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## NOTES ON HYGROPHORACEAE—VIII

Taxonomic and nomenclatural notes on some taxa of *Hygrocybe*

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Taxonomic status and nomenclature of several European taxa of *Hygrocybe* are discussed. It is argued why some new combinations, made in a previous paper (Arnolds, 1985b) were proposed. Three new taxa are described to replace incorrect names: *Hygrocybe cystidiata* Arnolds (= *H. obrussea* sensu Kühner), *H. lepida* Arnolds (= *H. cantharellus* sensu auct.) and *H. conica* var. *conicopalustris* (R. Haller ex) Arnolds (= *H. conicopalustris* R. Haller, nom. inval.). Three new combinations are proposed: *Hygrocybe miniata* (Fr.: Fr.) Kumm. var. *mollis* (B. & Br.) Arnolds, *H. virginea* (Wulf.: Fr.) Orton & Watl. var. *fuscescens* (Bres.) Arnolds and *H. persistens* (Britz.) Sing. var. *cuspidata* (Peck) Arnolds. The following names are reduced to synonyms of older or sanctioned names: *Hygrophorus quietus* Kühner = *Agaricus obrusseus* Fr.: Fr.; *Agaricus tristis* Pers. = *A. conicus* Schaeff.: Fr.; *Hygrocybe euroflavescens* Kühner = *Hygrophorus flavescens* C. H. Kauffm.; *Mycena acutoconica* F. Clem. = *Hygrophorus persistens* (Britz.) Britz.; *Hygrocybe aurantiolutescens* P. D. Orton = *Hygrophorus cuspidatus* Peck; *Hygrocybe pseudocuspidata* Kühner = *Hygrophorus cuspidatus* Peck; *Hygrocybe moseri* M. Bon = *Agaricus miniatus* Fr.: Fr.; *Hygrophorus strangulatus* P. D. Orton = *Agaricus miniatus* Fr.: Fr.; *Hygrophorus squamulosus* Ellis & Ev. = *Agaricus miniatus* Fr.: Fr.; *Hygrocybe vitellinoides* M. Bon = *Agaricus ceraceus* Fr.: Fr.; *Hygrocybe subceracea* Murrill = *Agaricus ceraceus* Fr.: Fr.; *Hygrophorus niveus* (Fr.) Fr. = *Agaricus virgineus* Wulf.: Fr. Descriptive notes are given on the holotypes of *Hygrocybe vitellinoides* M. Bon, *H. moseri* M. Bon, *Hygrophorus strangulatus* P. D. Orton and *Hygrocybe aurantiolutescens* P. D. Orton. Neotypes are designated and shortly described of *Agaricus miniatus* Fr.: Fr., *Agaricus ceraceus* Fr.: Fr. and *Agaricus obrusseus* Fr.: Fr.

In the framework of the 'Flora agaricina neerlandica' (see Bas, 1983) a revision was made of the genus *Hygrocybe* in the Netherlands and adjacent regions (Arnolds, in prep.). Some taxonomic and nomenclatural problems met during this work are discussed in this paper in alphabetic order of the epitheta. The yellow species with viscid stipe and pileus, placed in *Hygrocybe* subsect. *Inspidae*, e.g. *Hygrocybe glutinipes* and *H. vitellina*, will be treated in a separate paper since more extensive research in this group is necessary.

**acutoconica.**—*Hygrocybe acutoconica* (F. Clem.) Sing. was originally described from North America as *Mycena acutoconica* by Clements (1893: 38). In my opinion it

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is a synonym of *H. persistens* (Britz.) Sing. and the latter name is considered to have priority. See discussion on that epithet.

**alboviolacea.**—*Hygrophorus alboviolaceus* was informally described by Arnolds (1974a: 94) as 'nov. spec. ad interim.' The only collection is characterized by the white lower part of the stipe, separated by a sharp line from the violaceous grey upper part. However, I have observed such a silvery white base of the stipe later on in other species of *Hygrocybe* as well, among others in *Hygrocybe fornicata* (Fr.) Sing. and *H. pratensis* (Pers.: Fr.) Murrill, always in late autumn. The white 'stockinged feet' is caused by strong aeration of the outer tissue of the stipe, apparently due to cold and wet weather conditions. Also the presence of many spores with an abnormal shape, another difference with related species, points to deviating fruiting conditions. At present I regard *H. alboviolaceus* as a synonym of *Hygrocybe subviolacea* (Peck) Orton & Watl.

*Hygrophorus alboviolaceus* was treated as a distinct species of *Camarophyllus* by Cléménçon (1982: 50), but fortunately not validated on that occasion.

**ambigua.**—*Hygrocybe coccineocrenata* forma *ambigua* Kühner is regarded as a synonym of *H. coccineocrenata* var. *sphagnophila* (Peck) Arnolds. See there.

**aurantiaca.**—See for a discussion on *H. chlorophana* var. *aurantiaca* M. Bon the species epithet.

**aurantiolutescens.**—*Hygrocybe aurantiolutescens* was described by Orton (1969: 103) as a species close to *H. langei* (= *H. persistens*), but different in (1) the 4-spored (instead of 2-spored) basidia, (2) the pileus, being first scarlet or orange-scarlet (instead of orange-red with more yellow margin), (3) the lamellae, being 'pale then deeper chrome-yellow, sometimes becoming flushed orange' (instead of 'lemon or sulphur yellow, rarely tinged slightly chrome') and (4) the less persistently, more obtusely conical pileus.

In my opinion the shape of the pileus in typical *H. persistens* varies from obtusely to very acutely conical. The differences in colour of the lamellae are very subtle. Moreover, in an earlier key Orton (1960: 254) described the lamellae of *H. langei* as follows: 'Cap golden or lemon-yellow, sometimes orange or orange-red in places; stem and gills concolorous or yellow...'

Apparently the main difference between the two species is the number of sterigmata on the basidia, also stressed by Bon (1976b: 9). As I demonstrated before (Arnolds, 1974a) this is a most variable character in the entire conica-group of *Hygrocybe*. Among 17 collections of *H. persistens* (incl. var. *cuspidata*) in the Netherlands five were predominantly 4-spored (some 2- or 3-spored basidia present), five predominantly 2-(4-, 3-, 1-)spored; five were 4- and 2-(1-, 3-)spored intermixed in almost equal proportions, one was 3- and 2-spored intermixed and one collection was predominantly 1-(2-)spored (Arnolds, 1974a: 134, 138; 1983: 383).

I studied the isotype of *H. aurantiosplendens* (Orton 2797, E) and even in that collection I found two carpophores with mainly 4-spored basidia, one 4- and 3-spored intermixed and one predominantly 2-(3-, 4-)spored.

In view of these observations I consider *H. aurantio-lutescens* as a synonym of *H. persistens* var. *cuspidata*, differing from var. *persistens* only in the red pileus in young basidiocarps (see *cuspidata*).

**berkeleyanus.**—*Camarophyllus berkeleyanus* Cléménçon (1982: 55) is a superfluous renaming of *Hygrocybe berkeleyi* (P. D. Orton) Orton & Watling (see there).

**berkeleyi.**—*Hygrocybe berkeleyi* (P. D. Orton) Orton & Watl. (= *Camarophyllus berkeleyanus* Cléménçon, 1982 = *Hygrocybe ortonii* M. Bon, 1983) has the stature, habitat and microscopic characters of *H. pratensis* (Pers.: Fr.) Murrill. In fact it only differs in much paler colours of the basidiocarps: the pileus is ivory white at first, then pale ochre or isabella. These colours show strong qualitative resemblance to the colours of *H. pratensis*, ranging in that species from pale orange to orange-brown, and in fact differ only in intensity. Therefore I prefer to treat this taxon as a variety of *H. pratensis*, even if no intermediate forms are known at present (cf. Kuyper, 1986). The correct name in this rank is *Hygrocybe pratensis* var. *pallida* (Cooke) Arnolds (1985b: 477).

**cantharellus.**—*Agaricus cantharellus* was described by Schweinitz (1822: 88) from North America as a small, orange agaric with an undulating pileus and few, strongly decurrent lamellae, growing gregarious on rotting wood ('Gregarie crescit in truncis putredine consumtis et in terra lignosa frequens'). The morphological characters may apply to the fungus, usually named *Hygrocybe cantharellus* (Schw.: Fr.) Murrill, but the habitat and gregarious fruiting are quite deviating: *Hygrocybe cantharellus* sensu auct. is a terrestrial fungus, often growing amongst grasses or mosses. This discrepancy was noticed before by Rald (1986: 11). He synonymized *H. cantharellus* sensu auct. with *H. turunda* (Fr.: Fr.) P. Karst., but I do not agree with that point of view: *H. turunda* is in my opinion a species with a yellow pileus already in young basidiocarps, supplied with distinct brown scales, with broadly adnate or hardly decurrent lamellae and small spores ( $\pm 7-8.5 \times 4.5-5.5 \mu\text{m}$ ), broadened to the apex in face-view (Arnolds, 1974a: 174; 1986b). *Hygrocybe cantharellus* has an orange-red to scarlet pileus when young with concolorous or paler scales, distinctly decurrent lamellae and larger spores ( $\pm 8-11.5 \times 5-7 \mu\text{m}$ ), not broadened in face-view.

Consequently *H. cantharellus* sensu auct. is in need of a new name. It was well described and depicted by Boudier (1897: 12, pl. 1, fig. 1) as *Hygrophorus turundus* var. *lepidus*. I wish to use Boudier's name at the rank of species, but I prefer to describe it as a new species rather than to make a new combination because in this way I have the opportunity to link this name to a type collection.

### *Hygrocybe lepidus* Arnolds, *spec. nov.*

Pileus 7–22(–30) mm, semiglobatus vel convexus, dein plano-convexus, disco vulgo depressus vel umbilicatus, margine vulgo crenulatus, hygrophanus, miniatus vel aurantio-ruber, dein aurantio-flavus, siccus, disco squamulis parvis pilosis aurantiis obtectus. Lamellae (L = 16–30, l = 1–3(–7)) decurrentes, distantes, albae, dein cremeae vel pallide luteae, interdum pro parte aurantio-flavae. Stipes 15–50(–65)  $\times$  1.5–4 mm, aequalis, miniatus vel aurantio-ruber, dein aurantio-flavus, ad basium pallide luteus vel albidus. Caro concolor. Odor et sapor nulli. Sporae (7–)8–11.5  $\times$  (4.5–)5–7(–7.5)

$\mu\text{m}$ ,  $Q = 1.4-1.7(-1.9)$ , ellipsoideae(-oblongae) vel obovoideae(-oblongae), frequente pro parte phaseoliformae, haud lentiformae, interdum leviter strangulatae. Basidia 35-65(-72)  $\times$  7.5-11.5  $\mu\text{m}$ , clavata, 4-(2-)sporigera. Lamellarum acies fertiles. Lamellarum trama subregularis, cellulis brevis, 26-110  $\times$  (5.5-)9-20(-25)  $\mu\text{m}$ . Pileipellis cutiformis, ad discum trichodermiformis, hyphis ad septa strangulatis, cellulis exterioris subcylindraceis vel clavatis, 30-125  $\times$  (4.5-)7-17  $\mu\text{m}$ . Stipitipellis cutiformis, hyphis 2.5-5.5  $\mu\text{m}$  latis. Fibulae frequentes. Inter graminosis et muscos ad terram. — Holotypus: Netherlands, prov. Drenthe, Dwingeloo, Lheebroekerzand, near Kliploo, in juniper scrub, 8 Nov. 1968, *Barkman 8871* (WBS).

I refrain here from giving a description in English since several modern descriptions are available (e.g. Arnolds, 1974a; Kühner, 1976, 1979) and an extensive description based on collections from the Netherlands will be published in 'Flora agaricina neerlandica' Vol. 2 (Arnolds, 1986b).

It is interesting to know which species Schweinitz (1822) had in mind when describing *Agaricus cantharellus*, especially since this name was sanctioned by Fries in the Index of Systema (1832).

Rald (1986) suggested that *A. cantharellus* is identical with *Gerronema grossulum*, but this seems unlikely as the latter species has an olivaceous yellow pileus, whereas the former species was described as 'aurantiacus'. Kuyper (pers. comm.) noted that *A. cantharellus* fits in all respects with *Omphalina luteicolor* Murrill, a well known agaric growing gregariously on conifer logs that seems to be restricted to the Pacific northwest of America (Bigelow, 1970). However, as Schweinitz (1822) reported his species from eastern North America (Carolina), such an identity may be questioned too. For the time being I regard therefore *A. cantharellus* as a nomen dubium.

**ceracea** — *Agaricus ceraceus* was described and sanctioned by Fries (1821: 102) as a small species with an obtuse, yellow, viscid pileus,  $\pm$  13-25 mm broad, a thin, yellow stipe and broad, adnate to more or less decurrent lamellae ('adnato-decurrentibus'), common in meadows. The epithet has become confusing since Hesler & Smith (1963: 240) described *Hygrophorus ceraceus* from North America with a viscid stipe and rather broad spores, 5.5-8  $\times$  4-5  $\mu\text{m}$ . A similar fungus with a dry stipe and narrower spores (5-7.5  $\times$  2.5-3.5  $\mu\text{m}$ ) was redescribed by them as *Hygrophorus subceraceus* (Murrill) Murrill. Among the collections studied they listed also one from the Netherlands (*Moss Geesteranus 13478*). This concept of *H. ceracea* was followed by e.g. Kühner (1977: 74) and Moser (1978: 85).

I have argued before (Arnolds, 1974a: 206; 1983: 386) that Fries in his descriptions (1821: 102, 1838: 330, 1851: 138, 1874: 417) never attributed a viscid stipe to *Agaricus (Hygrophorus) ceraceus* and that the species that is widespread in N. W. Europe has no viscid stipe indeed. Consequently *Hygrocybe subceracea* Murrill is a synonym of *H. ceracea* and *Hygrophorus ceraceus* sensu Hesler & Smith is a misapplication.

The typification of *Agaricus ceraceus* is rather complicated. The authors are usually quoted as 'Wulf.: Fr.', but this is not correct since Fries (1821: 103) excluded *Agaricus ceraceus* Wulf. as a separate form ('b A. cer. Wulf. . .') with a dry pileus. Among the references under *A. ceraceus* Fr. are *Agaricus ceraceus* Sow. (1796: pl. 20) and *A. ceraceus* Pers. (1801: 336), but since these authors (indirectly) refer to *A. ceraceus* Wulf.

their names and concepts are not relevant from a nomenclatural point of view. It is remarkable, by the way, that Persoon, like Von Wulfen (in Jacquin, 1781: 105) described the pileus as not viscid, but that Fries (l.c.) enumerated Persoon's description under *Agaricus ceraceus* with viscid pileus. Whatever it may be, according to article 48 of IBCN ('When an author adopts an existing name but explicitly excludes its original type, he is considered to have published a later homonym that must be ascribed solely to him...') the sanctioned name *Agaricus ceraceus* must be ascribed to Fries.

In view of the existing confusion it seems useful to select a neotype of *Hygrocybe ceracea*. I failed to obtain well-annotated collections from South Sweden for this aim. The exsiccata distributed by Lundell & Nannfeldt as *Hygrocybe ceracea* (No. 542) represent in fact *H. chlorophana*, a quite different fungus with almost free lamellae and a trama of the conica type. In this case I prefer to select a well-annotated, rich collection from another region than the type locality.

Therefore I propose as neotype of *H. ceracea* (Fr.) Kumm. the collection *Arnolds 3095* (10 Nov. 1973, Wilp, Gelderland, the Netherlands), preserved at the Biological Station at Wijster (WBS). This material has been described and depicted before (Arnolds, 1983: 386, fig. 184, pl. 5C).

**chloroides.**—The combination *Hygrocybe conica* var. *chloroides* (Malençon) Arnolds was recently made (Arnolds, 1985b; Nov. 1985), but it is antedated by a publication by Bon (1985a: 52). See also discussion on *H. conica*.

**chlorophana.**—At present *Hygrocybe chlorophana* (Fr.: Fr.) Wünsche is usually regarded as a species with strictly regular trama, a lemon to chrome yellow, viscid to glutinous pileus, narrowly adnate, pale yellow lamellae and a yellow, viscid stipe. The pileipellis is an ixotrichodermium, whereas the stipitipellis is an ixocutis or an ixotrichodermium, 50–200(–550)  $\mu\text{m}$  wide.

A closely related species is *H. flavescens* (C. H. Kauffm.) Sing. (= *H. euroflavescens* Kühner, see there) with orange basidiocarps, a viscid to glutinous pileus and a dry to slightly viscid stipe, covered with a cutis or ixocutis  $\pm$  15–50(–60)  $\mu\text{m}$  wide. The situation has become more complicated by the description of *H. chlorophana* var. *aurantiaca* M. Bon (1976a: 42), combining orange colours with a viscid stipe, with a microscopical structure similar to typical *chlorophana*.

In the Netherlands these three taxa have been found as well (Arnolds, 1986b), but they could not always be clearly distinguished. Between *H. flavescens* and *H. chlorophana* var. *aurantiaca* intermediate forms were observed with a slightly viscid stipe covered with a rather thin,  $\pm$  40–70  $\mu\text{m}$  wide ixocutis. An additional complication is the fact that the macroscopic appreciation of the surface of the stipe may differ considerably from the microscopic analysis: a dry stipe to the touch may reveal a thick ixocutis, whereas an undoubtedly viscid stipe may be correlated with only a thin ixocutis. Therefore I am increasingly inclined to reunite *H. chlorophana* and *H. flavescens* into one species, possibly with several varieties. One fact restraining me for the moment is the lack, at least to my knowledge, of collections uniting pale yellow basidiocarps with a dry to subviscid stipe. See also *flavescens*.



**clivialis.**—*Hygrocybe clivialis* (Fr.) Orton & Watl. is considered a synonym of *H. fornicata* var. *fornicata* (see there).

