criteria are not sufficient to circumscribe genera in this family (p. 133). Three-spored asci, for example, are met with also in *Pyxidiophora badiorostris* n. sp., *P. bainemensis* (Bret. & Faur.) Lundq., and *P. grovei* (Hawksw. & Webst.) Lundq., and apically attenuated spores occur in a number of species of the genus. However, the stroma and the nature of the conidial state may be characters of weight and deserve an analysis.

A. trisporus Caill., the monotype, was collected from three provinces in Spain and four in France. I have examined seven French samples (PC) representing three gatherings:

Seine-et-Oise: Carrières sur Seine. Dried specimens on straw (1), on straw in alcohol (2), and on agar in formalin (3), 20.VII.1956. Montesson. On straw in lactophenol, 31.V.1967 (4), on agar in lactophenol, 12.VI.1967 (5), and on agar in alcohol, 7 & 12.VI.1967 (6). — *Oise*: Saint Gervais near Beauvais. On straw in alcohol-formalin-acetic acid, 21.III.1961 (7). All material was obtained from horse dung.

Only the gatherings from Carrières sur Seine and Montesson belong to the protologue of *A. trisporus*. These localities are situated NW of Paris ("Region parisienne"). Nos. 1 and 2 contain stromata and the imperfect state only, whereas all the others also have perithecia. Specimens with mature, pigmented spores are present on no. 6, and this would be suitable for a possible typification (cf. p. 142).

The agar cultures are not pure, but a mixture of infected dung and agar. Thus some other species are also present, i.a., a *Pyxidiophora* species. This occurs on nos. 3 and 5, where perithecia of *A. trisporus* could not be detected, and also mixed with fruit-bodies of this species on no. 6. Its perithecia are single or aggregated, (200-)230-300×70-95 μm, neck (115-)140-190×27-36 μm, peridial cells 10-19 μm in diam., neck cells 13-33×3.5 μm, spores slender, 38-50 μm long, with a middle septum, a subapical, brown, sometimes hollow, flattened patch, a 25-33×3 μm large protoplast, and a 9-12 μm long basal appendage. Truncate, cylindrical *Chalara* conidia, 9-15×4 μm were found, but no phialides.

My first thought was that this species could be a developmental stage of *A. trisporus*. Although not proved, it is possible that pigmented spores may be produced in immature fruit-bodies. The idea must be abandoned, however, since the differences in perithecia and spores are too great. Besides, *A. trisporus* has ochraceous, large stromata, 1-12 mm in diam. (according to Cailleux), recognizable also when sterile, whereas the *Pyxidiophora* perithecia in question at most form a minute, yellowish subiculum, if any at all.

Apart from no. 6, *A. trisporus* is represented also on nos. 4 and 7 with fructifications. In the two first-mentioned collections the perithecia measure 300-630×90-215 μm with a tapering, broad-based neck, 225-380×50-135 μm, and large neck cells, 17-42×6-10 μm. The spore width is stated to be 6-7 μm, which certainly includes the inflated wall; the protoplast is only 4-5 μm broad. The Saint Gervais specimens are even taller with perithecia up to 690 μm. Cailleux gives unusually low figures for the perithecial width, 40-60 μm, and he might have included the above-mentioned *Pyxidiophora* in his measurements. Even young fruit-bodies of *A. trisporus* are wider than that.

The imperfect state

Fig. 4. The ventricose-rostrate conidiophores, up to 55 μm long, have a few basal septa and produce chains of subcylindrical to narrowly obovoid (not ellipsoidal as in Cailleux's figure), probably holoblastic conidia, 11-17×4-5.5 μm, with conspicuous, mostly deciduous connectives.

The situation is complicated by the occurrence of typical *Chalara* phialides. They grow in fewer numbers on the stromata, mixed with the other kind of conidiophores, and are about the same size, but more regular in form with a cylindrical collarette. The conidia are of a size similar to those mentioned above, strictly cylindrical with truncate ends lacking connectives. Whether this *Chalara* is connected with the *Pyxidiophora* in question or whether *A. trisporus* has two anamorphs, I am unable to decide. Perhaps none of the two imperfects is associated with *A. trisporus*. The non-phialidic anamorph has recently turned up on badger dung from Harparbol, Almunge par., Uppland, Sweden (1.X.1979, Lqt 12415-d, UPS), and it is worth noting that neither

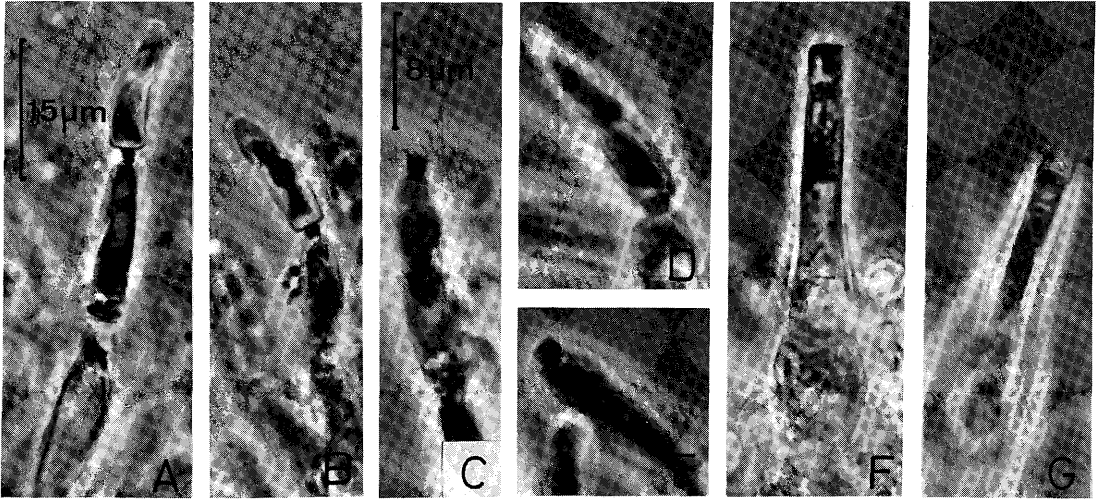


Fig. 4. *Ascolanthanus trisporus* from Carrières sur Seine, France, leg. Cailleux 20.VII.1956 (PC); formalin-preserved specimens on straw. Phase contrast. — A–E: Catenate conidia with tapering apex and distinct connectives; part of conidiophore visible in A. — F, G: *Chalara* phialides with cylindrical, truncate conidia without connectives found mixed with the afore-mentioned state; possibly not belonging to *A. trisporus*. Scales: B, G = A; D, E = C.

Chalara nor any *Pyxidiophora* perithecia could be detected on the material. Single-spore cultures have not yet been made.

When comparing *A. trisporus* with species of *Mycorhynchus*, *M. spinuliformis* (Speg.) Bret. & Faur. (\equiv *Copranophilus s.*) is the first one to be discussed.

Copranophilus Speg. 1909

The generic name has usually been placed in synonymy with *Mycorhynchus*. In 1964 I examined the type collection of *C. spinuliformis* Speg., the monotype (on cow dung from La Plata, XII.1908, LPS 1761), but failed to find any perithecia. Breton & Faurel (1968 p. 232) also searched in vain. Fortunately the description, illustration, and original drawing give a fairly good clue to the morphology of the species. Important information in the protologue seems to have been neglected: "Acervuli subglobosi parvi albo-cinerelli, spinuloso-hirti" and "Acervuli superficiales subglobosi tenelli (3–4 mm diam.); perithecia stromate centrali subgossypinulose dense constipata ...".

These phrases state, in fact, that the species has a 3–4 mm large, whitish, spiny-hairy stroma

and that the perithecia are densely aggregated on this stroma. Also Spegazzini's illustration (copied by Breton & Faurel) shows this distinctly. All these features suggest *Ascolanthanus*. On the dried collection of *A. trisporus* mentioned, the masses of conidia form a whitish powder on the stroma, which could correspond to what Spegazzini called "albo-cinerelli". The spinose-hairy surface may allude to the mat of erect conidiophores. There are on the whole very few characters, if any, to separate the two fungi. All measurements correspond roughly to one another in the two descriptions, except that the neck cells in *C. spinuliformis* are somewhat longer, 30–60 μ m, the perithecia are said to be "fuscidula" (apart from the hyaline ostiolum), and some peridial cells are "sinuoso-parenchymatico".