**conica.**—According to Kühner (1977: 84) the name *Hygrocybe conica* (Scop.: Fr.) Kumm. sensu stricto should be restricted to a blackening species with a yellow pileus at first. Such 'forms' have usually been described as *Hygrocybe tristis* (Pers.) Moell. (e.g. Moser, 1978: 86) or *H. conica* var. *chloroides* (e.g. Bon, 1976b: 5).

Fries (1821: 103) at first had a very wide concept of *Agaricus conicus*, including blackening and non-blackening forms with a colour of the pileus varying from yellow, orange and red to dark brown ('fuliginous'). The name must be applied to a blackening agaric since Fries (l.c.) wrote: 'Color variat; sed *fractus nigrescit!* quod nulla in affini specie vidimus.' He simultaneously described four forms (a) with yellow pileus, (b) later blackening, (c) with dark brown pileus, (d) with orange or scarlet pileus. In *Epicrisis* (1838: 331) Fries mentioned the yellow form as the most widespread form of a variable species ('Valde versicolor (etiam *laete coccineus!*), *vulgo flavus*, . . .'). If *Agaricus conicus* is typified with Fries' description from 1821 it seems reasonable indeed to restrict this name to the yellow taxon. The fungus with an orange to red pileus should have a different name, e.g. *Hygrocybe pseudoconica* J. Lange as suggested by Kühner (l.c.).

However, Fries (l.c.) listed numerous references in his protologue. In my opinion this name is typified by *Agaricus conicus* Schaeff. (1774: 2). His description and plate agree with the current use of the epithet *conicus* ('pileus . . . croceo-coccineo . . .; in senio totus nigrescens'). The authors are usually quoted as Scop.: Fr. It is true that *Agaricus conicus* Scop. (1772: 443) is an older valid name, but I reject this as type of *A. conicus* Fr. since Fries (1821) indicated Scopoli's description only by page number, not by name, under form d. (Voss & al., 1983; ICBN, art. 37.2). Under the main text he gave only a direct reference to *A. conicus* Schaeff. Schaeffer (l.c.) referred to *A. conicus* Scop. with a ?. This is quite understandable since it concerns a different species with a dark red ('coccineus'), conical pileus and yellow lamellae, without any suggestion of blackening.

Consequently I regard *Agaricus conicus* Schaeff. as the name sanctioned by Fries in 1821 and therefore this name can be maintained in its current concept. See also *conicopalustris*, *pseudoconica* and *tristis*.

**conicopalustris.**—The name *Hygrophorus conico-palustris* R. Haller (1953: 141) has not been validly published since Haller (l.c.) simultaneously proposed the name *Hygrocybe conico-palustris* (ICBN, art. 34). Bon (1985b: 38) made the new combination *Hygrocybe conicopalustris* (R. Haller) M. Bon, with a reference to the basionym *Hygrophorus conicopalustris* R. Haller and indicating between brackets 'nom. alternativum.' Apparently Bon (l.c.) intended to validate this name, but in my opinion he did not succeed since he neither gave a (reference to) a Latin diagnosis and an indication of the type, nor rejected one of Haller's names but instead used one of the names (*Hygrophorus conicopalustris*) as basionym for the other (*Hygrocybe conicopalustris*).

Consequently the name has still to be validated. However, in my opinion the only difference between *H. conicopalustris* and *H. conica* (forma *conica*) is the dwarfish size of basidiocarps in the former taxon, the cap diameters ranging from 4–10(–15) and

12–60(–70) mm, respectively. Therefore I accept *H. conicopalustris* only in the rank of variety and the following validation and new combination is proposed: **Hygrocybe conica** (Schaeff.: Fr.) Kumm. var. **conicopalustris** (Haller ex) Arnolds, var. nov.

A Latin diagnosis is provided by Haller (1953: 141). Holotypus: Switzerland, Kanton Aargau, Flachmoor bei Vogelrüti, nahe Mellingen, *R. Haller s.n.*, June–Aug. 1953 (ZT).

**constrictospora**.—*Hygrocybe constrictospora* Arnolds is a new name for *Hygrophorus strangulatus* sensu Arnolds (1974a, 1977). See Arnolds 1985b: 476, 1986a.

**cuspidata**.—Hesler & Smith (1963: 135) wrote that 'the bright red color at once distinguishes *H. cuspidatus* Peck from *H. acutoconicus*.' Elsewhere (l.c.: 139) they wrote 'When faded, specimens of *H. cuspidatus* are indistinguishable from specimens of *H. acutoconicus*. Unless the red color of the former is preserved in drying, herbarium specimens of the two are also indistinguishable.' I fully agree with these observations and therefore proposed (Arnolds, 1974a: 137, 1985b: 475) to reduce *H. cuspidatus* to a variety of *H. acutoconica*, the more so since intermediate forms with an entirely or partly orange-red pileus are sometimes found. Such an intermediate collection has been figured for instance by Bresadola as *Hygrophorus croceus* (1928: 348). The two taxa are usually well separated, however.

Since in my opinion *Hygrocybe persistens* has priority over *H. acutoconica* (see *persistens*) a new combination is necessary: **Hygrocybe persistens** (Britz.) Sing. var. **cuspidata** (Peck) Arnolds, *comb. nov.* (Basionym: *Hygrophorus cuspidatus* Peck in Bull. Torrey bot. Club 24: 141. 1897). See also *pseudocuspidata*.

**cystidiata**.—*Hygrocybe cystidiata* is described here as a new species in order to replace *H. obrussea* sensu Kühner & al. since *Agaricus obrusseus* Fr.: Fr. is an earlier synonym of *Hygrophorus quietus* Kühner (see *obrussea*).

### **Hygrocybe cystidiata** Arnolds, *spec. nov.*—Figs. 1–4

Pileus 25–70 mm latus, conicus vel campanulatus, dein convexus, umbonatus, citrinus vel aureus, glaber vel fibrilloso-striatus, siccus. Lamellae librae, ventricosae, distantes, crassae, albae vel pallide citrinae. Stipes 40–80 × 6–15(–30) mm, equalis, vulgo compressus, striatus-sulcatus, glaber, siccus, citrinus, ochraceus vel aurantio-luteus. Caro fragilis, tenuis, pilei et stipitis concolor. Odor et sapor nulli. Sporae 6.5–9.5 × (4.0–)4.5–5.5(–6.5)  $\mu\text{m}$ , Q = (1.3–)1.4–1.6(–1.8), ellipsoideae, ovoideae vel phaseoliformae. Basidia 39–46 × 7–9  $\mu\text{m}$ , 4-(2-, 3-)sporigera. Lamellarum acies fertiles; cheilocystidia (pseudocystidia) pauca, 90–130 × 8.5–17  $\mu\text{m}$ , subfusiformia, apices conica. Pleurocystidia nulla. Lamellarum trama regularis, cellulis 150–500 × 14–31  $\mu\text{m}$ , vulgo apice attenuatis. Pileipellis cutis, 40–50  $\mu\text{m}$  latus, hyphis 3.5–10  $\mu\text{m}$  latis, cylindricis, interdum pro parte minor erectis. Stipitipellis cutis, 30–70  $\mu\text{m}$  latus, hyphis pro parte ascendens vel erectis, 3.5–6  $\mu\text{m}$  latis, cylindricis. In pratibus ad terram. — Holotypus: Switzerland, Teufenthal, in Moos, 9 July 1953, *R. Haller* (herb. E. Horak 63/350).

Notes on the type.—Three well-dried basidiocarps. Pileus 20–42 mm broad, convex with umbo, ochre-brown. Lamellae free, strongly ventricose, distant, up to 5 mm wide. Stipe up to 42 × 7 mm.

Spores 6.5–8.5(–9.5) × (4–)4.5–5.5(–6.5)  $\mu\text{m}$ . Q = (1.3–)1.4–1.6(–1.8), ellipsoid, obovoid to phaseoliform, rarely ellipsoid-oblong, not constricted, not broader in front-view, with small, acute apiculus. Basidia 37–47 × 7–8(–9.5)  $\mu\text{m}$ , Q = (4.5–)5–6.5, slenderly clavate, 4-spored. Edge of lamellae sterile, but with scattered pseudocystidia, originating from the trama, projecting up to 65  $\mu\text{m}$  over the edge, 90–130 × 8.5–17  $\mu\text{m}$ , slenderly fusiform with conical apex, hyaline, thin-walled. Hymenophoral trama regular, made up of long, broad elements, 150–500 × 17–31  $\mu\text{m}$ , often tapering to the ends, but also with rounded ends, without long, twisted apex. Pileipellis a thin, dry cutis, 40–50  $\mu\text{m}$  broad, gradually passing into the trama, made up of rather loose, repent hyphae, 3.5–10  $\mu\text{m}$  wide, some ascending, with a few free ends. Pileitrama regular, made up of 9–23  $\mu\text{m}$  wide hyphae, in upper part with intracellular yellow pigment, with scattered, refractive, vascular hyphae, 4.5–7  $\mu\text{m}$  wide. Stipitipellis a cutis to almost a trichodermium, up to 70  $\mu\text{m}$  thick, made up of rather loosely interwoven, ascending to erect hyphae,  $\pm$  3.5–6  $\mu\text{m}$  wide. Clamps present.

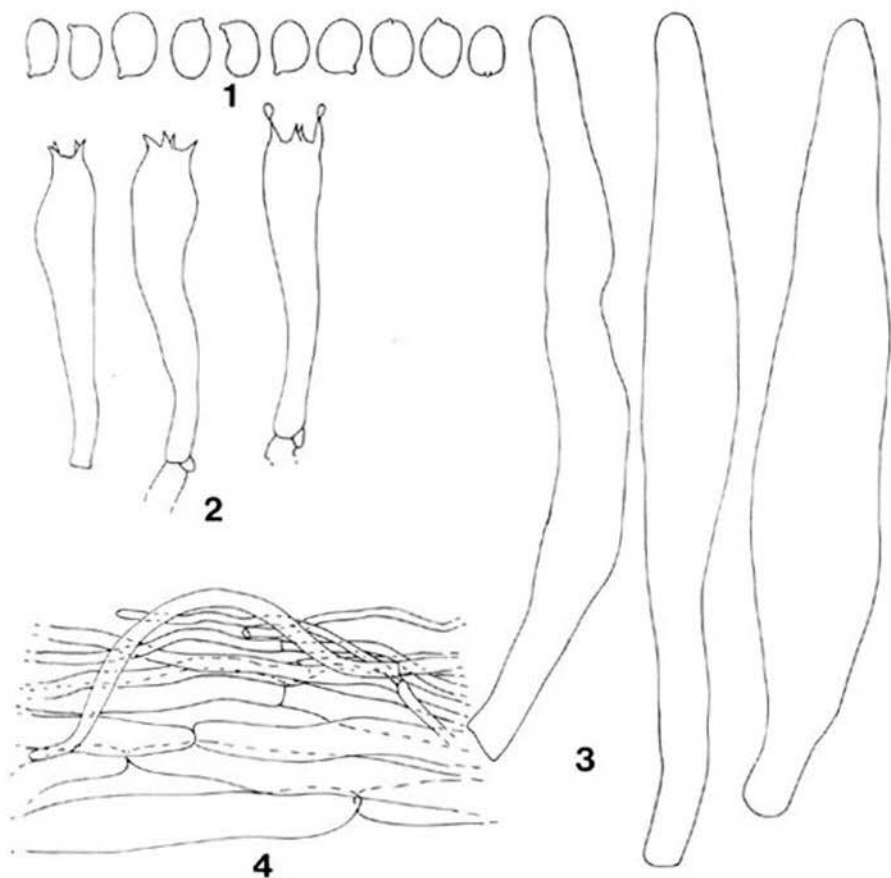
The microscopic details in the English description are entirely based on my study of the holotype. In spite of repeated requests no collections made by Kühner or Kristiansen were received on loan. For macroscopic characters of fresh specimens I have to refer to Kühner (1947: 20), Haller (1954: 84) and Kristiansen (1981: 120). *Hygrocybe cystidiata* is unknown from the Netherlands.

The name of this species refers to the large sterile elements along the edge of the lamellae. Since these elements originate from the trama they are considered as pseudocystidia. Pseudocystidia are regularly found in the section *Hygrocybe* (type: *H. conica* (Schaeff.: Fr.) Kumm.), although not constant in any species. These pseudocystidia are the projecting ends of (vascular) hyphae, of irregular shape, and are usually without septae at the base (Arnolds, 1974a, figs. 76, 77; Métrod, 1941). The pseudocystidia of *H. cystidiata* have a rather constant shape, a septum at the base and seem to be present in all collections, although they are often scarce, and absent from some lamellae.

*Hygrocybe cystidiata* is a very interesting species from a taxonomic point of view since it combines characters of the subgenera *Hygrocybe* (type: *H. conica*) and *Pseudohygrocybe* (type *H. coccinea* (Schaeff.: Fr.) Kumm.), viz.  $\pm$  conical pileus, free lamellae and strictly regular hymenophoral trama (*Hygrocybe*); small spores with small apiculus and slender basidia (*Pseudohygrocybe*) (Bon, 1977). It should be noticed that the elements of the hymenophoral trama are the shortest found in subgenus *Hygrocybe*, whereas in *Pseudohygrocybe* some species are found with approximately similar trama elements, e.g. *H. helobia* (Arnolds) M. Bon and *H. aurantioviscida* Arnolds (Arnolds, 1986b).

Bon (1977: 229) suggested that the difference in structure of the hymenophoral trama between the subgenera *Hygrocybe* and *Pseudohygrocybe* is as fundamental as between *Hygrocybe* and *Cuphophyllus* (= *Camarophyllus* sensu auct.), consequently that *Pseudohygrocybe* may be regarded as a genus in his own right. In my opinion the two groups are linked by too many intermediate forms to justify such a separation.

*Hygrocybe cystidiata* is related to *H. intermedia* (Passerini) Fay., a species with a similar habit and often with pseudocystidia, but with a red, at centre squamulose pileus, larger spores, broadly clavate basidia, and a pileipellis with a different structure (Arnolds, 1986b).



Figs. 1–4. *Hygrocybe cystidiata*. — 1. Spores  $\times 1000$ . — 2. Basidia  $\times 1000$ . — 3. Cheilocystidia  $\times 400$  (all from R. Haller, 9 July 1953, holotype).

**distans.**—*Hygrocybe distans* (Berk.) Bon & Chevassut is regarded as a synonym of *H. fomicata*. See there.

**euroflavescens.**—Kühner (1976: 463) introduced *Hygrocybe euroflavescens* as a new name for *H. flavescens* sensu Favre (1955), Orton (1960), Arnolds (1974a), auct. eur. on the basis of some discrepancies with the description of *H. flavescens* (C. H. Kauffm.) Sing., published by Hesler & Smith (1963: 211). The American collections should have a drier pileus, a more viscid stipe and lack the pruines on the stipe observed in European collections. In two American collections (*Bigelow 3296*, *Smith 63717*) Kühner (1977: 82) found the stipitipellis to be an ixotrichodermium.

However, in another American collection (*Smith 13713*) I observed only a thin ixocutis on the stipe, like in European collections (Arnolds, 1974a: 147). It is striking that Hesler & Smith (l.c.) placed *H. flavescens* in their subsection *Punicei*, characterized by a dry stipe, whereas the related *H. chlorophana* (Fr.) Wünsche was assigned to subsection *Psittacini*, characterized by a viscid to glutinous stipe. In their observations Hesler & Smith (l.c.) stressed the (almost) dry stipe surface of *H. flavescens* as the main difference with *H. chlorophana* and state that Kauffman too in his unpublished notes separated it from *H. chlorophana* by this character. This obviously contradicts Kühner's observations.

I could also not find any difference in the structure of the pileipellis between European and American collections of *H. flavescens*, ranging from a thin ixocutis (80  $\mu\text{m}$ ) to a thick ixotrichodermium (500  $\mu\text{m}$ ; see Arnolds, 1986b). The pruinosity of the stipe apex may have been overlooked or neglected by Hesler & Smith (1963) and, in any way, it is not a character of strong taxonomic importance in my opinion.

Taking everything into account, I do not see any reason to reject the name *H. flavescens* for the European collections. It is not impossible that the collections from North America, quoted by Hesler & Smith (l.c.: 212) are heterogeneous, also including collections with a viscid stipe. Such collections with orange basidiocarps can be assigned to *H. chlorophana* var. *aurantiaca* M. Bon (1976a: 42). It remains dubious whether *H. chlorophana* and *H. flavescens* are good species, after all (see *chlorophana*).

**flavescens.**—For a discussion on the nomenclature and taxonomic position of *H. flavescens* (Kauffm.) Sing., see *H. euroflavescens* and *H. chlorophana*.

**fornicata.**—*Hygrocybe fornicata* (Fr.) Sing. has been accepted in a wide sense, including *H. clivialis* (Fr.) P.D. Orton & Watling, *H. streptopus* (Fr.) Sing. & Kuthan, and *H. distans* sensu M. Bon (1976a). Two varieties can be distinguished: var. *fornicata* with a whitish to pale ochraceous pileus and var. *streptopus* (Fr.) Arnolds (1985b: 476) with a pale to dark grey-brown pileus. Variability, taxonomy and nomenclature were amply discussed in another paper (Arnolds, 1985a).

**fuscescens.**—Like the original author, Bresadola (1928), I prefer to distinguish this fungus as a variety of *Hygrocybe nivea* (= *H. virginea*): the stature, habitat and microscopic characters of the basidiocarps are completely identical. The only difference is the presence of a brown to greyish brown spot at the centre of the pileus. Occasionally even intergrading populations are found, in which part of the basidiocarps show a beige or pale brown centre of the pileus.

Since I did not accept the name *Hygrocybe virginea* until this paper a new combination is necessary: **Hygrocybe virginea** (Wulf.: Fr.) Orton & Watl. var. **fuscescens** (Bres.) Arnolds, *comb. nov.* (Basionym: *Hygrophorus niveus* var. *fuscescens* Bres., *Iconogr. mycol.* 7: pl. 330. 1928).

**griseopallida.**—*Hygrocybe griseopallida* Arnolds (1985) appears to be a form of *Hemimycena mairei* with almost smooth hyphae of the pileipellis (see Arnolds, 1986a).

*konradii*.—For a discussion on the variability of *Hygrocybe konradii* R. Haller, see pseudopersistens.

*langei*.—*Hygrocybe langei* Kühn. is regarded as a synonym of *H. persistens* (Britz.) Sing. See there.

*lepida*.—*Hygrocybe lepida* Arnolds is the valid name of *H. cantharellus* sensu auct. See that epithet.

*miniata*.—*Agaricus miniatus* was originally described by Fries (1821: 105) as a small fungus (pileus  $\pm$  13–25 mm; stipe  $\pm$  50  $\times$  2 mm) with a red, dry pileus and adnate, yellow and red ('flavo-miniatae') lamellae. The characteristic squamules were not mentioned by Fries until his description of *Hygrophorus miniatus* (Fr.: Fr.) Fr. in *Epicrisis* (1838: 330). However, since there is no contradiction between the descriptions from 1821 and 1838 it seems justified to maintain this name for a fungus with a red pileus with concolorous scales, as is custom nowadays.

The name *Hygrophorus miniatus* is interpreted in different ways by various authors. For instance Kühner (1976: 484) regards it as an alpine species with whitish yellow, yellow to orange-red lamellae and not constricted, ellipsoid, uninucleate spores, measuring 8–11  $\times$  (4–)5–6.5  $\mu$ m, Q = 1.5–1.8; Orton (1960: 249) as a lowland species with vermilion to orange-red lamellae at fist and not constricted, ellipsoid(-oblong) spores, measuring 7.5–10(-11)  $\times$  5–6(-7)  $\mu$ m. On the other hand it was described by Arnolds (1974a: 181; 1983: 389) as a species with pinkish red to orange-yellow lamellae, and spores broadened and often constricted in face-view. Such collections were also described by Kühner (1976: 481) from lowland habitats without giving them a formal name and by Orton (1960: 266) as *Hygrophorus strangulatus* (see also *strangulata*).

The only way to clarify this situation was to study some collections answering the original description by Fries (l.c.) and found in the same region. With this aim I investigated exsiccata, made by M. Moser (Innsbruck) near Femsjö and kindly put to my disposal. One of them (*Moser 80/372*, 1B) is designated here as neotype and described below.

Pileus in exsiccata 8–20 mm wide, expanded to applanate with depressed centre, dull brownish orange (when dried), with small, adpressed, concolorous scales around the centre. Lamellae broadly adnate, brownish pink. Stipe up to 25  $\times$  3 mm.

Spores [20/2]6.5–9(-9.5)  $\times$  4–5.5(-6)  $\mu$ m, Q = (1.3–)1.5–1.8, in side-view ellipsoid, ellipsoid-oblong to slightly obovoid(-oblong), in one basidiocarp not constricted, in another a small proportion weakly constricted; in front-view 5–6.5(-7)  $\mu$ m broad, Q = 1.2–1.5(-1.6), usually broadened towards the base, often constricted, obovoid, heart-shaped to obpyriform. Basidia 44–59  $\times$  5.5–8.5  $\mu$ m, slenderly clavate, 4-spored. Cheilocystidia in one basidiocarp absent, in another frequent, scattered or in small groups, 19.5–44  $\times$  2–3  $\mu$ m, subcylindrical, often tortuose or furcate. Hymenophoral trama subregular, made up of rather short elements, 39–140  $\times$  4–16  $\mu$ m. Pileipellis at centre a trichodermium, towards the margin a cutis with trichodermial tufts, made up of ascending and erect hyphae, constricted at the septae, with short elements; terminal elements

clavate, ovate or attenuate,  $20-59 \times 6.5-13.5 \mu\text{m}$ . Stipitipellis a cutis up to  $25 \mu\text{m}$  broad, made up of repent, cylindrical hyphae,  $2.5-5 \mu\text{m}$  wide, in places with erect hyphal tips, projecting up to  $45 \mu\text{m}$ . Clamps present.

Collections examined.—SWEDEN, Smoland, near Femsjö, 'Stensje'; along road amongst grass, 21 Sept. 1980, *M. Moser 80/372* (IB, neotypus).

Another collection from Femsjö (*M. Moser 80/287*, 17 Sept. 1980, IB) had similar microscopic characters, including spores broadened towards the base and often obpyriform.

The neotype is identical with *H. miniata* sensu Arnolds and *H. strangulata* (P. D. Orton) Svrček. *Hygrophorus miniatus* sensu Orton may be identical with *Hygrocybe calciphila* Arnolds (see Arnolds, 1986a). *Hygrocybe miniata* sensu Kühner seems to be a different fungus without appropriate name.

**mollis.**—*Hygrophorus turundus* var. *mollis* was originally described by Berkeley & Broome (1871: 434) as a golden yellow fungus with concolorous scales on the pileus ('Aureus; pileo . . . pilis mollibus brevibus radiantibus concoloribus . . .'). In the Netherlands such a fungus is not uncommon on acid, sandy and peaty soils. It is identical with *Hygrocybe miniata* in microscopical respect, including the characteristic ovoid to obpyriform spores in face-view (see *miniata*). The main difference is the yellow colour of the pileus in young basidiocarps, since older basidiocarps of *H. miniata* are discolouring yellowish as well. In addition the lamellae are pale yellow without the red or orange colours usually found in *H. miniata*. The two taxa are often found together and occasionally intermediate forms occur. Therefore it is not justified, in my opinion, to treat it as a separate species like done by e.g. Orton (1960: 249). I regard it as a variety: **Hygrocybe miniata** (Fr.: Fr.) Fr. var. **mollis** (B. & Br.) Arnolds, *comb. nov.* (Basionym: *Hygrophorus turundus* var. *mollis* B. & Br. in *Ann. Mag. nat. Hist.*, Ser. IV, 7: 434. 1871 (Notic. Br. Fungi 26).

*Hygrocybe mollis* sensu Moser (1967: 9) is identical with *H. helobia* (Arnolds) M. Bon. I studied Moser's collection, made 30 VII 1966 (IB) and found the hymenophoral trama made up of long elements, tapering to the ends,  $175-515 \times 14-32 \mu\text{m}$ , characteristic of *H. helobia* (see also Arnolds, 1974b: 90). *Hygrocybe mollis* sensu Moser has nothing to do with *H. moseri* M. Bon (see there).

**moseri.**—*Hygrocybe moseri* was described by Bon (1976a: 42) in order to rename *H. mollis* sensu Moser (1967: 9). However, Bon apparently did not study the authentic collections made by Moser since he indicated one of his own collections (3926B) as type and since his description shows great discrepancies with the description by Moser.

I studied a collection of *H. mollis* sensu Moser and found it to be identical with *H. helobia* (Arnolds) M. Bon as already suggested in 1974 (Arnolds, 1974b: 90). For details see discussion on *mollis*.

I also studied the holotype of *H. moseri* M. Bon (herb. Bon), consisting of one fragmented basidiocarp in bad condition. This study revealed some discrepancies between the type and the diagnosis by Bon: The hymenophoral trama is made up of short ele-

ments,  $38-66 \times 10.5-14 \mu\text{m}$  (Bon:  $100-300 \mu\text{m}$  long); the pileipellis is a trichodermium, made up of hyphae  $\pm 4.5-8$  (Bon:  $7-12(-16) \mu\text{m}$  wide; the spores measure  $7-8.5(-9) \times 4.5-5(-5.5) \mu\text{m}$  and are in front-view often broader to the base, obovoid to obpyriform (Bon in diagn.  $6-10 \times 4.5-6 \mu\text{m}$ ; in later key (1976b: 18)  $8-10 \times 4-5.5 \mu\text{m}$ ). It is remarkable that Bon's own notes on the type of *H. moseri*, kindly sent along with the collection, are in better accordance with my observations than with his own diagnosis: 'spores  $6.5-8.5 \times 4.5 \mu\text{m}$ ; hyphae de la trame courtes; hyphae d'épicutis  $\times (3-6-8(-12) \mu\text{m}$ .'

The type of *H. moseri* perfectly fits in with my concept of *H. miniata* (see there). Since the colours of the pileus in the type were described as 'jaune (un peu orangé sur le frais)' I synonymize it with *H. miniata* var. *mollis* (B. & Br.) Arnolds.

**murinacea.**—*Agaricus murinaceus* (Bull.: Fr.) was sanctioned by Fries (1821: 116) with references to i.a. *Agaricus murinaceus* Bull. (pl. 520) and *Agaricus nitratus* Pers. (1801: 356). The most important character according to Fries is the nitrose smell, which is found in several other species of *Hygrocybe* too: *H. ovina* (Bull.: Fr.) Kühner and *H. nitiosa* (Blytt) Mos. These species are reddening or blackening when touched and since Fries (l.c.) did not mention this character it is likely that *Agaricus murinaceus* Fr. and *A. nitratus* Pers. are identical. However, I reject the former name since it is typified by a plate by Bulliard (1791: pl. 520), representing a different fungus with very large, stout, dark brown basidiocarps, one of them tinged reddish on the pileus. In the accompanying description (Bulliard & Ventenat, 1812: 588) no characteristic smell is mentioned. In my opinion *A. murinaceus* Bull. may very well be identical with *Hygrophorus metapodius* (Fr.) Fr., in which case the epithet *murinaceus* has priority. Since I do not know *H. metapodius* personally, I do not want to make a final decision. Whatever it may be, *A. murinaceus* Bull. is not the same as *A. nitratus* Pers. and therefore the correct name of this well-known species is *Hygrocybe nitrata* (Pers.) Wünsche.

Another interesting point in favour of this concept is that Fries in 1874 (: 421) listed his *Agaricus murinaceus* 1821 as a synonym of *Hygrophorus nitratus* with explicit exclusion of the plate by Bulliard.

**nebularis.**—*Camarophyllus nebularis* Cléménçon has been invalidly published and is a synonym of *Hygrocybe griseopallida*. See there.

**nigrescens.**—Several authors (e.g. J. Lange, 1923: 24; Hesler & Smith, 1963: 113; Arnolds, 1974a: 112; Kühner, 1977: 84) have stressed the fact that *Hygrophorus puniceus* var. *nigrescens* was originally described by Quélet (1884: 503) as a taxon with a white pileus at first, later yellow with rose or orange fibrils. Moreover the basidiocarps are described as extremely large with the pileus 100 mm broad. These characters are copied in Quélet's later description of *Hygrophorus nigrescens* (1888: 254).

I reject this name for the smaller taxon with red pileus from the beginning, at present by most authors indicated as *H. nigrescens*. An alternative name is *Hygrocybe pseudoconica* J. Lange (see there).



**nitrata.**—*Hygrocybe nitrata* (Pers.) Wünsche is the correct name of *H. murinacea* sensu Fr., auct. eur. non Bull. See *murinacea*.

**nivea.**—*Hygrocybe nivea* (Fr.) Murrill is a synonym of *H. virginea* (Wulf.: Fr.) Orton & Watl. See there.

**obrussea.**—*Agaricus obrusseus* was described and sanctioned by Fries (1821: 104). The name has been used in widely different meanings since, e.g. sensu Konrad & Maublanc (1937: 386; = *Hygrocybe konradii* R. Haller); sensu Ricken (1910: 21; = *H. persistens* (Britz.) Sing.); sensu Bresadola (1928: 346, fig. 2; = *H. aurantiosplendens* R. Haller); sensu J. Lange (1940: 23; = *H. flavescens* (C. H. Kauffm.) Sing.) and sensu Kühner (1947: 20). The last-mentioned interpretation was accepted by most European mycologists, e.g. by Haller (1954: 84), Dennis & al. (1960: 80), Moser (1978: 87) and Kristiansen (1981: 120). Kühner (l.c.) described *H. obrusseus* as a species related to *H. conica* with a strictly regular hymenophoral trama, a yellow, campanulate pileus,  $\pm 30\text{--}70$  mm broad; free, strongly ventricose, pale yellow lamellae, a cylindrical, often compressed stipe,  $55\text{--}80 \times 6\text{--}15$  mm, without remarkable smell. This description indeed has much in common with the original diagnosis of *A. obrusseus* by Fries (l.c.), but Kühner overlooked one very important difference: Fries described the lamellae as adnate ('lamellis adnatis ventricosis distantibus') whereas they are free in Kühner's collections. The attachment of the lamellae is of fundamental importance within *Hygrocybe*: free lamellae are only found in subgenus *Hygrocybe* (trama regular), broadly adnate lamellae only in subgenus *Pseudohygrocybe* (trama subregular).

In my opinion *Agaricus obrusseus* Fr.: Fr. is nothing else than *Hygrophorus quietus*, described by Kühner (1947: 31) in the same paper. It is different from *H. obrussea* in the adnate lamellae, sweet smell like *Lactarius quietus*, constricted spores and subregular hymenophoral trama with short elements. The macroscopic characters of this species perfectly agree with Fries' *A. obrusseus*, except for the fact that Fries did not indicate a special smell. However, it is very likely that Fries missed the smell, especially since he did not describe a sweet smell for *Agaricus quietus* Fr.: Fr. (= *Lactarius quietus* (Fr.: Fr.) Fr.) either (Fries, 1821: 69: 'odor nullus').

This hypothesis is supported by the fact that Lundell & Nannfeldt (1979: 46) distributed *exsiccata* under the name of *Hygrophorus obrusseus*, which without any doubt belong to *H. quietus*, not to *H. obrussea* sensu Kühner. So proof has been given that the species with constricted spores really occurs in South Sweden, whereas the presence of *H. obrussea* sensu Kühner still has to be demonstrated. It is remarkable that Lundell & Nannfeldt also failed to notice the special smell of this fungus. Consequently I propose to select the collection described by Lundell & Nannfeldt at Uppsala as neotype of *Agaricus obrusseus* Fr.: Fr. For macroscopic characters I refer to their concise description (l.c.). Some notes on microscopic characters are:

Spores  $(7.5\text{--})8\text{--}8.5 \times 4\text{--}4.5\text{--}(5) \mu\text{m}$ ,  $Q = 1.7\text{--}2.0$ , ellipsoid-oblong, but in great majority ( $\pm 90\%$ ) weakly to strongly constricted in any view. Basidia  $41\text{--}51 \times 7\text{--}8.5 \mu\text{m}$ , slenderly clavate, 4-spored, clamped. Hymenial cystidia absent. Hymenophoral trama subregular, made up of short elements,  $30\text{--}65 \times 4.5\text{--}15 \mu\text{m}$ . Pileipellis a thin, dry cutis,

15–35  $\mu\text{m}$  thick, made up of repent hyphae, 2.5–5  $\mu\text{m}$  wide, with a few erect, free ends. Stipitipellis a cutis up to 45  $\mu\text{m}$  thick, made up of loose, repent hyphae, in places with erect ends, projecting up to 60  $\mu\text{m}$ .

Collections examined.—SWEDEN, Uppland, Uppsala, Carolinaparken; in sparse lawn under frondose trees, 29 Aug. 1959, *H. Belin s.n.* (Fungi Exsiccati Suecici nr. 2870; UPS, neotypus).

It is clear that *Hygrophorus obrusseus* sensu Kühner is in need of a new name. Since I could not find an appropriate name in literature I propose as new name *Hygrocybe cystidiata* Arnolds (see that epithet).

**ortonii**.—*Hygrocybe ortonii* M. Bon (1983: 27) is a superfluous renaming of *H. berkeleyi* (P. D. Orton) Orton & Watl. = *H. pratensis* var. *pallida* (Cooke) Arnolds.

**pallida**.—*Hygrocybe pratensis* var. *pallida* (Cooke) Arnolds is the name preferred here for *H. berkeleyi* (P. D. Orton) Orton & Watl. See that epithet.

**perplexa**.—*Hygrocybe perplexa* (A. H. Smith & Hesl.) Arnolds is the correct name for *H. sciophana* sensu auct. eur. nec Fr. See *sciophana*.

**persistens**.—*Hygrophorus conicus* var. *persistens* was described by Britzelmayr (1890: 200) with a very short, ambiguous diagnosis: 'weissl., St. u. H. blass  $\pm$ .-g.; H. klebr., sich nicht schwärz.' In 1893 (: 98) the variety was raised to the rank of species with an extended description: 'Sporen 10–16  $\times$  6–10  $\mu\text{m}$ . L. weissgeblich, z.g., H. meist klebrig; H. u. St. rotgelb bis blassgelb, sich nicht schwärzend; Heiden, Waldwies, A. (Augsburg, the author), dann s. häufig um N.; dem *H. conicus* v.' In 1899 an even more complete description was published, including the size and shape of the basidiocarps: pileus conical but also campanulate and expanding, 80 mm wide; stipe 100 mm long, lamellae 10 mm broad. Apparently these dimensions should be regarded as maximum values since the accompanying plate (figs. 75–77) shows basidiocarps with the pileus 35–65 mm broad and the stipe 50–85  $\times$  7–12 mm.

It is clear that Britzelmayr's species belongs to the group of *H. langei* = *H. acutoconica* (*Hygrocybe* subsect. *Macrosporae* R. Haller ex M. Bon). The stout basidiocarps and pale lamellae may suggest synonymy with *H. subglobispora* (P. D. Orton) Mos., but the elongate, in part constricted spores figured by Britzelmayr (l.c.) exclude this possibility and suggest a close relationship to *H. langei* Kühner. Bresinsky & Strangl (1966: 19) regarded the two species as identical and I agree with their view. A strong argument in favour of this opinion is that they actually found *H. langei* in great quantities in the localities indicated by Britzelmayr. They noticed also that they found only small to mediumsized basidiocarps, in this respect deviating from Britzelmayr's description (but not his plates!).