A phenomenon emphasized greatly by Breton & Faurel is the upside-down position of the spores in the ascus. As in the *Treleasia* case, I rather believe, as did Petch (1936), that Spegazzini never saw asci. The supposed ascus wall could be the aggregated inflated walls of the outer spores. Besides, when spores have been observed protruding from the perithecial ostiolum in other *Mycorhynchi* (or *Pyxidiophorae*), the broad and/or pigmented end always comes

first (cf. Fig. 3 C). Only one other species has been described with supposedly broad-based spores (Arnold 1972 a), viz. *M. fusco-olivaceus* G. Arnold, but the author is certainly mistaken about the orientation of these spores, as he neither discovered asci nor even mentioned this characteristic when comparing his species with others in the genus.

An intriguing detail on Spegazzini's drawing still remains to be explained: four, one-celled, elongate, hyaline bodies with a tapering end. They were called "éléments indéterminés" by Breton & Faurel, and were not mentioned by Spegazzini, not even in the legend. However, on the sketch kept in LPS 1761 the size is given to 12–15×3 μm. I do not hesitate to interpret these bodies as conidia. They have the same form and size as those of *A. trisporus*. Spegazzini was obviously uncertain about the origin of these conidia, and preferred to ignore them.

The taxonomic value of the stroma is limited as some *Mycorhynchus* spp. are more or less stromatic too. Thus the perithecia of *M. schotterianus* are said to be partly sunk in a soft, parenchymatous stroma. The caulicolous *M. petchii* (= *M. marchalii* sensu Petch) is described to have perithecia "clustered, superficially on, or partly embedded in, a delicate parenchymatous, pale brown stroma, forming subglobose tufts up to 0.5 mm diameter, or smaller and confluent in extended patches" (Petch 1936). Nevertheless, neither of these three authors nor Hawksworth & Webster, who also studied Petch's original specimens, have had any objections to range this fungus among the non-stromatic species of *Mycorhynchus*. In some cases the occurrence of a stroma is not even constant as a specific property (cf. *Pyxidiophora grovei*).

Conclusions

Ascolanathanus and *Copranophilus* are undoubtedly congeneric. Probably also their type species are conspecific, although no pigmentation was found in the spores of *C. spinuliformis*. If the stroma be accepted as a generic character, *Copranophilus* must be maintained for the stromatic species with *Ascolanathanus* as a synonym. In my opinion this is not taxonomically motivated and the genus can be merged with *Mycorhynchus*, i.e. *Pyxidiophora* s. lato. Nor is the peculi-

ar conidial state in *Copranophilus* a convincing argument for generic separation of the perfect state.

Acariniola Maj. & Wiśn. 1978 a—Fig. 5

This genus was established for two Polish species, *A. basalipunctata* Maj. & Wiśn. and *A. subbasalipunctata* Maj. & Wiśn. (the holotype), supposed to be parasites on mites in bark beetle galleries. In the same paper the similar *Thaxteriola moseri* Maj. & Wiśn. is described, also from Poland and with the same ecology. The latter fungus has also been recorded on mites in Louisiana, U.S.A. (Majewski & Wiśniewski 1978 b). All three species were thought to be organisms of unknown taxonomic position, and were placed in the "Thaxteriolae group", a name used by Thaxter (1920) for external arthropod parasites resembling Laboulbeniomyces, and characterized by an elongate, septate, apically tapering thallus with a black foot-cell and by formation of spores in the apical cell.

Majewski & Wiśniewski found that none of the species was confined to any particular host species or sex, or to any special part of the body of the mites, but they were most common on the legs. The thallus is said to be attached to the host by a dark foot, which in *T. moseri* possesses a "penetration pore". In the *Acariniola* species this pore is located near the middle of the thallus in the same cell.

When I saw the illustrations of these fungi I was struck by their extreme similarity to *Pyxidiophora* ascospores. By the courtesy of Dr T. Majewski in Warsaw (WA) I could examine five slides (incl. six paratypes) of the species, and my first impression was confirmed. The hoof-like, dark "foot" of *T. moseri* is a parallel of the pigmented body found in *Ascolanathanus trisporus* (= *Pyxidiophora spinuliformis*) and *Mycorhynchus subspinuliformis* Bret. & Faur. The "penetration pore", whatever function it may have, is present in *P. grovei* too (Fig. 10). A pigmentation in the middle part of the "thallus" is met with in *Mycorhynchus brunneocapitatus* Hawksw. & Webst. as well. The "thalli" often adhere to one another in bundles and with the same orientation as in discharged *Pyxidiophora* spores. The form of the protoplast is similar. The pointed "tip" of the "thalli" does not differ in outline from the basal elongation of the *Pyxidio-*

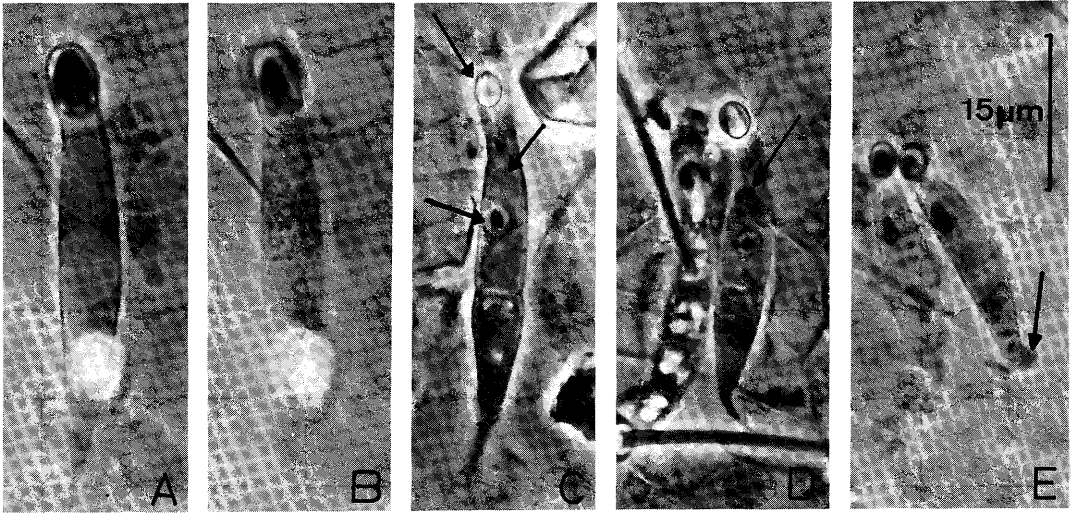


Fig. 5. Spores of *Acariniola* and "*Thaxteriola*" on mites from Zielonka Forest, Poland, leg. Pawlik (WR); specimens in polyvinyl-lactophenol. Phase contrast. — A, B: "*Thaxteriola*" *moseri* (slide 708); different focussations; the white spot is an artifact. — C, D: *Acariniola subbasalipunctata* (328); note the pigmented spots and the upper limit of the protoplast (arrows). — E: *A. basalipunctata* (140); germ hypha at arrow. Scale: A–D = E.

phora spore. A germinating spore was observed on slide 140 of *A. basalipunctata* (Fig. 5 E) and it looked exactly like the germ hypha illustrated on Fig. 3 H (*P. asterophora*) and Fig. 6 D, 7 (*P. arvernensis* (Bret. & Faur.) Lundq.). The authors' Fig. 3 C (left spore) may show the same phenomenon.

Majewski & Wiśniewski illustrate "thalli" with broken "tips" with diffuse, cytoplasmic globules inside, and postulate that the latter could be spores, but they have not seen such spores with certainty. The small, hyaline, ellipsoidal spores observed here and there on the mites are probably conidia of *Graphium* or ascospores of *Ceratocystis* species that also inhabit bark beetle galleries. The material is not very easy to study because of its treatment for several days in 50°C lactophenol and mounting in polyvinyl lactophenol; some finer details might have disappeared. Thus, a strongly inflated wall, like in most *Pyxidiophora* spores, could not be seen, nor the upper contour of the protoplast in *T. moseri*, not even by phase contrast.