Singer & Kuthan (1976: 10) distinguished *H. persistens* from *H. acutoconica* (= *H. langei*) on the basis of the presence of clamps and the gelatinized stipitipellis. However, clamps are constantly present in 4-spored forms of typical *H. acutoconica* (Arnolds, 1974a: 133, 1986b) with dry stipe. Indeed, the stipe in the latter species is dry to slightly

greasy and the stipe is a cutis. I cannot establish at the moment whether the viscid stipe in *H. persistens* sensu Sing. & Kuthan warrants the description of a different taxon. However, if this would be the case it should not be named *H. persistens* because Britzelmayer (l.c.) described only the pileus as viscid, not the stipe. Moreover, it is said to be an abundant species near Augsburg, which does certainly not apply to *H. persistens* sensu Sing. & Kuthan.

Consequently I regard *H. persistens* as conspecific with *H. acutoconica*. Unfortunately both *Hygrophorus persistens* (Britz.) Britz. and *Mycena acutoconica* F. Clem. were described in 1893. According to Stafleu & Cowan (1976: 350) the publication by Britzelmayer has become available at least as early as May 1893. In spite of strong efforts the exact date of publication of Clements' work could not be traced. Until further proof is given I regard it to be published in December 1893. Consequently in my opinion Britzelmayer's name has priority.

**pseudoconica.**—*Hygrocybe pseudoconica* J. Lange (1923: 24) is the correct name for the fungus, usually named *H. nigrescens* (Quél.) Quél. The latter epithet is rejected (see *nigrescens*).

I demonstrated earlier (Arnolds, 1974a) that the differences between *H. conica* and *H. pseudoconica* (as *H. nigrescens*), mentioned by European authors (e.g. Orton, 1960: 252; Moser, 1978: 87) do not exist in reality. This was confirmed by Kühner (1977). Hessler & Smith (1963: 109) shared this view with regard to the North American collections.

It may only be useful to distinguish between a small form with a pileus  $\pm 15-40$  mm (forma *conica*) and a larger form with a pileus  $\pm 40-70$  mm (forma *pseudoconica* (J. Lange) Arnolds, 1985b: 476), but variable in all other characters such as size of spores, number of sterigmata of the basidia and colour of the pileus, ranging from orange-yellow to red.

**pseudocuspidata.**—Kühner (1977: 105) introduced the name *Hygrocybe pseudo-cuspidata* for a fungus close to *H. langei* (= *H. persistens*), but with a red to orange-red pileus and stipe. Since no Latin diagnosis was provided the species was not validly published. In my opinion this fungus is identical with *H. persistens* var. *cuspidata* (Peck) Arnolds, originally described from North America (see *cuspidata*). An American collection of *H. cuspidata* (Hessler 24694, L) did not show any significant difference with collections from the Netherlands. If a European name is preferred over *H. cuspidata* the name *H. aurantiohutescens* P. D. Orton is available (see there).

**pseudopersistens.**—Bon (1978: 69, 1979b: 5) separated *Hygrocybe konradii* var. *pseudopersistens* from var. *konradii* on the basis of the red or orange-red colours on the pileus, especially near the margin, and on the stipe, especially near the apex. In var. *konradii* the entire pileus and stipe are said to be yellowish or orange. According to Bon (l.c.) occasionally the two varieties occur together and intermediate basidiocarps are known.

In the Netherlands the two colour forms are known as well, next to intermediate forms, e.g. basidiocarps combining a lemon yellow or orange-yellow pileus with an orange-red stipe (e.g. Bas 7100, L).

In my opinion and in view of the taxonomic concepts accepted in the 'Flora agaricina neerlandica' (Kuyper, 1986) the variation described above has to be expressed in the formal rank of formae. Therefore the combination *Hygrocybe konradii* forma *pseudopersistens* (M. Bon) Arnolds has been proposed (Arnolds, 1985b: 476).

*quieta*—*Hygrocybe quieta* (Kühner) Sing. is considered as a synonym of *H. obrussea* (Fr.: Fr.) Wünsche. See there.

*sciophana*—*Hygrocybe sciophana* (Fr.: Fr.) Wünsche is described by most European authors as a species close to *H. psittacina* with a similar habit and glutinous pileus and stipe. The pileus is dark brownish red, brick red or dark blood-red, the lamellae are first ascending, then  $\pm$  horizontal, adnate to strongly emarginate (like *H. psittacina*), orangeish brown to flesh coloured, the stipe is concolorous with the pileus or paler. Representative descriptions have been published by e.g. Jossierand (1933: 366), Kühner & Romagnesi (1953: 52) and Svrček (1970: 125); plates by Ricken (1910: pl. 8, fig. 7), Bresadola (1928: pl. 339), Konrad & Maublanc (1937: pl. 387, fig. 2) and Kotlaba (in Svrček 1970, pl. 77).

In my opinion this interpretation is deviating in some important characters from the original description. *Agaricus sciophanus* has originally been described by Fries (1821: 102) as a species, related to *H. pratensis*, but also intermediate between *H. psittacina* and *H. laeta* ('Affinis A. pratenti, medius inter psittacinum et laetum') with similar, orange-brown to fulvous colours ('subtestaceus, sordide fulvescens') as *H. pratensis* and decurrent lamellae. In 1838 (: 329) and 1874 (: 417) the description is almost identical and the similarity with *H. pratensis* is stressed again (1874: 'Habitus et color opace fulvescens *H. pratensis*, sed tenuis...'). This description is deviating from the usual interpretation of *Agaricus sciophanus* as outlined above, e.g. in the colours and the decurrent lamellae. In fact that fungus does not remind to *H. pratensis* at all. In my opinion *Agaricus sciophanus* Fr. is likely to be in fact a form of the variable *H. laeta* (Pers.: Fr.) Kumm., which is characterized by  $\pm$  decurrent lamellae and rather often has a colour of the pileus reminding *H. pratensis*.

These discrepancies have been noticed before in Europe by Jossierand (1933: 364) and apparently also by Kühner & Romagnesi (1953: 550) who listed this species in the index of the 'Flore analytique' as '*sciophanus* Qué. (nec Fr.)'.

The use of the epithet *sciophanus* for the brownish red fungus with emarginate lamellae is apparently based on Fries' description in *Monographia* (1851: 137) where the lamellae were described as 'attenuato adnatae, primitivè leviter ascendentes', and on the plate in *Icones selectae Hymenomycetes* (1882: pl. 167, fig. 1), showing ascending, narrowly adnate lamellae, also in mature basidiocarps. This plate indeed represents *H. sciophana* sensu auct. eur. non Fr. 1821. In the description it is stressed that the attachment of the lamellae is not characteristic of *H. sciophana* ('lamellarum insertio minus typica').

However, the latter descriptions are not important from a nomenclatural point of view. Therefore, Smith & Hesler (1954: 328) rightly introduced the name *Hygrophorus perplexus* for a North American taxon that is very close to the current interpretation of *H. sciophana* by European authors. The lamellae are described by Smith & Hesler (l.c.)

as 'amber yellow' when young, then 'apricot yellow'. In the collections from the Netherlands the lamellae are orange, orangeish brown, greyish orange to flesh-coloured like the descriptions by most European authors. However, Rea (1922: 303) described the lamellae 'of the same colour as the pileus [deep tawny or brick colour], or yellowish' and Kühner & Romagnesi (1953: 52) as 'jaune d'or foncé, se teintant de rose-brique avec l'âge, au moins dans le fond.' So it seems that orangeish yellow lamellae fit into the variation of this species, too. Another small discrepancy between European and North American collections is the size of the spores:  $6-8 \times 4-5 \mu\text{m}$  according to Smith & Hesler (l.c.) against  $(6.5-7-9(-10) \times 4.5-6(-6.5) \mu\text{m}$  in the collections from the Netherlands. Jossierand (1933: 367) measured them  $6.5-9 \times 5-6.5 \mu\text{m}$ . This difference seems not to be significant as well.

Thus I reject the name *H. sciophanus* for the species discussed here and propose to call it *Hygrocybe perplexa* (A. H. Smith & Hesl.) Arnolds (1985b: 477).

**sphagnophila.**—*Hygrophorus miniatus* var. *sphagnophilus* was first described by Peck (1901: 856). Hesler & Smith (1963: 146) studied the type and observed large spores,  $9-12(-14) \times 5.5-7(-8.5) \mu\text{m}$ , and a pileipellis made up of 'septate, constricted, fuscous hyphae, the terminal elements clavate.' They regarded it as a variety of *Hygrophorus turundus* (Fr.: Fr.) Fr. with a red pileus at first, with scales not or only slightly darker than the ground colour, occurring in *Sphagnum* bogs. *Hygrophorus turundus* var. *turundus* sensu Hesler & Smith has a scarlet pileus with dark brown scales.

Orton (1960: 262) has demonstrated that *Agaricus turundus* Fr.: Fr. is a species with a yellow pileus with dark scales (see *turundus*). He renamed the red species *Hygrophorus coccineocrenatus* (= *H. turundus* sensu Hesler & Smith). Therefore I proposed the combination *Hygrocybe coccineocrenata* var. *sphagnophila* (Peck) Arnolds (1985b: 475).

Kühner (1976: 463, 495) rejected the epithet *sphagnophila* for apparently the same fungus, because Hesler & Smith (1963: 146) mentioned the occurrence of cuneate spores in the type of *H. miniatus* var. *sphagnophilus*, next to ellipsoid and subovoid spores. In my opinion the occurrence of some apparently aberrant spores cannot be a reason to reject this epithet. Therefore I regard *H. coccineocrenata* forma *ambigua* Kühner as a synonym of var. *sphagnophila*. The rank of this taxon is a matter of personal judgement.

**squamulosa.**—*Hygrophorus squamulosus* Ellis & Ev. is distinguished by Hesler & Smith (1963: 160) as a species close to *H. miniata* (Fr.: Fr.) Fr., but different because of the presence of cheilocystidia and possibly in the thicker, more squamulose pileus. Among the material studied they listed also a collection (*Bas 694*) from the Netherlands.

Arnolds (1974a: 185) showed that the occurrence of poorly differentiated marginal hairs in part of the collections of *H. miniata* has no taxonomic relevance. This is also demonstrated in the neotype of *H. miniata*, designated in this paper (see *miniata*): one basidiocarp has numerous cheilocystidia, whereas in another basidiocarp they are lacking completely.

**strangulata.**—*Hygrophorus strangulatus* was described by Orton (1960: 266) as a small species with a slightly greasy, red pileus, 5–35 mm wide, when dry minutely golden-

scurfy-scaly around centre when young; yellowish lamellae, often flushed orange to entirely orange-red; smooth, red stipe, 18–48 × 1–4 mm; ellipsoid-oblong spores, constricted in some views, 7–9 × 4–5  $\mu\text{m}$  and a pileipellis made up of broad hyphae, 6–16  $\mu\text{m}$  wide, with a thin layer of very narrow hyphae (1–2  $\mu\text{m}$ ) over these. The macroscopic appearance and microscopic structure of the pileipellis are a kind of intermediate between *Hygrocybe* subsect. *Coccineae* with a smooth pileus (pileipellis a cutis) and subsect. *Squamulosae* with a squamulose pileus (pileipellis a trichodermium, at least at the centre). Indeed, Orton (l.c.: 249, 221) keyed-out *Hygrophorus strangulatus* in these two groups. Reid (1968: 6) described under that name a species with distinct scaly pileus. On the other hand Arnolds (1977: 250) described as *H. strangulatus* collections with a smooth to slightly velvety pileus and a pileipellis made up of repent, slender hyphae, 2.5–6  $\mu\text{m}$  wide, constituting a cutis. Kühner (1976: 476) found discrepancies between two collections made by Orton, for instance in the number of nuclei in the spores: Orton 3619 was binucleate, Orton 4162 uninucleate.

In order to clarify this situation I studied the isotype of *Hygrophorus strangulatus* (Orton 1554, 5 XI 1958, Witley Common, Surrey; E). The type consists of four basidiocarps in good condition. The spores measured 6.8–8.7(–10.3) × 4.7–5.3(–5.6) × (4.8–)5.1–6.1(–6.3)  $\mu\text{m}$ , in side-view ellipsoid or ellipsoid-oblong, some obovoid, exceptionally slightly constricted, Q = (1.4–)1.5–1.7; in front-view almost all broader towards the base, obovoid or obpyriform, often ( $\pm$  70%) constricted. Basidia 39–47.5 × 6.5–7.5  $\mu\text{m}$ , 4-spored. Hymenophoral trama subregular, made up of short elements, 28–103 × 4.5–13  $\mu\text{m}$ . Pileipellis at centre a trichodermium, towards the margin a cutis with trichodermial fascicles of ascending hyphae, constricted at the septae, made up of short elements, at the tips ellipsoid or clavate, (23–)37–63 × 5.5–9.5  $\mu\text{m}$ , a few hyphae with slender, cylindrical, hair-like projections, 1.5–3  $\mu\text{m}$  wide.

These characters perfectly agree with *H. miniata* in the meaning accepted here (see *miniata*) and consequently I regard *H. strangulatus* P. D. Orton as a synonym of that species. This synonymy is not at all unexpected since *H. strangulatus* was described as common, whereas *H. miniatus* sensu Orton (1960: 248) is an uncommon fungus with non-constricted spores, according to Orton (in a letter) characteristic of calcareous soils. Fries (1821: 106, 1838: 330) regarded *H. miniatus* as a common species. *Hygrocybe miniatus* sensu P. D. Orton may be identical with *Hygrocybe calciphila* Arnolds (1985b: 475).

Kühner (1976: 475) also made a critical study of the *miniatus-strangulatus* complex and arrived at similar conclusions. However, he denied a synonymy of these two names because he had another concept of *H. miniata* as an alpine to subalpine fungus with not constricted spores, not broadened in face-view. The fungus from the lowlands with obpyriform spores was described by Kühner (l.c.) without formal name.

I studied several other collections of *H. strangulata* made by Orton (all in E). Orton 1220 (25 X 1957) has spores 6.5–7.5 × 3.5–4.5  $\mu\text{m}$ , in all views ellipsoid to oblong, a minor proportion ( $\pm$  20%) weakly constricted, and on the pileus a well developed ixocutis, in places even up to 180  $\mu\text{m}$  thick, made up of thin repent hyphae, 2.5–5  $\mu\text{m}$  wide. In my opinion this collection belongs to *H. marchii* (Bres.) Sing. Orton 3620 (14

IX 1969) has spores  $6.5-8 \times (3.5-4-4.5 \mu\text{m})$ , not broader in face-view, often (30-40%) constricted in face-view. The pileipellis is a cutis, at the centre with rather many erect hyphae, made up of cylindrical hyphae,  $4.5-6 \mu\text{m}$  wide. This collection may very well be identical with *H. constrictospora* Arnolds (= *H. strangulata* sensu Arnolds). Orton 2987 (12 XI 1967) and Orton 4539 (22 I 1973) are similar to the type and consequently represent *H. miniata* (Fr.: Fr.) Fr. It is no wonder that Orton's *H. strangulatus* has caused much confusion!

**streptopus.**—*Hygrocybe streptopus* (Fr.) Sing. & Kuthan is considered as a variety of *H. fornicata* (see there).

**subvitellina.**—*Hygrocybe subvitellina* M. Bon non Imai is a synonym of *H. ceracea*. See discussion on *H. vitellinoides*.

**tristis.**—*Hygrocybe tristis* (Pers.) F. H. Møll. is usually regarded as a blackening species, close to *H. conica*, but with a yellow to greenish yellow pileus, e.g. by Moser (1978: 86). *Agaricus tristis* was originally described by Persoon (1796: 49) with the pileus '... primum virescente-aurantio, mox nigrescente...', consequently also with orange colours. He referred to plates by Bulliard of *Agaricus croceus* (pl. 50 and 524, fig. 3) and by Schaeffer of *A. conicus* (1774: pl. 2, fig. 9). These plates represent typical *H. conica*. In 1822 (: 234) Persoon quoted these plates under *Agaricus conicus* and *A. tristis* is not mentioned anymore. It is inevitable to regard *A. tristis* as a superfluous name change of *A. conicus*.

I regard the (greenish) yellow collections of *H. conica* as a variety, viz. var. *chloroides* (Malençon) M. Bon (see chloroides).

**turunda.**—At least four recent interpretations exist from the name *Agaricus turundus* Fr.: Fr. (1821: 106): (1) sensu J. Lange (1940: 27), Kühner & Romagnesi (1953: 52), Hesler & Smith (1963: 143), auct. eur. p.p. maj. with a red pileus supplied with brown scales, pale lamellae and large, ellipsoid spores ( $\pm (8.5-9-12.5 \times 5.5-7.5 \mu\text{m})$ ); (2) sensu F. H. Møller (1945: 155), P. D. Orton (1960: 270) with a yellow or orange-yellow pileus from the beginning with brown scales and slightly smaller, elongate spores ( $8.5-11(-12) \times 4.5-5.5(-6 \mu\text{m})$ ); (3) sensu Moser (1967: 9), Arnolds (1974a: 174; 1986b) with a yellow or orange-yellow pileus from the beginning with brown scales and small spores, broadened to the apiculus in face-view ( $7-8.5(-10.5) \times 4.5-5.5(-6 \mu\text{m})$ ); (4) sensu Rald (1986: 10) with a red to yellow pileus with concolorous scales, deeply decurrent lamellae and ellipsoid spores ( $8-12 \times 5-7.5 \mu\text{m}$ ).

Orton (1960: 262) has indicated that *Agaricus turundus* was originally described by Fries (1818: 199, 1821: 106) as a species with a yellow pileus with grey scales ('luteo cinereo-squamuloso'). He renamed *Hygrophorus turundus* sensu Kühn. & Romagn. as *H. coccineocrenatus* P. D. Orton. *Hygrocybe turunda* sensu Rald is identical with *H. cantharellus* sensu auct. (= *H. lepida* Arnolds, see there).

*Hygrocybe turunda* sensu F. H. Møller, P. D. Orton and sensu Moser, Arnolds are similar in macroscopic characters, but have very different spores as stressed earlier by Kühner

(1976: 472). At the moment it is not clear which interpretation is identical with *Agaricus turundus* Fr.: Fr. This question can only be answered by study of authentic collections from South Sweden.

**virginea.**—*Agaricus virgineus* Fr. has been rejected earlier by me (1974a: 81) as a nomen confusum, a point of view followed by e.g. Cléménçon (1982). This rejection was based on the sanctioning description (1821: 100) and later descriptions (1851: 133, 1874: 414) by Fries. However, this discussion was not complete since *A. virgineus* Fr. is typified by *A. virgineus* Wulf. in Jacq., and the description and plate by Von Wulfen had not been studied at that time. Von Wulfen (in Jacquin, 1781: 104) described *A. virgineus* as an entirely white agaric with a striate pileus when moist and decurrent lamellae. The accompanying plate (15, fig. 2) shows rather small basidiocarps with the pileus  $\pm 15$  mm broad and the stipe  $\pm 30-40 \times 3-4$  mm, exactly like the present concept of *Hygrocybe nivea* (Fr.) Murrill. Since *Agaricus virgineus* was sanctioned by Fries (1821: 100) and *niveus* was only accepted as a variety, the correct name of this species is *Hygrocybe virginea* (Wulf.: Fr.) Orton & Watl., after all.

It must be stressed that this name change does not alter my taxonomic point of view, namely that *H. nivea* and *H. virginea* sensu Orton (1960), Moser (1978), auct. eur. p.p. maj. are one and the same, variable taxon with pileus measuring 10–50(–95) mm, the stipe (15–)20–60(–90)  $\times$  2–7(–15) mm, spores (6.5–)7–12.5  $\times$  3.5–7.5  $\mu$ m and basidiocarps with predominantly 2-spored, 4-spored, or intermixed 2- and 4-(1)-spored, rarely predominantly 3-spored basidia (Arnolds, 1974a: 81; 1986b). *Hygrophorus virgineus* sensu Quélet (1888), Henry (1929), Bataille (1948) with a thick, not striate pileus and small spores (5.5–7.5  $\times$  3.5–5.5  $\mu$ m) is a different taxon, in my opinion identical with *Hygrocybe pratensis* var. *pallida* (Cooke) Arnolds (= *H. berkeleyi* (P. D. Orton) Orton & Watl.) (see berkeleyi).

**vitellinoides.**—*Hygrocybe vitellinoides* was described by Bon (1979a: 39) as a nomen novum for *H. subvitellina* M. Bon (1976a: 41), a later homonym of *H. subvitellina* (Imai) Ito.

According to Bon (l.c.; 1977: 205) it is a species with an egg-yellow to orange, lubricous to slightly viscid pileus,  $\pm 20-30$  mm broad; broadly adnate to more or less decurrent, yellow lamellae; a dry, yellow stipe  $\pm 10-30 \times 2-4$  mm, sometimes a weak smell of *Hygrocybe quieta*, spores  $\pm 7-8 \times 3.5-4$   $\mu$ m, in majority constricted; the pileipellis an ixocutis to ixotrichodermium above a hypocutis; the stipitipellis a dry cutis. This description matches the descriptions of *H. ceracea* by Arnolds (1974: 202, 1983: 386) and of *H. subceracea* by Kühner (1977: 73) very well, except perhaps for the well-developed hypodermium in *H. vitellinoides*.

I studied the type of *H. subvitellina* (Bon 741014, Herbarium M. Bon), consisting of a single fragmented basidiocarp in very poor condition and found the spores (6–)6.5–7.5  $\times$  3.5–4  $\mu$ m, about 60 % constricted; the basidia 32–39  $\times$  6–7.5  $\mu$ m, 4-spored; the hymenophoral trama subregular, made up of short elements, 20–56  $\times$  5–17  $\mu$ m, and the pileipellis a thin ixocutis made up of repent hyphae, 2–5  $\mu$ m wide. I could neither recognize a well differentiated hypoderm nor erect slender hyphae as figured by Bon



(1977: 211, fig. 2-C), but I must admit that it was hardly possible to reinflate the tissues of the exsiccatum, even in boiling KOH.

In fact it is difficult to find reliable differences between *H. subvitellina* and *H. ceracea* in Bon's own key (1976: 14, 15). *Hygrocybe subvitellina* was keyed-out in a group with the 'lamellae more or less decurrent . . . with omphalioid habit'; *H. ceracea* in a group with 'the lamellae adnate, rarely subdecurrent, habit more or less collybioid or subconical.' However, in the next description of *H. subvitellina* the habit is described as 'omphalioid or collybioid when the lamellae are slightly decurrent.' Bon (l.c.) quoted a plate of *H. citrina* by Lange (1940: pl. 167A) that shows a fungus with adnate gills, for the rest deviating from both *H. vitellinoides* and *H. ceracea* in the lemon yellow basidiocarps. The only remaining difference between these species is the size of the basidiocarps: 10–30(–35) mm in *H. vitellinoides*, 20–50 mm in *H. ceracea*. It is remarkable that Bon in a later publication (1977) extensively discussed the relationship of *H. vitellinoides* and *H. vitellina*, which are different species indeed, but hardly spends a word to the affinity with *H. ceracea*.

According to Bon (1977: 208) *H. vitellinoides* is extremely common, whereas *H. ceracea* (1976: 15) is said to be rather rare or overlooked. This statement again is remarkable since *H. ceracea* is one of the classical species, described already by Fries (1821: 103) as 'vulgaris' which is true for entire North-West Europe.

My conclusion is that *H. vitellinoides* is a synonym of *H. ceracea* (Fr.: Fr.) Fr. See also that epithet.

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## ARE YEAST CELLS OF ENDOMYCETALES HOMOLOGUES OF CONIDIA OF EUROTIALES?

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Similarities in structure, symmetry, and size of asci and ascospores indicate a phylogenetic relationship between the Endomycetales (Endomycetes, Hemiascomycetes) and the Eurotiales and Erysiphales of the Ascomycetes. Their anamorphs which form catenate conidia from meristematic zones and which are released by disjunctive structures, are also similar. The structures in the septa of hyphal Endomycetales termed micropores or plasmodesmata, are considered to be disjunctive pegs.

The Endomycetales (Endomycetes, Hemiascomycetes) include the ascus-forming yeasts. As a rule only budding cells are present and relatively few species form septate hyphae. The Eurotiales are plectomycetous Ascomycetes with septate hyphae. Their asci and conidia-forming structures develop on or in the aerial mycelium. The asci and ascospores of typical members of the two orders are similar and peculiar within the Ascomycota. The asci are spherical or nearly so, botryose or catenate, with a thin, often evanescent wall. The ascospores are relatively small (mostly 3-7  $\mu\text{m}$ ), aseptate, hyaline or reddish brown and often ornamented. They are either oblate-bivalvate-saturnoid or spherical-ellipsoidal-fusiform (Fig. 1).

Redhead & Malloch (1977) suggested the yeasts with galeate (helmet- or hat-shaped) ascospores were related to *Ceratocystis*, *Ophiostoma*, and other genera of the Ophiostomataceae, which also include a small number of species with galeate ascospores (e.g. *Ceratocystis fimbriata* Ellis & Halst. and *Europhium trinacriiforme* Parker). Consequently, they classified the Ophiostomataceae within the Endomycetaceae, restricting this family to taxa with mainly galeate ascospores. The Ophiostomataceae, having dark, thick-walled ascospores with usually ostiolar beaks, have been classified in the Sphaeriales, next to the Microascaceae, or in a separate order Ophiostomatales. Their asci are evanescent at an early stage, and the small, often reniform, lunate, or allantoid ascospores are extruded in sticky droplets.

Since the Eurotiales (including Gymnoascales) have never been suspected to be related to the Endomycetales, typical members of the two orders were studied by both light (LM) and transmission electron microscopy (TEM). For comparative purposes the Erysiphales and some other Ascomycetes were also included in the study.

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## MATERIALS AND METHODS

The following cultures from the CBS culture collection were studied by LM from freshly grown cultures on cornmeal and other agar media: *Briosia cubispora* (Berk. & Curt.) v. Arx (342.74), *Byssosascus striatisporus* (Barron & Booth) v. Arx (642.66), *Byssochlamys fulva* Olliver & Smith (146.48), *Cephaloascus fragrans* Hanawa (183.71), *Dipodascus australiensis* v. Arx & Barker (625.74), *Hormoascus platypodis* (Barker & Kreger-van Rij) v. Arx (4111), *Neosartorya fischeri* (Wehmer) Malloch & Cain (544.65), *Saccharomyces capsularis* Schiöning (5063), *Talaromyces flavus* (Klöcker) Stolk & Samson (387.48), *Triadelfia pulvinata* Maggi & al. (744.84) and *Wallemia sebi* (Fr.) v. Arx (411.77).

The following strains were studied by TEM: *Ascoidea africana* Batra & Francke-Grossmann (377.68), *Ascoidea rubescens* Brefeld (111.48), *Cephaloascus albidus* Kurtzman (389.77), *Ceratocystis fimbriata* Ellis & Halst. (740.70), *Eleutherascus tuberculatus* Samson & Luiten (389.77), *Gelasinospora tetrasperma* Dowding (880.69), *Geotrichum terrestre* (v.d. Walt & Johannsen) Weijman (6697) *Hormoascus ambrosiae* (v.d. Walt & Scott) v.d. Walt & al. (6003) and *Ophiostoma ulmi* (Buisman) Nannf. (427.71).

For TEM the strains were cultured on yeast-malt agar for 4 days at 20°C. Material was fixed in 5% glutaraldehyde and postfixed with 1% osmium tetroxide. Ultrathin sections of the material embedded in an Araldite-Epon mixture were cut with a diamond knife and stained by consecutive treatments with saturated uranyl acetate and Reynolds lead citrate solution as described by van der Walt & al. (1974).

## RESULTS AND DISCUSSION

The Eurotiales include several families, including the Trichocomataceae sensu Malloch & Cain (1972), the Gymnoascaceae and the Onygenaceae. The Trichocomataceae are characterized by 'phialidic' anamorphs with conidia formed in basipetal chains and separated from each other by double septa with disjunctive structures (disjunctors). Typical teleomorphic genera are *Eurotium*, *Byssochlamys*, *Hamigera*, and *Eupenicillium*, with anamorphs classified in *Aspergillus* (including *Cladosarum*), *Paecilomyces*, and *Penicillium* (Fig. 1a, b). Several Gymnoascaceae and Onygenaceae include anamorphs belonging to the genera *Briosia*, *Coremiella*, *Geomyces*, and *Oidiodendron* (Fig. 1d-f), in which the conidia are also catenate and are also separated by double septa with disjunctors. In the species of these genera conidiogenous hyphae become septate in a meristematic zone and conidia are delimited in basipetal sequence or at random. The disjunctive structures in and between the septa of the conidia are small, but usually visible by light microscopy as central or ring-like pegs or other excrescences. In *Aspergillus* and *Paecilomyces*, the disjunctors are especially visible in young states when the double septa are formed (Hanlin, 1976; Roquebert, 1981). Such septa apparently have no central pores, which occur in the septa of the vegetative hyphae of all Ascomycetes. In *Aspergillus*, *Penicillium*, and *Paecilomyces* the meristematic, conidiogenous hyphae develop in the apex of ampulliform or obclavate-lanceolate cells (the phialides) but are often inconspicuous (Fig. 1a, b).

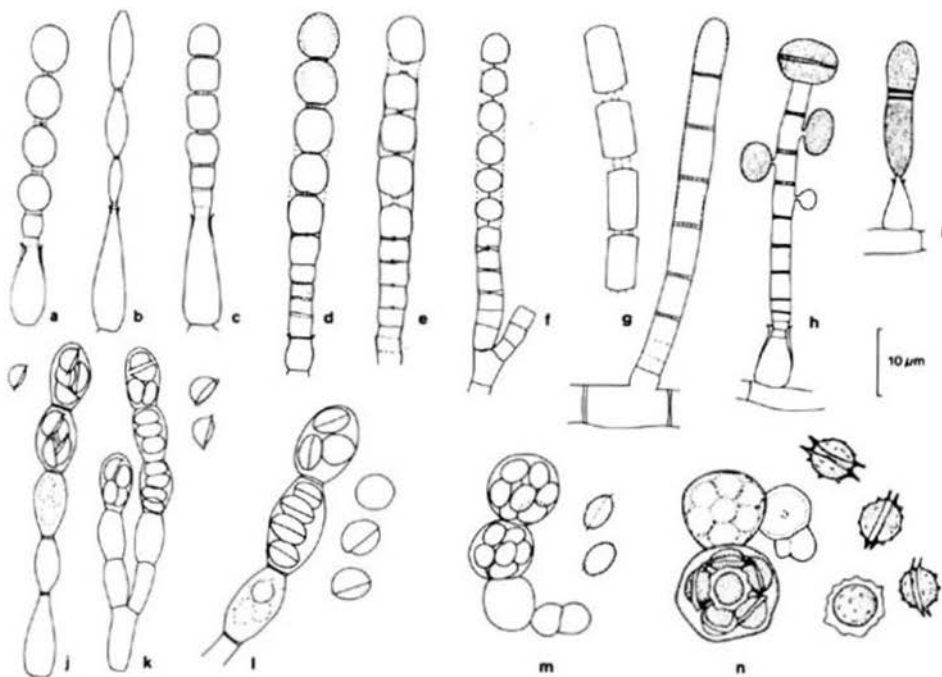


Fig. 1. Catenate conidia and catenate asci in *Endomycetales* and *Eurotiales*, and conidiogenous cells in *Arthrinium* and *Triadelphia*. a. *Aspergillus* anamorph of *Neosartorya fischeri*; b. *Paecilomyces* anamorph of *Byssoschlamys fulva*; c. *Wallemia sebi*; d. *Briosia* spec.; e. *Briosia* (*Coremiella*) *cubispora*; f. anamorph of *Byssosascus striatisporus*; g. *Geotrichum* anamorph of *Dipodascus australiensis*; h. *Arthrinium sphaerospermum*; i. *Triadelphia pulvinata*; j. *Cephalosascus fragrans*; k. *Hormoascus platypodis*; l. *Saccharomycopsis capsularis*; m. *Talaromyces flavus*; n. *Neosartorya fischeri*.

*Aspergillus* isolates with distinct, long conidiogenous hyphae have been classified in a separate genus *Cladosarum*, which has not been accepted by subsequent authors (e.g. Raper & Fennell, 1965). Distinct ampulliform cells forming conidiogenous hyphae are absent in *Onygenaceae* and *Gymnoascaceae*.

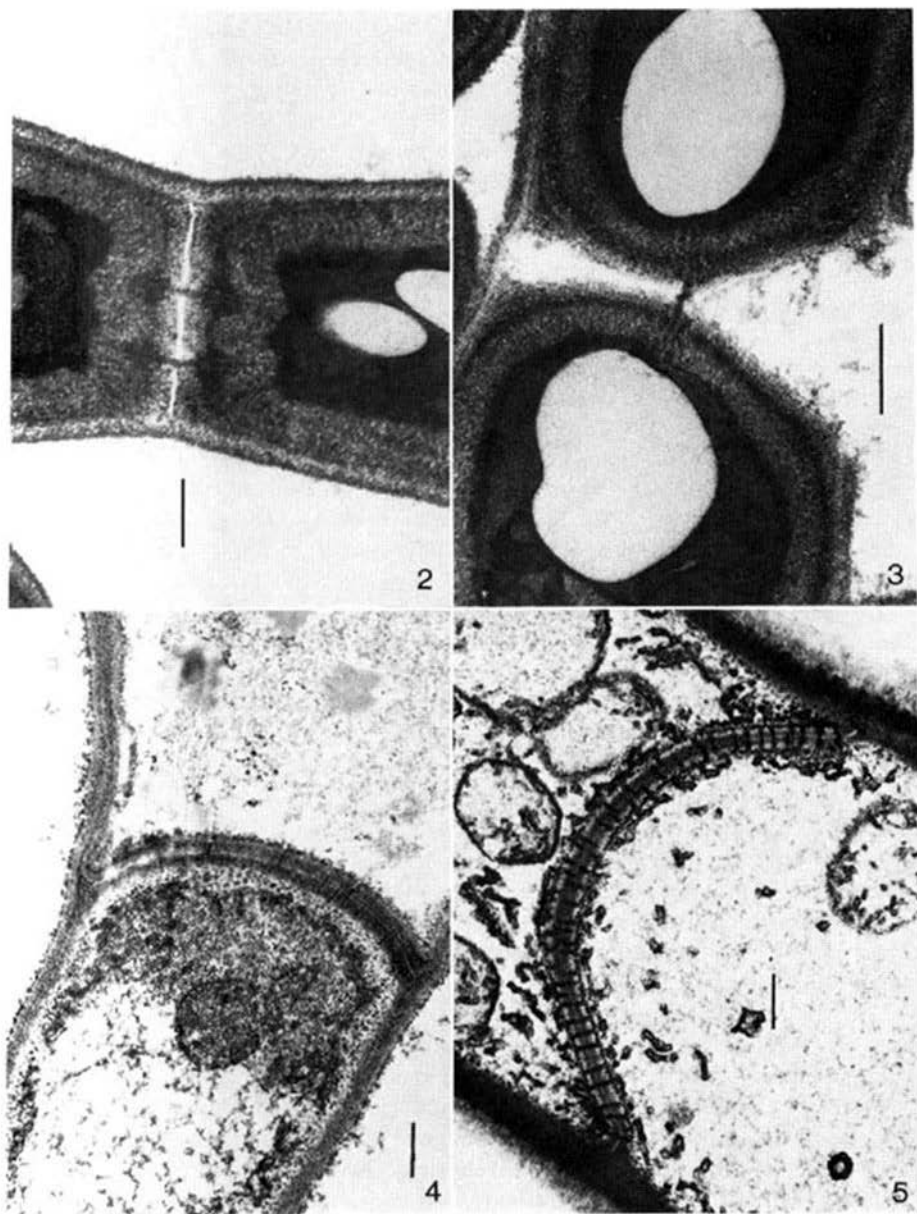
Similar releasing structures occur in filamentous *Endomycetales*, e.g. in species of *Ascoidea*, *Dipodascus* (anamorph: *Geotrichum*), *Saccharomycopsis*, and *Endomyces* (Fig. 1g). The releasing structures have been demonstrated by TEM in ultrathin sections of the double septa of the hyphae or connected conidia and were formerly interpreted as micropores, plasmodesmata, or closure lines. However, they never have a channel, but are visible by TEM even in young states as electron-opaque lines or pegs which apparently do not connect the lumina of neighbouring cells (Figs. 2–5). These structures were discovered in *Geotrichum candidum* Link by Wilsenach & Kessel (1965) and subsequently in several other species of *Geotrichum* and other genera of the *Endomycetes*

(van der Walt & von Arx, 1985). When the two septa bulge, the pegs extend (Fig. 3), the hyphal wall is broken and the cells separate. Extending pegs were previously also observed by Kreger-van Rij & Veenhuis (1973) in *Arthroascus javanensis* (Klöcker) v. Arx and in *Yarrowia lipolytica* (Wickerh. & al.) v.d. Walt & v. Arx. They were demonstrated by Cole & Samson (1979) by SEM in *Geotrichum candidum* (their figure 7.9, p. 109). They considered these structures to be connectives; we would prefer the term disjunctive (disjunctive pegs), this conforming with the classical term disjunctor (Hawksworth & al., 1983).