These species apparently form fruit-bodies in the bark beetle galleries. Their slimy spores aggregate at the ostiolum, and become transported by passing mites, probably also by beetles. Such

an adaptation explains the higher concentration of spores on the legs of the vectors.

Majewski & Wiśniewski considered the septation an important character, and restricted the three-celled spores to *T. moseri* and the two-celled spores to the *Acariniola* species. Such features are not of generic status in *Pyxidiophora*. A couple of spores of *A. basalipunctata* were even found to have an extra septum near the base. However, *T. moseri* is clearly distinct from the other two by its peculiar, hoof-like, pigmented body ($8 \times 5.5 \mu\text{m}$) with a pore. The total spore size is $45\text{--}50 \times 5.5\text{--}6.5 \mu\text{m}$ ($41\text{--}54 \times 4.5\text{--}6 \mu\text{m}$; orig. diagnosis), and the basal elongation c. $5\text{--}6 \mu\text{m}$. The upper part of the spore is verruculose.

The *Acariniola* species are separated only with difficulty. Their spores have about the same size (*A. basalipunctata*: $34\text{--}51 \times 4.5\text{--}8 \mu\text{m}$; *A. subbasalipunctata*: $24\text{--}53 \times 3\text{--}7 \mu\text{m}$; orig. measurements), a flattened, brown, pore-less, subapical body ($4 \times 3 \times 1.5\text{--}2 \mu\text{m}$; my meas.), and a small, brown ring ($2\text{--}2.5 \mu\text{m}$; my meas.) above the septum. Their basal elongation is $5\text{--}11 \mu\text{m}$ long and their protoplasts resemble each other with the rounded upper tip far below the pigmented body. In *A. basalipunctata* the upper [sic!] cell and in

A. subbasalipunctata the lower [sic!] cell is verruculose, but the other cell may also be partly roughened. The material seen by me is too scarce to allow definite conclusions as to the taxonomy of the *Acariniolae*, particularly as their fruit-bodies are unknown. The two fungi may be conspecific. The names *A. subbasalipunctata* and *T. moseri* are here combined into *Pyxidiophora*, whereas a transfer of *A. basalipunctata* should be postponed pending further studies.

It shall be added that *Thaxteriola* (Spegazzini 1918) is a genus quite unrelated to *Pyxidiophora*.

Dr T. Majewski (in litt.) now shares my opinion about the nature of his species, but prefers not to join me in the new combinations.

Specimens examined. The WA material was collected by C. Pawlik from the Zielonka Forest near Poznan, Poland, on vectors of *Dendrolaelaps* and *Proctolaelaps* in galleries of *Hylurgus ligniperda* (Fbr.) and *Myelophilus piniperda* (L.) on *Pinus silvestris*. — *A. basalipunctata*: 3.III.1974 (slide 140), 6.IV.1974 (241, on *Dendrolaelaps*; not publ.), 13.V.1974 (364). — *A. subbasalipunctata*: 6.IV.1974 (241), 5.V.1974 (328), 13.V.1974 (364). — *T. moseri*: 13.V.1974 (364), 9.III.1975 (708).

Synopsis

Pyxidiophoraceae G. Arnold 1972 a emend. Lundq.

Pyxidiophora s. lato and its synonyms were referred by earlier authors to either pycnidial fungi or to the Hypocreaceae s. lato. Müller & von Arx (1962), however, placed *Pyxidiophora* s. str. in the Hypomycetaceae, and *Mycorhynchus* in the Hypocreaceae s. str. How these families should be defined will not be treated here. Information on their history and various circumscriptions is given in Rogerson (1970), who accepted only one family in the order, viz. Hypocreaceae. His approach was adopted by Müller & von Arx (1973). A contrasting standpoint was taken by Arnold (1968, 1972 b), who maintained the Hypomycetaceae in a very narrow sense (3–4 genera) and excluded *Pyxidiophora* s. str.

That this genus has been placed in one or other of these families is understandable. The resemblance, particularly to *Hypomyces*, is obvious as regards perithecial colour, spore morphology, habitat, and lack of paraphyses. But the ascial

form and structure and manner of spore discharge are different, and the two genera are probably not akin. Even more far-fetched is to place *Pyxidiophora* s. str. among the *Nectriae*, as proposed by Clements & Shear (1931).

The first to realize the exclusiveness of *Pyxidiophora* s. lato was Spegazzini (1909) in a comment on *Copranophilus*: “Genus eximium cum *Treleasia* familiolam *Nectriaceis* nonnihil aberrantem certe constituens”. Arnold (1972 a) arrived at the same conclusion, and erected the new family Pyxidiophoraceae for *Pyxidiophora* s. str. and *Mycorhynchus*. He considered it related to the Melanosporaceae because of its deliquescent asci. If this theory be correct, the Pyxidiophoraceae may not even belong to the Hypocreales, as Rogerson (1970) did not include the Melanosporaceae in this order.

Whether the imperfect states could contribute to the family classification here is uncertain. *Chalara* is found in *Pyxidiophora* and one species of *Hypomyces*, but does not seem to occur in *Melanospora* (Tubaki 1958). On the other hand, authorities such as Nag Raj & Kendrick (1975) and Arnold (1972 b) do not mention any connection between *Chalara* and *Hypomyces*. The latter author lists 11 imperfect genera for the Hypomycetaceae and 7 for *Hypomyces*, and claims that the conidial states in question characterize the species only.

As far as is known only two genera constitute the family Pyxidiophoraceae: the type genus in a wide sense and the monotypic *Mycorhynchidium* Mall. & Cain (Malloch & Cain 1971). The latter taxon, which was originally placed in the Hypocreaceae, differs merely by its cleistocarpic state. This feature is given little taxonomic weight by some modern authors, but a generalization is not defensible. In this case I regard the cleistocarpic state as being a good generic criterion. A minor emendation of the family limits is thus necessary:

Non-stromatic or stromatic; ascocarps ostiolate and long-necked or closed, ± light-coloured, membranaceous. Paraphyses lacking. Asci unitunicate, non-amyloid, soon deliquescent. Spores fusiform to clavate to cylindrical, usually basally elongate, with one or a few transverse septa, rarely one-celled, mature hyaline but often ultimately with limited, brown pigmentation, particularly in the upper part. Conidial state hyphomycetous, phialidic and holoblastic (?).

Saprophytic, especially coprophilous, rarely parasitic.

Pyxidiophora Bref. & Tav. emend. Lundq.

Brefeld & von Tavel 1891 p. 188. — Orig. monotype: *P. asterophora* (Tul.) Lindau.

Rhynchomyces Sacc. & March. in March. 1885 p. 60, nom. illeg.; non *Rhynchomyces* Willk. 1866. — *Mycorhynchus* Sacc. in Sacc. & D. Sacc. 1906 p. 418. — Orig. monotype: *R. marchalii* Sacc.

Treleasia Speg. 1896 p. 236. — Orig. monotype: *T. sacchari* Speg.

Copranophilus Speg. 1909 p. 410. — Monotype: *C. spinuliformis* Speg.

Ascolanthanus Caill. 1967 p. 1473. — Monotype: *A. trisporus* Caill. nom. illeg. (not typified) = *Pyxidiophora spinuliformis* (Speg.) Lundq.

Acariniola Maj. & Wiśn. 1978 a p. 7. — Holotype: *A. subbasalipunctata* Maj. & Wiśn.

Perithecia free or partly sunk in a soft, light-coloured stroma or subiculum, hyaline to ochraceous, rarely partly brown, long-necked. *Peridium* pseudoparenchymatous, membranaceous, two-layered, with an outer layer of isodiametric cells below and elongate, cylindrical cells in the neck. *Paraphyses* absent. *Asci*, where observed, subclavate to ellipsoidal, unitunicate, rapidly dissolving, without or rarely with a non-functional apical ring, non-amyloid, 2–3–4(–8?)-spored. *Spores* parallel to one another in the ascus, at maturity aggregating in slimy masses on the ostiolum, subclavate to fusiform or cylindrical, attenuated particularly at the base, 0–4-septate at a late stage, usually with a gelatinized and swelling, smooth or verruculose wall, mature hyaline but often finally with an apical or subapical, lateral, brown body or with smaller pigmented spots or girdles. Conidial states, where known, phialidic (*Chalara*) and holoblastic (?). — Coprophilous or saprophytic on other substrates, rarely mycoparasitic.