Several Endomycetales with septa with disjunctive pegs have ascospores which are similar in size, shape, symmetry, structure, and pigmentation, to those of Eurotiales. *Saccharomycopsis capsularis* Schiöningg, for example, has bivalvate, smooth, hyaline ascospores (Fig. 1b) as do *Narasimhella hyalinospora* (Kuehn & al.) v. Arx and *Leucothecium emdenii* v. Arx & Samson of the Eurotiales (Gymnoascaceae) and several teleomorphs of *Aspergillus*. *Leucothecium emdenii* includes an unnamed, *Geotrichum*-like anamorph with catenate, cylindrical conidia with disjunctive structures. The species of the yeast genus *Endomycopsella* (von Arx & Yarrow, 1984) have saturn-shaped, verrucose, slightly pigmented ascospores with equatorial furrows, which correspond in all characters with the ascospores of species of *Eurotium*, *Emericella*, and *Neosartorya*, all with *Aspergillus* anamorphs (Fig. 1n). The conidia of *Endomycopsella* species are not catenate but single with a truncate base and the septa have disjunctive pegs.

The ascospores of *Dipodascus geotrichum* (Butler & Petersen) v. Arx are bivalvate, walnut-shaped, relatively large, with a thick, ornamented wall and a longitudinal furrow. This species has a *Geotrichum* anamorph and is closely related to *Dipodascus australiensis* which has ellipsoidal or irregular, hyaline, sheathed ascospores lacking a furrow (von Arx, 1981). Ascospores similar in shape and structure to those of *Dipodascus geotrichum* but much smaller, are characteristic of the genus *Schwanniomyces*, which includes yeasts without hyphae. *Byssoschlamys* and *Talaromyces*, two related, probably indistinguishable genera of the Eurotiales, include species with similar, ellipsoidal ascospores, but which usually lack distinct furrows (Fig. 1m). *Byssoschlamys* and *Talaromyces* include *Paecilomyces* anamorphs (Fig. 1b), which often are classified in *Penicillium* subgenus *Biverticillatum* (Pitt, 1980).

Ampulliform, phialide-like cells forming meristematic conidiogenous hyphae also occur in the anamorphic states of *Physalospora*, *Apiospora* (Sphaeriales), and some related genera (von Arx, 1985). These anamorphs are classified in *Arthrinium*, *Dictyoarthrinium*, *Papularia*, *Nigrospora*, *Triadelphia*, and other genera (Fig. 1h, i). In most species the conidiogenous hyphae are narrow and thin-walled. The hyphae either form a single apical conidium or they elongate, becoming many-celled by the formation of often thick and pigmented septa and forming supplementary conidia by lateral budding. The darkened septa in the conidiogenous hyphae of *Arthrinium* or *Dictyoarthrinium* species or in the conidia of *Triadelphia* species, are reminiscent of the disjunctive thickenings of Endomycetales and Eurotiales. It may be noted that the conidia are usually bivalvate, with equatorial furrows, as are the ascospores of numerous Endomycetales and Eurotiales.



Figs. 2-5. Hyphal septa of Endomycetales. 2, 3. *Geotrichum terrestre*; 4. *Ascoidea africana*; 5. *Ascoidea rubescens*. Electron micrographs, showing septa with disjunctives (2, 3, bar  $\times 0.25 \mu\text{m}$ ; 4, 5, bar  $\times 0.5 \mu\text{m}$ ).



The hyphomycete *Wallemia sebi* also forms conidiogenous hyphae from ampulliform cells (Fig. 1c). The conidiogenous hyphae become closely septate and the conidia are connected by disjunctive structures. The septa of the vegetative hyphae have central, tube-like pores surrounded by a thickened wall (Terracina, 1974; Cole & Samson, 1979).

Similar central pores in the septa of the vegetative hyphae are known in the ambrosial yeast genera *Ambrosiozyma* and *Hormoascus* (Fig. 10), which are characterized by galeate ascospores (Fig. 1k) and an association with wood-attacking beetles. The thickened septa with central pores have been compared with the dolipores of the Basidiomycetes (Kreger-van Rij & Veenhuis, 1969), but are quite different in their ultrastructure. The septal pores are plugged by dark material.

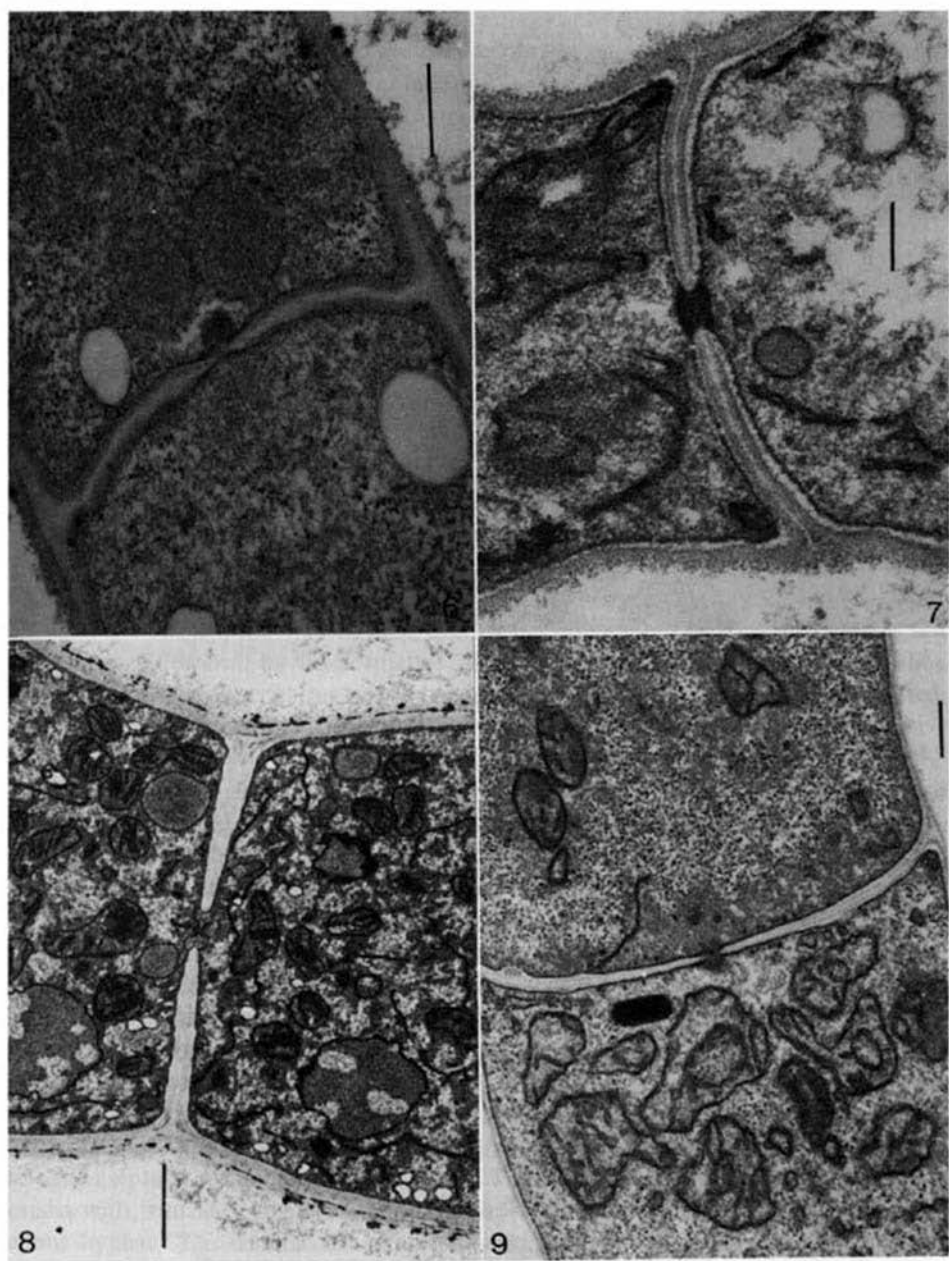
Galeate, helmet-, or hat-shaped ascospores may be considered to be asymmetrically bivalvate with a more distinct, basal brim. No taxa with galeate ascospores are known in the Eurotiales, but they are common in the Endomycetales. The genera *Hansenula* and *Pichia* are characterized by galeate or hemispherical, bivalvate ascospores. The species of *Ascoidea* have many-spored asci, galeate, ascospores and the hyphal septa have numerous disjunctive pegs. *Ascoidea rubescens* and *A. africana* form broad hyphae with septa with distinct, dark pegs (Figs. 5, 6). In *Dipodascus magnusii* (Ludwig) v. Arx the pegs are arranged in a ring near the margin of the septum (van der Walt & al., 1983). *Geotrichum terrestre* has rather thin hyphae with thick septa with one or a few pegs (Fig. 2, 3).

The classification of *Cephaloascus fragrans* (Fig. 1j) either in Endomycetales or Ophiostomatales or in separate order, is often questioned (Redhead & Malloch, 1977; Kurtzman, 1977). Its hyphae have thick septa with rather narrow central pores (Fig. 11). Two conjugating, neighbouring hyphal cells form a thick, apparently diploid hypha, on which erect, thick-walled, pigmented ascophores arise and which bear an apical brush of asci. The asci develop on an ampulliform ascogenous cell and are arranged in basipetal chains, as are the conidia in *Aspergillus* and related genera. In *Cephaloascus fragrans* the asci contain four small, galeate ascospores (Fig. 1j).

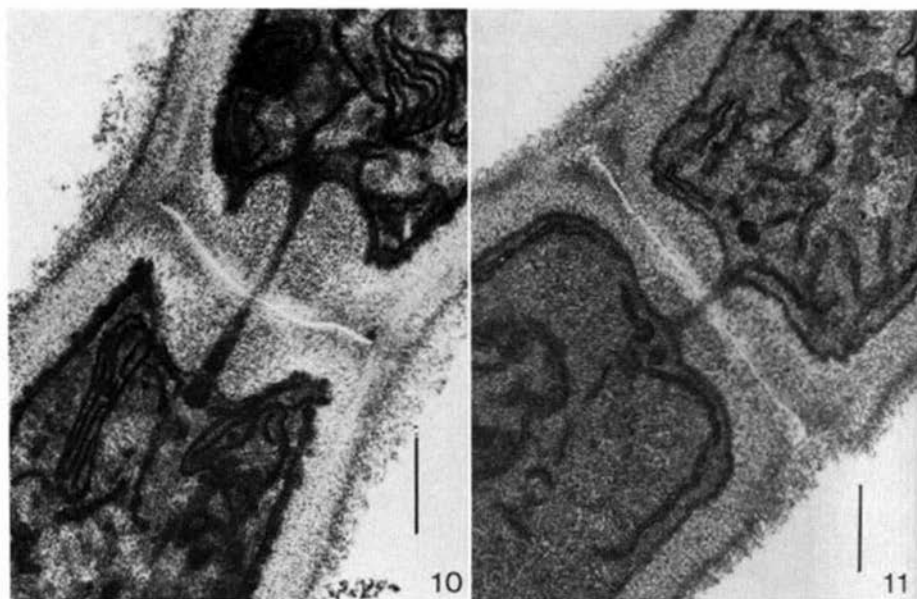
Typical genera of the Ophiostomatales are *Ophiostoma*, *Ceratocystis*, *Ceratocystiopsis*, and *Europhium*. The latter genus is characterized by non-ostiolate, dark ascomata and by galeate ascospores. The ascomata are embedded in a superficial mycelium. The *Lep-tographium* (*Verticicladiella*) anamorphs have conidiophores reminiscent of the ascophores of *Cephaloascus fragrans*.

*Ceratocystis* has been restricted to species with *Chalara* anamorphs, and *Ophiostoma* has been reintroduced for species which include anamorphs belonging to *Graphium*, *Sporothrix*, and some related hyphomycete genera (von Arx, 1974; de Hoog, 1974). Transmission electron microscope studies show that species of both *Ceratocystis* and *Ophiostoma* have relatively thick hyphal walls and septa with a central pore occluded by dark material (Fig. 6, 7). Some chemical characters have been introduced by Weijman & de Hoog (1975) and de Hoog & Scheffer (1984) to delimit the two genera.

*Ceratocystis fimbriata* is apparently the only species of the genus having galeate ascospores with a basal brim. In its *Chalara* anamorph conidia develop in basipetal sequence from a meristematic zone inside a tube-like conidiogenous cell and are cylindrical, aseptate, and hyaline. Disjunctives are apparently absent and the conidia, after release, form



Figs. 6-9. Hyphal septa of Ascomycetes. 6. *Ceratocystis fimbriata*; 7. *Ophiostoma ulmi*; 8. *Gelasinospora tetrasperma*; 9. *Eleutherascus tuberculatus*. Electron micrographs, showing septa with central pores (6, 9, bar  $\times 0.5 \mu\text{m}$ ; 7, bar  $\times 0.25 \mu\text{m}$ ; 8, bar  $\times 1 \mu\text{m}$ ).



Figs. 10–11. Hyphal septa in *Hormoascus* and *Cephaloascus*. 10. *Hormoascus ambrosiae*; 11. *Cephaloascus albidus*. Electron micrographs, showing thickened septa with narrow pores (10, bar  $\times 0.5 \mu\text{m}$ ; 11, bar  $\times 0.25 \mu\text{m}$ ).

mucoïd droplets. Some other *Chalara* species form septate conidia and the septa may be rather thick, occasionally darkened.

The Endomycetales are distinguished from the Eurotiales and from the other Ascomycetes by the absence of ascomata and specialized ascogenous hyphae. They usually develop in aqueous or very moist environments. Further distinguishing characters are the absence of septal pores and Woronin bodies in the hyphae (when present), and the absence of chitin (glucosamine) in the cell walls. In this connection it may be noted that, at least in some species of *Penicillium*, *Aspergillus*, and *Trichoderma*, the cell walls of the conidia do not contain glucosamine, but mainly mannose, galactose, and glucose. Glucosamide, in higher amounts than in the conidia, has been observed in the vegetative hyphae and in germ tubes (Martin & al., 1973, Benitez & al., 1976; Cole & al., 1979; Barreta-Bergter & al., 1981).

#### CONCLUSIONS

The similarity in the presence of disjunctive structures and the absence of glucosamide in the cells and hyphae of the Endomycetales and the conidial chains of the Eurotiales, suggests that these structures are homologous. Three phylogenetic lines have to be

considered. The 'aquatic' line leads to the main part of the Endomycetales, which are dependant on aqueous environments for their reproduction and dispersal. The 'aerial' line is represented by the Eurotiales, the Erysiphales, and other ascomycetes. They form superficial reproductive structures and the ascospores and conidia are dispersed by air under dry conditions. The third phylogenetic line includes fungi and yeasts primarily associated with insects and adapted to dispersal by animals. They develop in cavities, often as ambrosia fungi (Ophiostomatales, *Cephaloascus*, *Hormoascus*, *Ambrosiozyma*, and other entomogenous yeasts and fungi).

The Endomycetales, Eurotiales, Ophiostomatales, and Erysiphales may have been evolved from fungi with similar, aseptate ascospores and with spherical or obovate asci. Such species now are included in *Eleutherascus*, which was classified tentatively in the Pezizales by von Arx (1971). The genus includes four species. The asci develop singly or in small clusters from conjugating cells of the aerial mycelium and are spherical or nearly so, with a relatively persistent wall without operculum. Ascospores with a peridium are absent. *Eleutherascus lectardii* (Nicot) v. Arx has spherical, pale, spiny ascospores. It also has been classified in the Endomycetales as *Hemiascosporium spinulosum* by Batra (1973). By TEM, the hyphae are seen to have relatively thin walls and the septa to have distinct central pores, similar to those of typical Ascomycetes, e.g. *Gelasinospora tetrasperma* (Figs. 8, 9). *Eleutherascus tuberculatus* has also spherical, spiny ascospores and differs from *E. lectardii* by the formation of an anamorph with small, aseptate, hyaline conidia. *Eleutherascus cristatus* v. Emden and *E. peruvianus* Huang have pigmented, spiny ascospores with equatorial furrows.

The 'phialides' of *Aspergillus*, *Penicillium*, *Paecilomyces*, *Wallemia*, *Arthrimum*, and related genera should not be confused with the 'phialides' of *Fusarium*, *Phialophora*, *Clonostachys*, and many other genera, which do not form conidiogenous hyphae with a meristematic base and in which the conidia have no disjunctives. The conidia form usually wet, mucoid masses, but may also be arranged in 'false', often oblique chains. The 'phialoconidia' of *Aspergillus* and related genera are similar to the 'arthroconidia' of *Briosia*, *Coremiella*, and their relatives (Fig. 1). Cain (1972) and others connected the Eurotiales with the Hypocreales, which is not justified. Both differ fundamentally in the structure of ascospores, asci, ascospores, and anamorphs.

Müller & von Arx (1962) connected the Erysiphales (powdery mildews) with the Pezizales. They are also similar to the Eurotiales in that they form reproductive structures on a superficial mycelium and have non-ostiolate ascospores, spherical or obovate asci, and aseptate, hyaline or pale ascospores. The *Oidium* anamorphs also form aseptate conidia with truncate ends in basipetal chains from meristematic bases of erect conidiogenous hyphae. The conidia are separated from each other by two adjacent, bulging septa.

The catenate conidia of the Eurotiales and Erysiphales also should not be confused with the catenate conidia formed in acropetal chains, which also release by bulging scars or disjunctors (e.g. *Monilia*, *Chrysonilia*, *Cladosporium*, or *Ramularia*).

In our opinion, the Endomycetales, Eurotiales (including Gymnoascales), Erysiphales, and Ophiostomatales should be maintained in their present delimitation. An alternative classification based exclusively on the shape and symmetry of the ascospores, would be less than desirable. The shape of the ascospores, however, can be useful to delimit 'natural' groups especially within the Endomycetales and Eurotiales.

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## THE ASCOMYCETE GENUS GYMNOASCUS

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The ascomycete genus *Gymnoascus* is expanded, comprising all Gymnoascaceae with lenticular or discoid (not bivalvate), pigmented ascospores and with ascomata without long, circinate, arcuate, or comb-like appendages. Several species hitherto classified in separate genera are transferred to *Gymnoascus*. *Gymnoascus udagawae* spec. nov. is described. A key to the 14 accepted species is given. *Gymnoascus durus* Zukai is transferred to *Ascocalvatia*. A checklist of all fungi described in *Gymnoascus* is given.

Within the fungi classified in the Gymnoascaceae, von Arx (1971, 1974, 1977) distinguished three phylogenetic entities, which can be recognized easily by the shape and symmetry of the ascospores. The genera *Myxotrichum* Kunze, *Pseudogymnoascus* Raillou, and *Bysoascus* v. Arx are characterized by ellipsoidal or fusiform ascospores having longitudinal furrows in *Bysoascus striatisporus* (Barron & Booth) v. Arx and being smooth or striate by crests in the species of the other genera (Müller & von Arx, 1982; Currah, 1985). The asci are usually spherical, with a distinct cylindrical stalk. Currah classified the three genera in a new family Myxotrichaceae; von Arx (1986) included them in the Onygenaceae, which were emended comprising all Eurotiales with ellipsoidal or fusiform ascospores.

The species of *Amauroascus* J. Schröt., *Arachnotheca* v. Arx, and *Auxarthron* Orr & Kuehn are characterized by spherical ascospores with an ornamented, reticulate, pitted, or striate, often thick wall. They may be related to *Emmonsella* Kwon-Chung, *Ajellomyces* McDonough & Levis, *Xylogone* v. Arx & Nilsson, and related genera, which have spherical, but apparently smooth and hyaline ascospores.

The Gymnoascaceae are now restricted to genera characterized by dorsiventrally flattened, bivalvate, lenticular, or discoid ascospores. Several genera are characterized by such ascospores, but von Arx (1974, 1977) accepted only a limited number including *Gymnoascus* Baranetzky (ascospores discoid, pigmented), *Arachniotus* J. Schröt. (ascospores lenticular, pigmented) and *Narasimhella* Thirumalachar & Mathur (ascospores bivalvate, hyaline). *Arachniotus ruber* (Tiegh.) J. Schröt. was selected as type species of *Arachniotus*, which was not accepted by Orr & al. (1977). They reintroduced the name *Gymnascella* for two species with discoid ascospores and 'naked' ascomata. Similar species with lenticular ascospores were classified in *Pseudoarachniotus* Kuehn. Currah (1985) restricted *Arachniotus* to *A. ruber* and transferred several other species to *Gymnascella*.

The present study began, when a specimen growing on a decaying hoof of a cow was collected. The specimen was identified as *Gymnoascus reticulatus* Zukai, which also

was collected on a hoof. Zukal (1887) described the fungus as follows (translated from German).

Ascomata roundish in outline, orange-reddish, about 500  $\mu\text{m}$  in diameter, covered with a network of hyphae, which are about 5  $\mu\text{m}$  broad, distinctly septate, and reddish; asci botryose, nearly spherical, about 13  $\mu\text{m}$ ; ascospores lenticular, yellow, thick-walled, about 6.4  $\mu\text{m}$ . No type specimen in existence.

On the present specimen, the ascomata are pulvinate, 200–400  $\mu\text{m}$  and orange or pale reddish. They are covered by a network of rather thick-walled, 3–4  $\mu\text{m}$  broad, near the septa 4.5–6  $\mu\text{m}$  broad, smooth or verruculose hyphae. The spherical asci have a diameter of 12–16  $\mu\text{m}$  and a thin but rather persistent wall. The ascospores are lenticular, roundish in face view, elliptical in lateral view, have an equatorial, band-like thickening and measure 6–7  $\times$  4–5  $\mu\text{m}$ . Young ascospores are yellow and become orange or ochraceous when mature.

Cultures on hay infusion agar show a poor growth and remain sterile. Ascomata with mature ascospores were observed only on sterilized pieces of hooves. The fungus apparently is highly keratinolytic. In other characters it represents a typical member of *Gymnoascus*. It differs from *G. reessii* mainly by larger ascospores with an equatorial band and by thicker peridial hyphae without seta-like branches.

The presence of an ascomatal peridium with or without seta-like branches in *Gymnoascus* and *Gymnascella* and its absence in *Arachniotus* is not adequate for the delimitation of genera. In some species a peridium is present when the ascomata develop on the natural substrate or in fresh isolates, but is absent in subcultures. *Arachniotus*, *Pseudoarachniotus*, *Petalosporus*, *Plunkettomyces*, *Disarticulatus*, and *Gymnascella* consequently are synonymized with *Gymnoascus*, which is emended as follows.

### GYMNOASCUS Baranetzky

*Gymnoascus* Baranetzky in Bot. Ztg 30: 158. 1872. — Type: *G. reessii* Baranetzky.

*Gymnascella* Peck in Ann. Rep. N. Y. St. Mus. 35: 153. 1884. — Type: *Gymnascella aurantiaca* Peck.

*Arachniotus* J. Schröt. in Krypt.-Fl. Schlesiens 3(2): 210. 1893. — Type: *A. ruber* (Tiegh.) J. Schröt.

*Pseudoarachniotus* Kuehn in Mycologia 49: 694. 1957. — Type: *P. roseus* Kuehn.

*Waldemaria* Batista & al. in Atas Inst. Micol. Recife 1: 5. 1960. — Type: *W. pernambucensis* Batista & al. (= *G. dankaliensis*).

*Petalosporus* Ghosh & al. in Mycopath. Mycol. appl. 21: 36. 1963. — Type: *P. nodulosus* Ghosh & al.

*Plunkettomyces* Orr in Mycotaxon 6: 33. 1977. — Type: *P. littoralis* Orr.

*Gymnoascoides* Orr & al. in Mycotaxon 5: 459. 1977. — Type: *Gymnoascoides petalosporus* Orr & al.

*Disarticulatus* Orr in Mycotaxon 6: 35. 1977. — Type: *D. devroeyi* Orr.

*Acitheca* Currah in Mycotaxon 24: 63. 1985. — Type: *A. purpurea* Currah.

Colonies expanding, lemon yellow, ochraceous, orange, or red; ascomatal initials composed of a clavate or cylindrical ascogonium surrounded by a coiled antheridium, or of two coiled hyphal tips; ascomata embedded in the aerial mycelium, non stipitate,



occasionally pulvinate and covered or surrounded by a peridium composed of a loose network of hyaline or pigmented hyphae which may bear lateral hyphal tips or short setae; asci irregularly disposed, often botryose, sessile, without croziers, spherical or nearly so, with a thin but rather persistent wall, 8-spored; ascospores discoid or lenticular, round in face view, ellipsoidal or quadrangular in lateral view, aseptate, with or without equatorial thickenings or furrows, yellow, orange, ochraceous, or reddish brown when mature; conidia occasionally present, separated from each other or from the conidiogenous cell by double septa, which may be adjacent or separated by empty parts of the hypha.

*Gymnoascus* species are isolated from soil, dung, and plant debris, occasionally from hooves, nails, feathers, or hairs. On the natural substrate the ascومات are often covered with a network of hyphae, which may be absent or reduced in pure culture or when grown in moist chambers. Only a relatively small number of species includes anamorphs. These belong to the form genera *Malbranchea* and *Chrysosporium*, but are unnamed.

## KEY TO THE SPECIES

- |       |  |                        |
|-------|--|------------------------|
| 1 a.  | Ascospores with an equatorial depression or furrow (Fig. 1a, e)  | 2                      |
| b.    | Ascospores without equatorial furrow or depression   | 3                      |
| 2 a.  | Equatorial depression of the ascospores deep, distinct   | <i>G. ruber</i>        |
| b.    | Equatorial depression of the ascospores shallow  | <i>G. desertorum</i>   |
| 3 a.  | Ascospores 3–4 $\mu\text{m}$ in diameter, ascومات with a distinct peridium                                     | 4                      |
| b.    | Ascospores 4–7 $\mu\text{m}$ in diameter, ascومات with or without peridium                                     | 6                      |
| 4 a.  | Ascospores lenticular, with equatorial thickening  | <i>G. alatosporus</i>  |
| b.    | Ascospores without equatorial thickening, usually discoid (Fig. 1h)  | 5                      |
| 5 a.  | Peridial hyphae stiff, with spine-like, often recurved branches  | <i>G. reessii</i>      |
| b.    | Peridial hyphae thin, without spine-like branches  | <i>G. petalosporus</i> |
| 6 a.  | Ascospores lenticular and with equatorial thickenings (Fig. 1b, c, d)  | 7                      |
| b.    | Ascospores discoid or lenticular and without equatorial thickenings  | 10                     |
| 7 a.  | Colonies lemon-yellow, arthroconidia present, isolated from animals of marine environments                     | <i>G. littoralis</i>   |
| b.    | Colonies not lemon-yellow  | 8                      |
| 8 a.  | Keratinolytic, ascومات with a peridium of thick hyphae   | <i>G. reticulatus</i>  |
| b.    | Not keratinolytic, ascومات without peridium of thick hyphae  | 9                      |
| 9 a.  | Ascospores 5.5–7 $\mu\text{m}$ , with a distinct equatorial thickening and occasionally with polar thickenings | <i>G. dankaliensis</i> |
| b.    | Ascospores 4.5–6 $\mu\text{m}$ , with a broad equatorial band  | <i>G. punctatus</i>    |
| 10 a. | Ascospores lenticular, with distinct poles; colonies lemon-yellow (Fig. 1f)                                    | <i>G. citrinus</i>     |
| b.    | Above characters not combined  | 11                     |
| 11 a. | Ascospores 6–7 $\times$ 4–5 $\mu\text{m}$ , thick-walled; colonies expanding, orange                           | <i>G. devroeyi</i>     |
| b.    | Ascospores smaller, usually discoid (Fig. 1g)  | 12                     |
| 12 a. | Colonies orange or ochraceous, anamorphs absent  | <i>G. aurantiacum</i>  |
| b.    | Colonies lemon-yellow or pale, anamorphs present   | 13                     |
| 13 a. | Colonies restricted, conidia 2–3.5 $\mu\text{m}$ broad   | <i>G. nodulosus</i>    |
| b.    | Colonies expanding, conidia predominant, 6–15 $\times$ 4–5 $\mu\text{m}$                                       | <i>G. udagawae</i>     |

Most species are well described and correctly delimited by Currah (1985) as *Arachnionotus*, *Gymnascella*, *Gymnoascoides*, and *Gymnoascum*. *Gymnascella* sensu Currah is polyphyletic; two species have to be retained in *Narasimhella* Thirumalachar & Mathur

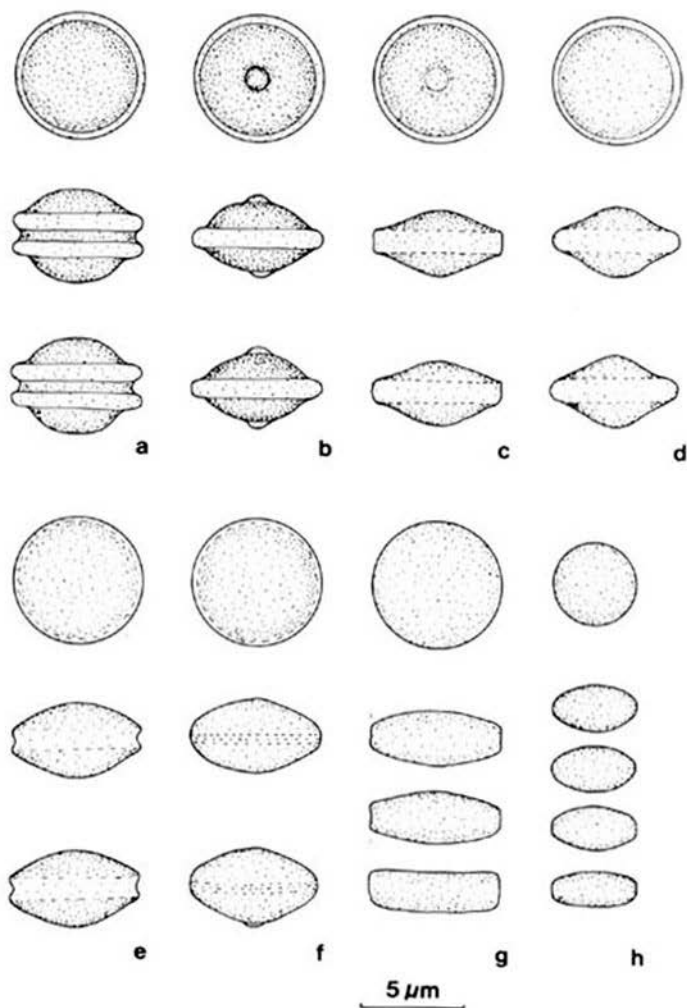


Fig. 1. Ascospores of *Gymnoascus* species in face and lateral view. — a. *G. ruber* (CBS 592.71). — b. *G. dankaliensis* (CBS 294.66). — c. *G. punctatus* (CBS 279.64). — d. *G. littoralis* (CBS 454.73). — e. *G. desertorum* (CBS 634.72). — f. *G. citrinus* (CBS 863.72). — g. *G. aurantiacus* (CBS 655.71) and *G. reessii* (CBS 111.12).

(type species: *N. poonensis* Thirumalachar & Mathur). This genus differs from *Gymnoascus* by unequally bivalvate, hyaline ascospores, obovate asci formed from croziers, and by often stipitate ascomata. *Narasimhella* is closely related to *Ctenomyces serratus* Eidam, *Leucosphaera emdenii* v. Arx & Samson and other species with similar, unequally bival-

vate, hyaline ascospores. The mycelial yeast *Saccharomycopsis capsularis* Schöningg also has bivalvate, smooth, hyaline ascospores and a relationship to the above mentioned Gymnoasaceae has to be considered (von Arx & van der Walt, 1986).

## CHECKLIST

List of species described as *Gymnoascus* (G.), *Arachniotus* (A.), *Gymnascella*, *Pseudarachniotus* (Ps.), and *Petalosporus* (P.).

Accepted names are printed *spaced* or in **bold-face type** (if new).

*P. filamentosus* Orr & Kuehn in Mycologia 64: 62. 1972. — *Gymnascella filamentosa* (Orr & Kuehn) Currah = *G. nodulosus*.

*G. alatosporus* Natarajan in Proc. Indian Nat. Sci. Acad. 37: 124. 1971.

*A. albicans* Apinis in Mycol. Pap. 96: 45. 1967. — *Arachnotheca albicans* (Apinis) v. Arx in Gen. Fungi, 2nd ed., p. 98. 1974.

*P. anodosus* Kuehn & al. in Mycopath. Mycol. appl. 23: 30. 1964 = *G. nodulosus*.

*G. aurantiacus* (Peck) Sacc., Syll. Fung. 8: 823. 1889 is based on *Gymnascella aurantiaca*, the type species of *Gymnascella* Peck.

*Ps. aurantiacus* Kamyschko in Niv. Sist. Niz. Rast. 4: 224. 1967. — *G. aurantiacus* (Currah, 1985).

*G. aureus* Eidam in Jber. schles. Ges. Kultur 64: 161. 1887. — *Amauroascus aureus* (Eidam) v. Arx in Persoonia 6: 375. 1971.

*G. bifurcatus* (Orr) v. Arx in Gen. fungi, 3rd ed., p. 132. 1981. — *Macronodus bifurcatus* Orr in Mycotaxon 5: 283. 1977 = *Auxarthron conjugatum* (Kuehn) Orr & Kuehn (Currah, 1985).

*G. bourquelotii* Boudier in Bull. Soc. mycol. Fr. 8: 44. 1882 is a nomen dubium. No type specimen in existence.

*G. brevisetosus* Kuehn in Mycologia 48: 813. 1956 = *Auxarthron zuffianum* (Morini) Orr & Kuehn.

*G. californiensis* (Orr & Kuehn) Apinis in Mycol. Pap. 96: 12. 1964. — *Auxarthron californiense* Orr & Kuehn.

*G. candidus* Eidam in Jber. Schles. Ges. Kultur 6: 161. 1887 is a nomen dubium. No type specimen in existence.

*G. citrinus* (Masse & Salmon) v. Arx, *comb. nov.* — *Arachniotus citrinus* Masse & Salmon in Ann. Bot. 16: 62. 1902 (basionym).

*G. confluens* Sartory & Bainier in Bull. Soc. mycol. Fr. 29: 261. 1913 is a nomen dubium. No type specimen in existence. The neotype CBS 352.66 is identical to *G. aurantiacus* (Apinis, 1964).