Particular attention should be drawn to the pigmented body of the spores, since it has been allotted a diagnostic value at the specific level (Hawksworth & Webster 1977). The taxonomic importance of this phenomenon seems exagger-

ated. There may be species in the genus that are unable to develop such a stage, but certainly others that regularly or only sporadically do it. A pigmentation is known in ten or eleven species of *Pyxidiophora*. Its protective function must be practically nil, nor is it connected with the physiological maturation of the spores. It may be an evolutionary whim.

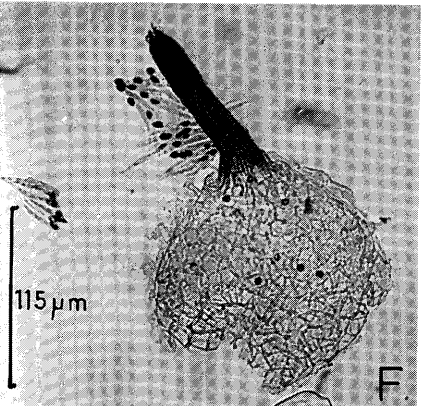
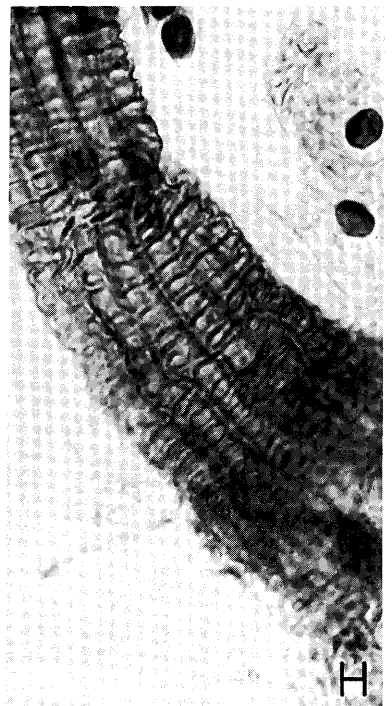
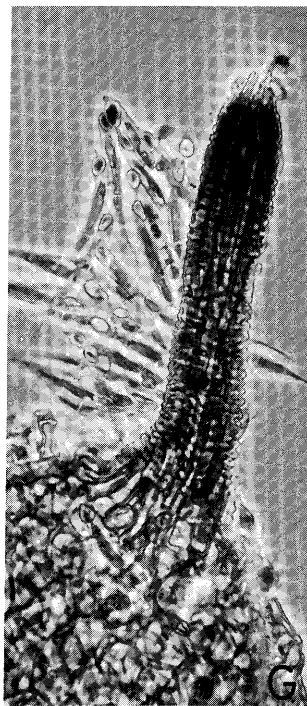
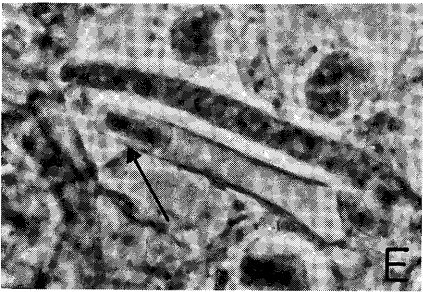
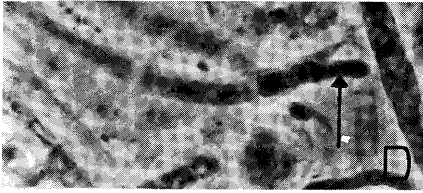
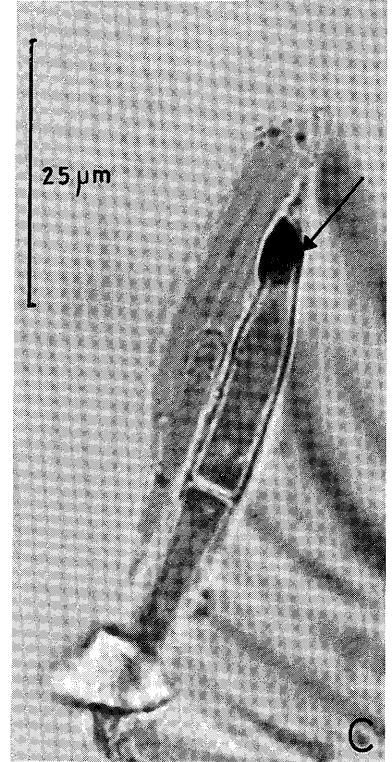
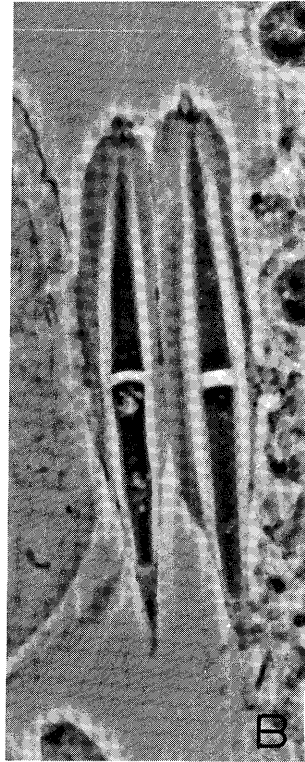
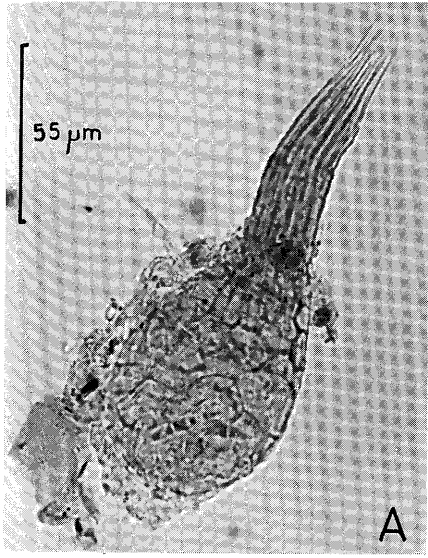
Hawksworth and Webster accepted 12 species in *Mycorhynchus* including *Copranophilus*. With the addition of *Pyxidiophora* s. str., *P. badiorostris* n. sp., *Treleasia*, *Ascolanthanus*, and *Acariniola* the number increases to 20, but 5–7 of these species have a dubious status. It has not been my ambition to revise them all, as they have been given good treatments by other authors. Apart from those already analysed, only the three Swedish species shall be fully described.

Pyxidiophora arvernensis (Bret. & Faur.) Lundq. comb. nov.—Figs. 6 A–E, 7

Mycorhynchus arvernensis Bret. & Faur. 1968 p. 249.

Non-stromatic; perithecia yellowish, glabrous or with a few thick, septate, hyaline hairs, narrowly pyriform, 130–170×45–65 μm, long-necked; neck tapering, 65–105×20–30 μm, composed of elongate, cylindrical cells, 10–18×3–4.5 μm, which are drawn out into pointed beaks around the ostiolum; peridial cells rounded to angular, 7–18 μm in diam. *Paraphyses* lacking. *Asci* not seen. *Spores* clavate-fusiform, 48–57×5–7 μm, swelling to 10 μm in width, hyaline; protoplast at first fusiform, often truncate at base, then rounding up at the ends, 38–48×3.5–4 μm, with a septum in or just below the middle; the inflated wall contracted above into a point, often slightly constricted below the apex, and basally elongated into a whip-like, 6–10 μm long appendage. At maturity a flattened, rounded or angular, brown body, 5–6×4×1.5–2.5 μm, occasionally develops in the spore wall laterally below the apex.

Fig. 6. A–E: *Pyxidiophora arvernensis*. Lqt 3429-b (UPS). — F–H: *Pyxidiophora badiorostris* n. sp., Lqt 2776-e (UPS). Material in lactic blue. Figs. B, D, E, G taken in phase contrast. — A: Perithecium. — B: Spores showing the inflated wall and the shape of the protoplast. — C: Spores; note the pigmented spot (arrow). — D: Germinating spore (arrow). — E: *Chalara* phialide with conidium (arrow). — F: Crushed perithecium and spores. — G, H: Perithecial neck. Scales: B, D, E, H = C; G = A.



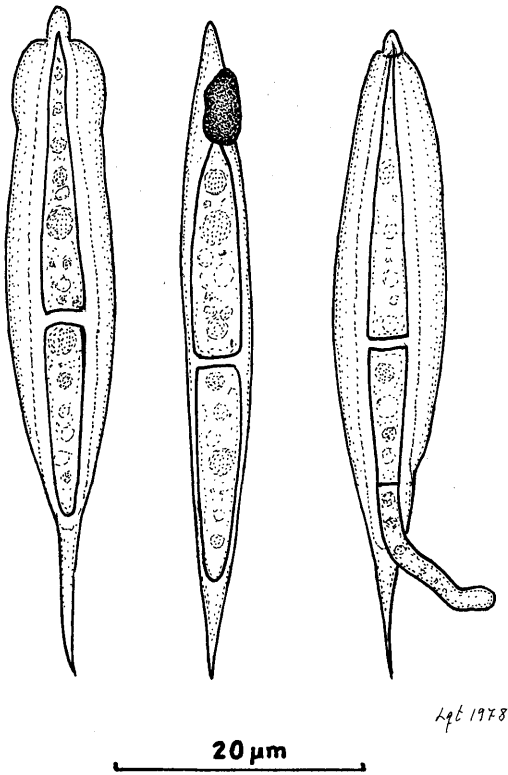


Fig. 7. *Pyxidiophora arvernensis*. Lqt 3429-b (UPS). Spores; one with a germ hypha.

Specimens examined. Sweden: Jämtland, Åre par., Storlien, in subalpine region, on reindeer dung, 17.VI.1962, Lqt 3429-b (UPS). — Uppland, Rasbokil par., NW of Lake Lafssjön, on roe deer dung, 25.X.1964, O. Eriksson 2510 (UPS). — Finland: Kuusamo, Kuusamo par., SSW of Liikasenvaara near Oulankajoki River, on hare dung, 24.VIII.1978, Lqt 11679-a (UPS, slide). New to Northern Europe.

All specimens are developed in moist chamber cultures. The species was hitherto known only on cow and horse dung from Clermont-Ferrand in France. Breton & Faurel did not observe any pigmentation in the spores, nor the strong inflation of the spore wall. They also stated that the length of the cells hardly exceed $10\ \mu\text{m}$, and that the "pseudospore"—i.e. the basal elongation without protoplast—is absent (p. 256). I consider all these differences versus the Nordic specimens to be either within the normal variation of the species or be founded on incomplete observations (cf. comment under *Pyxidiophora*

and *P. grovei*). The pseudospore could be difficult to distinguish from the protoplast in young spores. A new study of authentic specimens may be needed to settle these questions.

The type of *P. arvernensis* (leg. Breton 3.X.1965) is said to be placed in Paris (PC), but "is not available" there (J. Mouchacca in litt.). Nor has Dr André Breton (Clermont-Ferrand) any material in his possession, since he left all of it to the late L. Faurel (Breton in litt.). It is possible that collections of this species and other *Pyxidiophorae* are still among Faurel's mycological remains, and have not yet been filed in PC. Dr Breton also took the trouble to send me fresh horse dung from the type locality, the Cournon Bridge at Allier River, but *P. arvernensis* did unfortunately not develop in my moist chamber cultures.

The imperfect state. Fig. 5 E. A hyaline *Chalara* is present on Lqt 3429-b, growing mixed with the perithecia. Both states seem to originate from the same hyphae, but the connection remains to be proved by single-spore cultures. The phialides are lageniform, $25\text{--}38\ \mu\text{m}$ long, with a $5.5\text{--}8\ \mu\text{m}$ wide venter and a $3\text{--}4\ \mu\text{m}$ wide, cylindrical collar. The conidia are $6\text{--}19 \times 3\text{--}3.5\ \mu\text{m}$, cylindrical, truncate, one-celled, hyaline.

Pyxidiophora asterophora (Tul.) Lindau—Figs. 1–3

Lindau 1897 p. 351.

Hypomyces asterophorus Tul. in Tul. & Tul. 1860 p. 14; non *H. asterophorus* (Fr.) Tul., *ibid.* ≡ *Asterophora lycoperdoides* (Bull. ex Mérat) S. F. Gray, stat. con. — *Pyxidiophora Nyctalidis* Bref. & Tav. 1891 p. 189, nom. superfl. for *H. asterophorus* Tul. — Lectotype selected here on *A. lycoperdoides* from Héricy, France, Herb. L. R. Tulasne (PC).

Imperfect state: *Chalara brefeldii* Lindau nom. nov. in Rabenh. 1906 p. 750. — *Polyscytalum fungorum* Sacc. 1886 p. 336; non *Chalara fungorum* (Sacc.) Sacc. 1877. — Orig. coll. from Hocking Wood, England, IX.1880, leg. C. B. Plowright and J. M. Du Port (not seen).

Illustrations. Tulasne & Tulasne 1865 Pl. IX: 4–10. — Plowright 1881 Pl. 147: c–h (partly after the Tulasnes). — Brefeld & von Tavel 1891 Pl. V: 51, 52. — Maire 1911 Pl. XVI: 1. — Müller & von Arx 1962 Fig. 317. — Parguey-Leduc 1977 Fig. 1 d. Copied illustrations are excluded here.

Specimens examined. France: Seine-et-Marne, Héricy, "In Ag. adusto et Nyctali superposita", VIII–IX.1858, leg. L. R. Tulasne as *Hypomyces asterophorus* and *Nectria microscopica* Tul. in sched.

(PC, lectotype). — *Germany: Westfalen, Münster, Hiltrup, near the railway station, "auf Nyctalis asterophora auf Russula adusta", IX.1889, leg.?, Herb. F. von Tavel as Pyxidiophora Nyctalidis nob. (ZT).*

I have examined all material of *Asterophora lycoperdoides* in Herb. Tulasne, but found the pyrenomycete on the collection from Héricy only. Four samples originate from Chaville in Seine-et-Oise (25.VII.1860; end of July, 1860; VII–VIII.1860; VIII.1860), and one from Meudon in Seine-et-Oise (25.X.1857). One is without a locality and date. The Tulasnes (1865) stated that they saw the chlamydosporic fungus "hundreds of times . . . in the neighbourhood of Versailles [close to Chaville], Compiègne etc.", but only rarely the ascophorus state, which was first discovered "around Fontainebleau in August 1858". This place alludes to Héricy, which is situated close to Fontainebleau. In 1860 the authors reported the species as a whole on both *Asterophora lycoperdoides* and *A. parasitica* (Bull. ex Fr.) Sing. from "Fontebellaqueo . . . agri versaliensis, Modoni nempe, Cavillae, etc."

As regards Brefeld's herbarium, it is not mentioned in Lanjou & Stafleu's index of collectors (1954) and is said to be unknown (Stafleu & Cowan 1976). I have received negative answers from Munich (M), Münster (MSTR), and also from the Botanical Garden in Münster, of which Brefeld was the director in the 1880's. But Dr I. Friederichsen in Hamburg (HBG) has kindly informed me that in 1935–36 all the cryptogamic collections of the Botanical Institute in Münster were sent by Prof. Mevius to the Berlin Museum. The unopened boxes were kept in the cellar during the war and escaped the destruction on March 1, 1943. In an institutional report in Willdenowia 2, p. 783, 1961, Brefeld's herbarium is stated to be accessible, but this does not accord with information received from Dr B. Hein, Curator of the Berlin Herbarium. He has searched in vain for *P. nyctalidis* and other Brefeldian collections.

Fortunately there is an authentic sample of *P. nyctalidis* in Zürich (ZT). This syntype can be used for lectotypification if one of the proposals to change Art. 59 be accepted (p. 122). In such a case also the Tulasnes' material of the species will receive syntype status as part of the protologue of *P. nyctalidis*.

Distribution. *P. asterophora* is undoubtedly rare. Apart from France and Germany it is reported only from England (Plowright 1882) and U.S.A. (Berkeley 1875). Saccardo (1883) listed also Finland (Karsten 1873) and Italy, but the Italian collection in Herb. Saccardo (PAD) and the Uppsala copy of Karsten's Fungi Fenn. Exs. No. 512 do not exhibit the pyrenomycete. The same is certainly true for the Couans' (1867) records from Brittany, as there is no indication that perithecia were seen. Further information on the bibliography of the species is given by Arnold (1976).

The imperfect state. Figs. 1, 2. This was placed in *Polyscytalum* by Saccardo (1886), in *Chalara* by Lindau (1906), in *Paecilomyces* by Tubaki (1958 p. 206), and again in *Chalara* by Nag Raj & Kendrick (1975) in their monograph of this genus. There is still some uncertainty about the correct epithet of the anamorph. The latter authors rejected the name *Chalara brefeldii* as a nomen dubium, as they had not been able to locate and examine the type. Nor could they get enough information from the description. They obviously allude to Brefeld & von Tavel's publication, but overlooked that *C. brefeldii* and *Polyscytalum fungorum* are both founded on Plowright's English material. This type collection, if it exists, has apparently not been re-studied.

***Pyxidiophora badiorostri* Lundq. sp. nov.**
—Figs. 6 F–H, 8

From Latin *badius*, chestnut-brown, and *-rostris*, beaked, referring to the brown perithecial neck.

Nonstromatica; perithecia semi-immersa, vulgo dispersa, 230–295×105–140 μm , globosa, longicollia, \pm glabra; collum 95–145×21–28 μm , sursum decrescens, apice conico, valde transverse rugosum, badium. *Peridium* membranaceum, semipellucidum, flavidum, cellulis externis angulatis vel rotundatis, 10–23 μm diam.; cellulae externae colli elongatae, 10–20×4.5 μm , circa ostiolum longe acutae, cristis crassis, badiis, transversis, anastomosantibus obtectae. *Paraphyses* carentes. *Asci* trispori, 45–50×10–20 μm , subclavati, inamyloidei, cito deliquescentes. *Sporae* 38–52×4.5–5.5 μm , longe clavato-fusiformes, basim versus attenuatae, hyalinae; protoplastus 27–38×3–3.5 μm , utrinque acutus tum rotundatus, infra medium 1(–2)-septatus; paries sporarum praesertim apicaliter tumescens, appendicem basalem, 14–18 μm longam formans, maturitate corpore brunneo, applanato, rotundato, subapicali, 5–6×4.5×2 μm , instructus. Species coprophila.

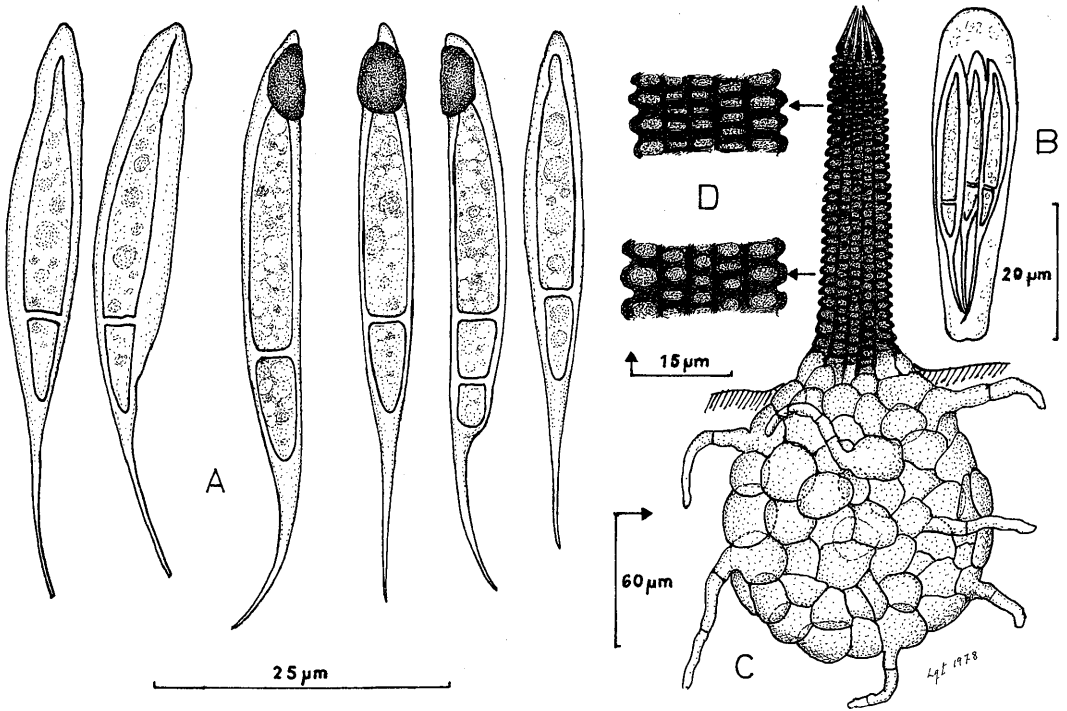


Fig. 8. *Pyxidiophora badiorostris* n. sp. A, B: Lqt 3165 (UPS, holotype). C, D: Lqt 2776-e (UPS). — A: Spores at hyaline and pigmented stages. — B: Young, three-spored ascus. — C: Perithecium. — D: Detail of the perithecial neck.

Non-stromatic; *perithecia* scattered or aggregated, $230\text{--}295 \times 105\text{--}140 \mu\text{m}$, rounded, long-necked, glabrous or with a few thick, hyaline hairs; neck $95\text{--}145 \mu\text{m}$ long, $21\text{--}28 \mu\text{m}$ wide below, $13\text{--}15 \mu\text{m}$ wide above, conical at the tip, rugose, chestnut-brown. *Peridium* membranaceous, semi-transparent, yellowish, with thin-walled, angular to rounded, $10\text{--}23 \mu\text{m}$ large outer cells; neck cells cylindrical, $10\text{--}20 \times 4.5 \mu\text{m}$, forming 5–6 visible longitudinal rows, pointed around the ostiolum, covered with brown, thickened, transverse, anastomosing ridges and plates. *Paraphyses* lacking. *Asci* unitunicate, 3-spored, $45\text{--}50 \times 10\text{--}12 \mu\text{m}$, subclavate, non-amyloid, without apical apparatus, deliquescing. *Spores* gathering around the ostiolum in slimy masses, $38\text{--}52 \times 4.5\text{--}5.5 \mu\text{m}$, hyaline, elongate, clavate-fusiform, with a drawn-out base; protoplast $27\text{--}38 \times 3\text{--}3.5 \mu\text{m}$, with acute, later rounded ends, 1(–2)-septate below the middle; outer spore wall swelling, particularly in the upper part of the spore, giving it an obtuse

although tapering profile, often slightly constricted below the apex, and forming a $14\text{--}18 \mu\text{m}$ long basal elongation. At maturity a brown, flattened, rounded body, $5.5\text{--}6 \times 4.5 \times 2 \mu\text{m}$, is laid down subapically and laterally in the spore wall. Coprophilous.

Specimens examined. Sweden: Ångermanland, Ytterlännäs par., Västertorp, on cow dung, 20.VIII.1961, Lqt 3165-e (UPS, holotype); isotypes in K, S, TRTC. — Jämtland, Hammerdal par., Fyrås, on cow dung, 14.VIII.1960, Lqt 2776-e (UPS).

The specimens appeared after 23–28 days in moist chamber cultures. *P. badiorostris* is easily distinguished from all other *Pyxidiophorae* by its brown, rugose perithecial neck. No distinct stroma has been observed, nor any conidial state.

Pyxidiophora bainemensis (Bret. & Faur.) Lundq. comb. nov.

Mycorhynchus bainemensis Bret. & Faur. 1968 p. 246.

Acariniola basalipunctata Maj. & Wiśn. 1978 a p. 9

This may be a synonym of *Pyxidiophora subbasali-punctata* (Maj. & Wiśn.) Lundq.; see comment under *Acariniola*.

Mycorhynchus brunneo-capitatus Hawksw. & Webst. 1977 p. 331

This species could be the same as *Pyxidiophora microspora* (Hawksw. & Webst.) Lundq.; see comment under that name.

Pyxidiophora caulicola (Hawksw. & Webst.) Lundq. comb. nov.

Mycorhynchus caulicola Hawksw. & Webst. 1977 p. 331.

Pyxidiophora fusco-olivacea (G. Arnold) Lundq. comb. nov.

Mycorhynchus fusco-olivaceus G. Arnold 1972 a p. 190.

Pyxidiophora grovei (Hawksw. & Webst.) Lundq. comb. nov.—Figs. 9, 10.

Mycorhynchus grovei Hawksw. & Webst. 1977 p. 333.

Perithecia free or gregarious on a stroma, yellowish, glabrous or with a few thick, hyaline hairs, globose, long-necked, 200–290×70–95 μm; neck cylindrical to tapering, pointed, 100–190 μm long, 20–28 μm wide below, c. 14 μm wide above, composed of cylindrical cells, 15–31×3–4 μm, ending in narrow beaks around the ostiolum; outer peridial cells rounded to angular, 9–18(–23) μm in diam. *Paraphyses* absent. *Asci* 3-spored, c. 55×20 μm, ellipsoidal, evanescent. *Spores* clavate-fusiform, (43–)48–58×4.5–6 μm, swelling up to 8 μm in width, hyaline to yellowish; protoplast at first fusiform, often truncate at base, then rounding up at the ends, 38–45×3–4.5 μm, with a transverse septum in or just below the middle; the inflated wall forms an acute apex and a 13–16 μm long, whip-like, basal elongation. At maturity a subapical, flattened, round or angular, brown body, 4–5×3–4×1.5–2.5 μm, occasionally with a central pore, is formed laterally in the spore wall.

Specimens examined. Sweden: Uppland, Forsmark par., Röngrund, on fresh sheep dung, 26.IX.1962, Lqt 3788-a (IMI, PC, S, UPS). Haga par., Åtorpet, on fresh

elk dung, 18.XI.1979, Gunnerbeck 3477-d (UPS). Uppsala, Marieberg, on sheep dung, 23.VII.1964, Lqt 4302-c (UPS). New to northern Europe.

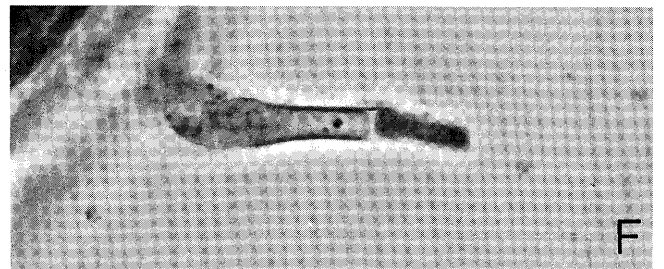
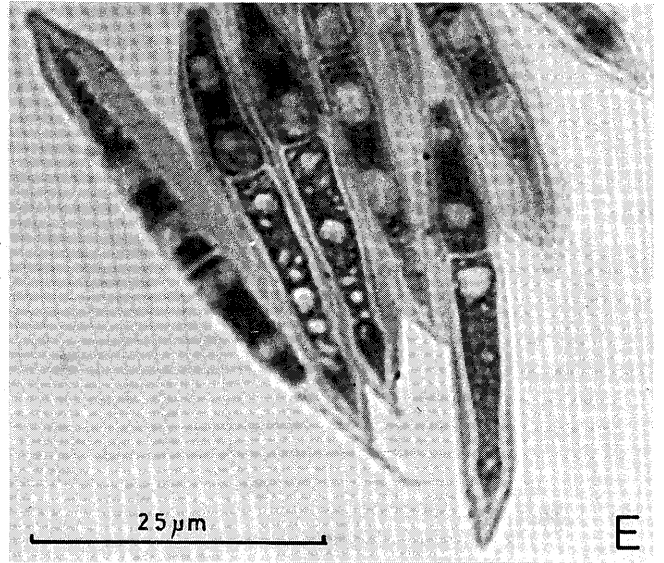
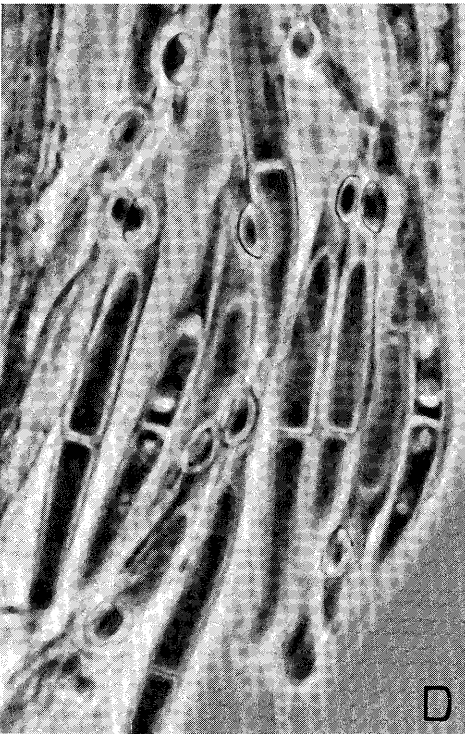
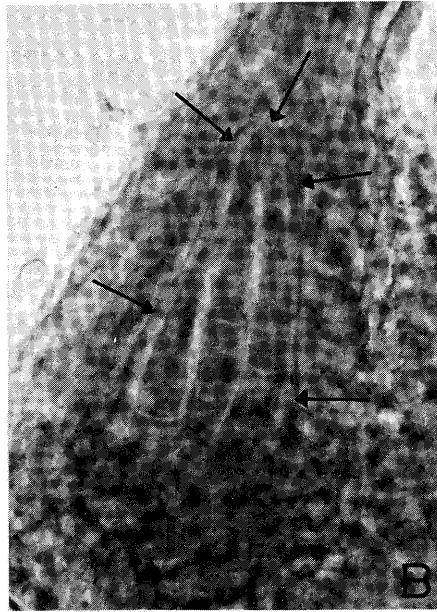
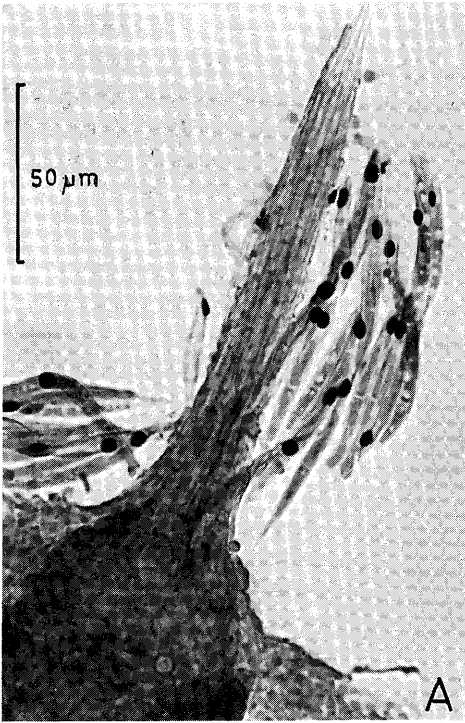
The only find hitherto known is on horse dung from Liverpool, England (Grove 1932 as *Mycorhynchus marchalii*; Hawksworth & Webster 1977). The Swedish specimens appeared after 11–12 days in moist chamber. They are accompanied by a *Chalara* state (Fig. 8 F), indistinguishable from that found together with *P. arvernensis*. Neither in this case has the connection been proved.

According to the original description, *P. grovei* deviates from my specimens by smaller neck cells (10×3 μm), slightly longer spores (53–65 μm), and absence of a pigmented stage and a stroma. However, Dr David Hawksworth (Kew) has told me (in litt.) that he has re-examined the type collection of *P. grovei* and discovered three pigmented spores, and found that the neck cells could be up to 32 μm long. He also remarks that the tendency to form a stroma seems to be general in the genus, and he does not attach much taxonomic importance to it.

The related *Pyxidiophora petchii* (Bret. & Faur.) Lundq. (= *Mycorhynchus marchalii* sensu Petch 1941) matches Swedish material in some respects too, for example as regards the occurrence of a stroma and the size of the neck cells. On studying the original slides (in BM), Breton & Faurel (1968) also detected two pigmented spores. On the other hand, *P. petchii* is caulicolous and its peridial cells are much too small, only 7–10 μm in diam. Furthermore, Petch's spore measurements are unreliable in this case. They were stated to be 40–63×6–7 μm, but both Breton & Faurel and Hawksworth & Webster (1977), who investigated dried material in Kew, could not find spores exceeding 53 μm in length. Dr Hawksworth has kindly compared material of my 4302-c with both *P. grovei* and *P. petchii*, and found it to accord with the former species. Particularly the longer and slender spores and the larger peridial cells distinguish *P. grovei* from *P. petchii*.

Pyxidiophora marchalii (Sacc.) Lundq. comb. nov.

Rhynchomyces marchalii Sacc. in March. 1885 p. 60.



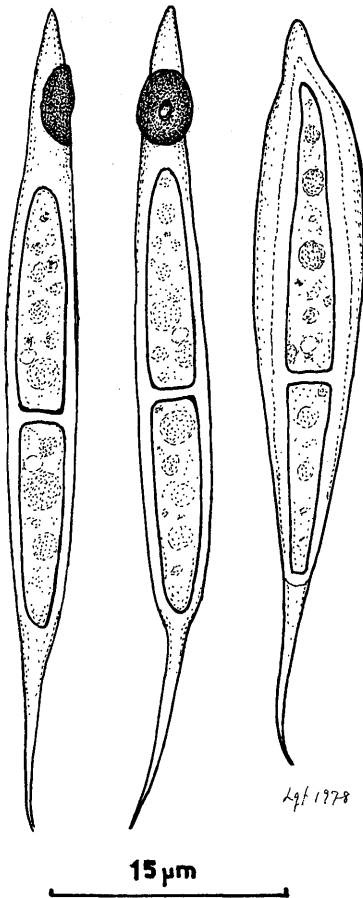


Fig. 10. *Pyxidiophora grovei*. Lqt 4302-c (UPS). Spores at pigmented and hyaline stages.

***Pyxidiophora microspora* (Hawksw. & Webst.) Lundq. comb. nov.**

Mycorhynchus microsporus Hawksw. & Webster. 1977 p. 336.

Mycorhynchus brunneocapitatus Hawksw. & Webst. (1977 p. 331) may be a synonym. The only tangible difference between the two is the pigmented spores in *M. brunneocapitatus*. Dr Hawksworth reports (in litt.) that he has investi-

gated a rich material of *P. microspora* without finding any pigmentation, whereas such occurred regularly in mature spores of *M. brunneocapitatus*. I am not fully convinced that this difference is constant. Dr Hawksworth suggests that if the species be united, *microsporus* is the epithet to be preferred.

***Pyxidiophora moseri* (Maj. & Wiśn.) Lundq. comb. nov.**

Acariniola moseri Maj. & Wiśn. 1978 a p. 5. The species is discussed under *Acariniola*.

***Pyxidiophora petchii* (Bret. & Faur.) Lundq. comb. nov.**

Mycorhynchus petchii Bret. & Faur. 1968 p. 244. See comment under *P. grovei*.

***Pyxidiophora schotteriana* (Bret. & Faur.) Lundq. comb. nov.**

Mycorhynchus schotterianus Bret. & Faur. 1968 p. 250.

***Pyxidiophora spinuliformis* (Speg.) Lundq. comb. nov.**

Copranophilus spinuliformis Speg. 1909 p. 410. See comment under *Copranophilus*.

***Pyxidiophora subbasalipunctata* (Maj. & Wiśn.) Lundq. comb. nov.**

Acariniola subbasalipunctata Maj. & Wiśn. 1978 a p. 7. See comment under *Acariniola*.

***Mycorhynchus subspinuliformis* Bret. & Faur. 1968 p. 252.**

The status of this species is doubtful. Although lacking(?) a stroma and a conidial state, it is very close to *Pyxidiophora spinuliformis* (incl. *Ascolanthes trisporus*) in certain perithecial and sporal characters. It has, to mention one, the same kind of two-capped pigmentation of the spores. The species should be studied anew.

Fig. 9. *Pyxidiophora grovei*. A, B, D-F: Lqt 4302-c (UPS). C: Lqt 3799-a (UPS). Material in lactic blue. Figs. B-D, F taken in phase contrast. — A: Perithecium with pigmented spores. — B: Perithecium with a young, three-spored ascus visible through the wall (arrows mark the outline of the ascus). — C-E: Spores; compare the form of the ends of the protoplasts in the pigmented and the hyaline spores. — F: *Chalara* phialide with a conidium. Scale: B-D, F = E.

Ascolanthanus trisporus Caill. 1967 p. 1474; not validly published.

As has been elucidated earlier in the present paper, the differences between this species and *Copranophilus spinuliformis* Speg. are insignificant. If the former is to be accepted as an independent species, its name must first be validated by a typification. Cailleux (1967, 1973) mentioned but did not specify the type. Since a valid publication of a name requires an indication of the type (Article 37), one must require that at least some clue to it shall be *published*, irrespective of whether the type is marked in the herbarium or not. This is also the interpretation of Hawksworth (1974 p. 156), who cites an example directly applicable here.

Dubious names

Hypomyces fusisporus Tul. in Tul. & Tul. 1865 p. 55

The perithecia are said to be whitish to dingy, elongate, 150–200×50–60 μm, the asci broadly obovoid, 4-spored, and the spores obovoid-fusiform, 50×10 μm, with a cuspidate base.

The type collection is from Chaville in Seine-et-Oise, France, 3.VII.1860, Herb. Tulasne (PC). It has the text "perexigua, Sphaeromematis aemula, in Ag. adusto nyctaliifero" and a poor drawing of a spore that is hyaline, claviform with a mucronate apex and a longitudinal row of three oil drops(?) in the middle.

M. Cornu (XI.1887), Maire (1911), and Arnold (6.I.1965) studied the material without finding any pyrenomycete, and they all treated *H. fusisporus* as a synonym of *H. asterophorus* Tul. (= *Pyxidiophora a.*). I can verify that the species is no longer present on the scarce substrate, which is *Asterophora parasitica* (Bull. ex Fr.) Sing.

The smooth-walled chlamydospores typical of this agaric are also found here. The Tulasnes were acquainted with these spores, which they naturally thought to be parasitic and specifically distinct from *H. asterophorus*. They consequently established a new species, *Hypomyces baryanus*, solely for these chlamydospores, but the name is illegitimate according to Art. 59.3 (Tulasne & Tulasne 1860 p. 13).

Treleasia? musicola Speg. 1909 p. 411

Authentic specimens are lacking according to Breton & Faurel's (1968 p. 232) and my own

examination of the type collection (on banana leaves, La Plata, 30.IX.1906, C. Spegazzini, LPS 1752). Only nine empty leaf fragments are left, and an enclosed drawing almost identical to the published illustration. The species looks like a member of *Pyxidiophora*, except that the asci have a short, narrow stipe and a tapering tip. If this is correctly interpreted, *T. musicola* may not belong in *Pyxidiophora*, but Spegazzini may also have made a mistake (cf. *T. sacchari*).

Treleasia sacchari Speg. 1896 p. 235

This species is discussed under *Treleasia*. It is certainly a representative of *Pyxidiophora* s. lato. No type specimens exist.

Excluded species

Mycorhynchus betae (Hollr.) Sacc. & D. Sacc. 1906 p. 418

Sphaeronaema betae Hollr. 1904 p. 202. This is a coelomycete.

Mycorhynchus exilis (Höhn.) Sacc. & D. Sacc. 1906 p. 418

Rhynchomyces exilis Höhn. 1902 p. 1021. This is a coelomycete.

Acknowledgements. I am greatly indebted to Dr E. Gunnerbeck, Uppsala, for discussions on the nomenclature and for his opinions on my manuscript, to Dr D. Hawksworth, Kew, for his help with the identification of *P. grovei* and for valuable remarks on various taxonomic problems in the genus, and to Dr A. Parguey-Leduc, Paris, for sending me excerpts of F. Durand's unpublished thesis. I have also benefitted from correspondence in the matter with Dr E. Müller, Zürich, Dr A. Breton, Clermont-Ferrand, Dr R. Cailleux, Paris, Dr T. Majewski, Warsaw, and the Curators of the Berlin (B), Hamburg (HBG), Munich (M), Münster (MSTR), and Paris (PC) Herbaria. Loans from PC, ZT, and WR are also acknowledged.

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