*G. corniculatus* Orr & Plunkett in Mycopath. Mycol. appl. 21: 11. 1963 = *G. reesii* (Samsno, 1972).

*G. dankaliensis* (Castellani) v. Arx, *comb. nov.* — *Trichophyton dankaliense* Castellani in J. trop. Med. Hyg. 40: 315. 1937 (basionym). — *A. dankaliensis* (Castellani) v. Beyma in Antonie van Leeuwenhoek 8: 107. 1942.

*G. demonbreunii* Ajello & Cheng in Mycologia 59: 682. 1967. — *Neogymnomyces demonbreunii* (Ajello & Cheng) Orr (Currah, 1985). Subcultures of the type are sterile.

*G. desertorum* (Moustafa) v. Arx, *comb. nov.* — *A. desertorum* Moustafa in Trans. Br. mycol. Soc. 61: 392. 1973 (basionym).

*G. devroeyi* (Orr) v. Arx, *comb. nov.* — *Disarticulatus devroeyi* Orr in Mycotaxon 6: 35. 1977 (basionym).

*G. dugwayensis* Orr & Kuehn in Mycologia 64: 65. 1972 = *G. reessii* (Currah, 1985). A subculture of the type proved to be sterile.

*G. durus* Zukal in Ber. dt. bot. Ges. 8: 295. 1890 (basionym). — *Keratinophyton durum* (Zukal) Currah in Mycotaxon 24: 156. 1985. — *Ascocalvatia dura* (Zukal) v. Arx, *comb. nov.* No type specimen in existence.

Zukal (1890) described the fungus as follows (translated from German): Ascomata spherical, 1–1.5 mm in diameter, white or pale brownish, aggregated in a stroma, hard, with an about 140  $\mu$ m thick covering composed of thick-walled filaments; asci in irregular balls, spherical, 8-spored, 6–7  $\times$  5–6  $\mu$ m, surrounded by branched, tapering filaments; ascospores cylindrical or ellipsoidal, with truncate ends, pale yellow when mature. 3–4.5  $\times$  2.5  $\mu$ m.

This description agrees with that of *Ascocalvatia alveolata* Malloch & Cain (1971). Both species are congeneric, probably conspecific. The genus is a typical Onygenaceae (Malloch & Cain, 1971). The fungus is rare. I observed it about 20 years ago on a cadaver of a salamander. Cultures on agar media from germinating ascospores remained sterile.

The fungus which Currah (1985) identified with *Gymnoascus durus* differs in spherical ascomata with a dark wall composed of angular cells and in discoid ascospores with a thickened and distinctly pitted margin. It represents a probably undescribed species of *Anixiopsis* = *Aphanoascus*.

*Ps. echinulatus* Dutta & Ghosh in Mycologia 55: 775. 1963. — *Amauroascus echinulatus* (Dutta & Ghosh) v. Arx — *Narasimhella echinulata* (Dutta & Ghosh) v. Arx — *Mallochia echinulata* (Dutta & Ghosh) v. Arx & Samson. This species has to be classified in the Eurotiaceae, because the lenticular, bivalvate ascospores have an equatorial furrow and are echinulate.

*G. eidamii* Cocconi in Mem. Accad. Sci. Inst. Bologna 5: 32. 1891 = *Auxarthron zuffianum* (Currah, 1985).

*A. flavoluteus* Kuehn & Orr in Mycologia 51: 864. 1959 = *G. dankaliensis* (Currah, 1985). Subcultures of the type differ slightly from typical strains of *G. dankaliensis* by paler colonies and the presence of arthroconidia.

*G. flavus* Klöcker in Hedwigia 41: 80. 1902. — *Talaromyces flavus* (Klöcker) Stolk & Samson in Stud. Mycol. 2: 10. 1972 (Onygenaceae).

*A. glomeratus* Müller & Pacha-Aue in Nova Hedwigia 15: 544. 1968. — *Arachnotheca glomerata* (Müller & Pacha-Aue) v. Arx in Persoonia 6: 376. 1971.

*G. gypseus* Nannizzii in Atti Accad. Fisiocr. Sienna 2: 94. 1927. — *Nannizzia gypsea* (Nannizzi) Stockdale in Sabouraudia 1: 45. 1961.

*Ps. halophilus* Pawar & al. in Mycopath. Mycol. appl. 40: 100. 1970 = *G. dankaliensis* (von Arx, 1971).

*A. hebridensis* Apinis in Mycol. Pap. 96: 41. 1964. This is a *Chryso sporium* species (von Arx, 1971).

*Ps. hyalinusporus* Kuehn & al. in Mycopath. Mycol. appl. 14: 215. 1961. — *Narasimhella hyalinuspora* (Kuehn & al.) v. Arx in Persoonia 6: 374. 1971.

*A. indicus* Chattop. & Das Gupta in Trans. Br. mycol. Soc. 42: 72. 1959 = *Talaromyces flavus* (Stolk & Samson, 1972).

*A. intermedius* Apinis in Mycol. Pap. 96: 45. 1964. — *Talaromyces intermedius* (Apinis) Stolk & Samson in Stud. Mycol. 2: 21. 1972.

*G. intermedius* Orr in Mycotaxon 5: 470. 1977 = *G. reessii* (von Arx, 1981). Currah (1985) accepted this species.

*G. johnstonii* (Masse & Salmon) Orr & Kuehn in Mycopath. Mycol. appl. 21: 8. 1963 is a nomen dubium. No type specimen in existence.

*Gymnascella kamyschkoi* Orr & al. in Mycologia 69: 137. 1977 = *G. aurantiacus* (Currah, 1985).

*A. lanatus* Apinis in Mycol. Pap. 96: 39. 1964 is a nomen dubium. No type specimen in existence.

*A. lectardii* Nicot in Bull. Soc. mycol. Fr. 85: 319. 1969. — *Eleutherascus lectardii* (Nicot) v. Arx in Persoonia 6: 378. 1971.

*G. littoralis* (Orr) v. Arx, *comb. nov.* — *Plunkettomyces littoralis* Orr in Mycotaxon 6: 33. 1977 (basionym).

*G. longitrichus* Orr & Kuehn in Mycopath. Mycol. appl. 21: 9. 1963 = *G. reessii* (Currah, 1985).

*G. luteus* Sacc., Syll. Fung. 11: 437. 1894. — *Talaromyces luteus* (Sacc.) Stolk & Samson in Stud. Mycol. 2: 23. 1972.

*Ps. marginosporus* Kuehn & Orr in Mycopath. Mycol. appl. 19: 257. 1963 (basionym). — *Narasimhella marginospora* (Kuehn & Orr) v. Arx, *comb. nov.*

*Narasimhella marginospora* is closely related to *N. poonensis* Thirumalachar & Mathur (1966), but differs by the less distinct equatorial rim of the ascospores and by the absence of stipitate ascomata. *Narasimhella hyalinuspora*, the third species, has ascospores without a distinct rim. In all species the outer (upper) volva of the ascospores has a thicker wall than the inner (lower) volva, which may be covered with some granulae. A strain isolated in 1978 from dung received from India (CBS 125.78) forms distinct, stipitate, orange ascomata and oblate ascospores without rim or brim (Fig. 2).

*G. myriosporus* Rostr. in Meddr. Groenland 18: 12. 1894 is a doubtful species. No type specimen in existence. Probably a *Thelebolus* has been described.

*A. niger* (J. Schröt.) Kuehn & al. in Mycopath. Mycol. appl. 25: 106. 1965. — *Amauroascus niger* J. Schröt.

*G. nodulosus* (Ghosh & al.) v. Arx, *comb. nov.* — *P. nodulosus* Ghosh & al. in Mycopath. Mycol. appl. 21: 36. 1963 (basionym).

*G. ossicola* Rostr. in Bot. Tidskr. 21: 45. 1897. — *Nannizzia ossicola* (Rostr.) Apinis, but is a doubtful species. No type specimen in existence.

*G. petalosporus* (Orr & al.) v. Arx in Persoonia 9: 397. 1977 is based on *Gymnoascoides petalosporus* Orr & al. in Mycotaxon 5: 459. 1977.

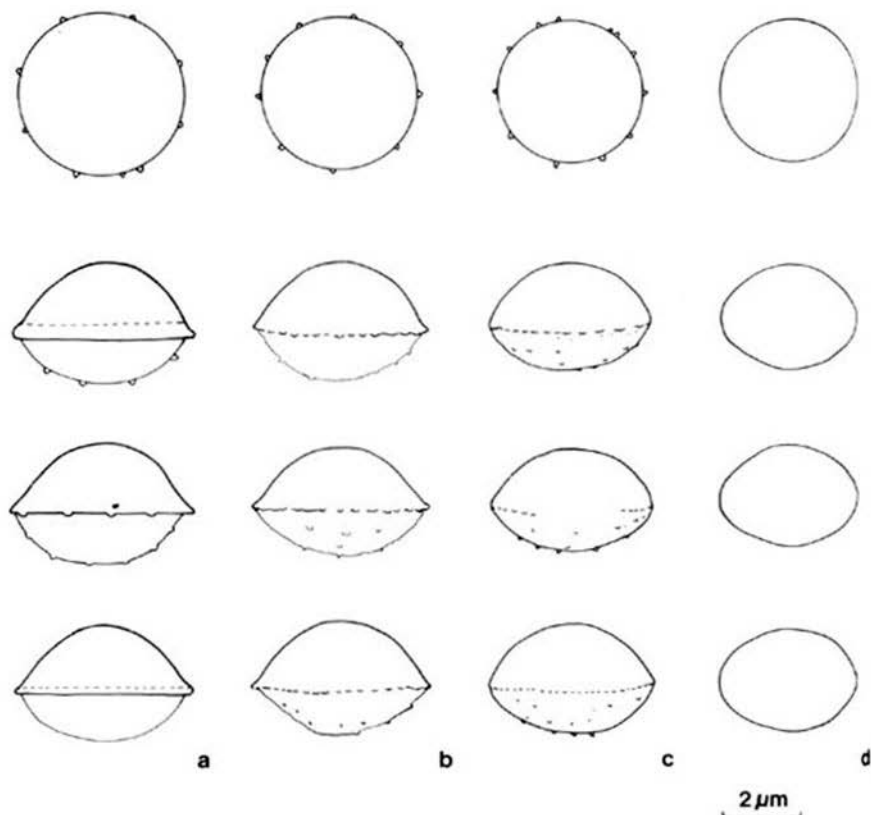


Fig. 2. Ascospores of *Narasimhella* species in face and lateral view. — a. *N. poonenis* (CBS 393.71). — b. *N. marginospora* (CBS 115.54). — c. *N. hyalinospora* (CBS 548.72). — d. *Narasimhella* spec. (CBS 125.78).

*G. punctatus* (Dutta & Ghosh) v. Arx, *comb. nov.* — *Ps. punctatus* Dutta & Ghosh in *Mycologia* 56: 153, 1964 (basionym).

*A. purpureus* Müller & Pacha-Aue in *Nova Hedwigia* 15: 552, 1968. — *Talaromyces purpureus* (Müller & Pacha-Aue) Stolk & Samson in *Stud. Mycol.* 2: 57, 1972.

*G. reessii* Baranetzky in *Bot. Ztg* 30: 158, 1872.

*G. reticulatus* Zukal in *Verh. zool.-bot. Ges. Wien* 37: 40, 1887.

*Ps. reticulatus* Kuehn & Goos in *Mycologia* 52: 40, 1960. — *Amauroascus reticulatus* (Kuehn & Goos) v. Arx in *Persoonia* 6: 375, 1971 (but see Currah, 1985).

*A. reticulatus* Kuehn in *Mycologia* 49: 57, 1957 = *Amauroascus kuehneii* v. Arx in *Persoonia* 6: 376, 1971.

*G. rhoustogonylinus* Wener & Cain in Can. J. Bot. 48: 325. 1970 = *Pseudogymnoascus roseus* Raitio (Samson, 1972).

*G. roseus* (Raitio) Apinis in Mycol. Pap. 96: 8. 1964. — *Pseudogymnoascus roseus* Raitio. Currah (1985) synonymized *Pseudogymnoascus bhattii* Samson with *Ps. roseus*, but it differs by the absence of a *Geomyces* (*Chryso sporium*) anamorph and by the colour of the colonies.

*Ps. roseus* Kuehn in Mycologia 49: 695. 1957 = *G. dankaliensis* (Castellani) v. Arx (von Arx, 1971).

*G. ruber* Tiegh. in Bull. Soc. bot. Fr. 24: 159. 1877 is also known as *A. ruber*.

*G. setosus* Eidam in Bot. Zentbl. 10: 107. 1882. — *Myxotrichum setosum* (Eidam) Orr & Plunkett in Can. J. Bot. 41: 1470. 1963.

*G. siglerae* v. Arx in Gen. Fungi, 3rd ed., p. 132. 1981 = *Uncinocarpus reessii* Sigler & Orr in Mycotaxon 4: 461. 1976. The ascospores are similar to those of *G. reessii*: 4–5  $\mu$ m in diameter, discoid or slightly lenticular, pale brown when mature. *Uncinocarpus* can be accepted as a separate genus of the Gymnoascaceae, when *G. uncinatus* is included in it. Both species form superficial ascomatal structures with long, thick-walled, apically circinate setae and include *Malbranchea* anamorphs (Currah, 1985). In pure culture only the anamorphs develop; asci are formed in moist chambers on hairs mixed with soil.

*G. stipitatus* Lindfors in Svensk bot. Tidskr. 14: 270. 1920. — *Myxotrichum stipitatum* (Lindfors) Orr & Kuehn in Can. J. Bot. 41: 1471. 1963.

*A. striatisporus* Barron & Booth in Can. J. Bot. 44: 1060. 1966. — *Byssosascus striatisporus* (Barron & Booth) v. Arx in Persoonia 6: 377. 1971.

*G. subumbrinus* A. L. Smith in Trans. Br. mycol. Soc. 5: 424. 1917 = *Auxarthron umbrinum* (Boud.) Orr & Plunkett in Can. J. Bot. 41: 1446. 1963.

*G. sudans* Valionis in Vyt. Didziojo Mat. Gamtos Fak. Darbei 11: 115. 1936 = *Byssochlamys nivea* Westling (Stolk & Samson, 1971).

*Ps. terrestris* Thirumalachar & Mathur in Mycopath. Mycol. appl. 40: 102. 1970 = *G. dankaliensis* (von Arx, 1971).

*Ps. thirumalacharii* Mathur in Mycopath. Mycol. appl. 40: 101. 1970 = *G. dankaliensis* (von Arx, 1971).

*A. trachyspermus* Shear in Science 16: 138. 1902. — *Talaromyces trachyspermus* (Shear) Stolk & Samson in Stud. Mycol. 2: 32. 1972. *T. spiculispurus* (Lehman) C. R. Benjamin is a synonym.

*A. trisporus* Hotson in Mycologia 28: 500. 1936 = *Byssochlamys nivea* Westling (Stolk & Samson, 1971).

*Ps. trochleosporus* Kuehn & Orr in Mycologia 64: 58. 1972 = *G. ruber* Tiegh. (Currah, 1985).

*Gymnoascus udagawae* v. Arx, spec. nov. — Fig. 3

Coloniae expandae, citrino-luteae; mycelium ex hyphis septatis hyalinis, 1.5–4  $\mu$ m in diam. compositum; asci aggregati, sessiles, globosi vel subglobosi, tenui-tunicati, 8-sporei, 8–11  $\mu$ m in diam.; ascosporeae dorsiventrali compressae, discoideae, flavae, 4–5  $\times$  2.5–

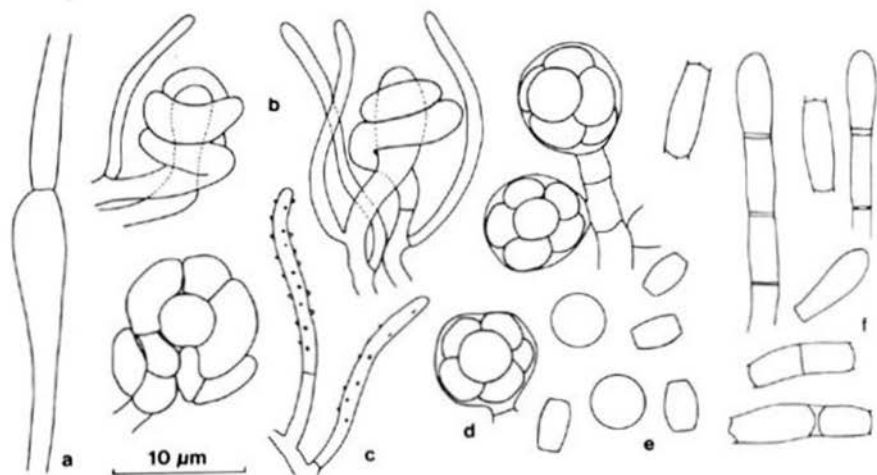


Fig. 3. *Gymnoascus udagawae* (CBS 950.69). — a. Swollen hypha. — b. Initials. — c. Verrucose hyphae surrounding the ascogonia. — d. Asci. — e. Ascospores in face and lateral view. — f. Conidia.

3.5  $\mu\text{m}$ ; arthro- e aleurioconidia numerosa, cylindracea vel clavata, hyalina, 0- vel 1-septata, 6–15  $\times$  3–5  $\mu\text{m}$ .

Typus exsiccatus CBS (CBS 950.69, IFO 8921, ATCC 24072).

This species is known by a soil isolate from Japan, described and depicted by Udagawa and Takada (1968) as *A. hebridensis* Apinis. It differs from other species with lemon yellow colonies by the daily growth rate of the aerial mycelium (3–4 mm at 25°C on hay infusion agar), the relatively small, lenticular ascospores without equatorial thickenings and the abundant formation of relatively large conidia. Young ascogonia are surrounded by delicate, hyaline, often verrucose hyphae extending the asci (Fig. 3).

*G. umbrinus* Boudier in Bull. Soc. mycol. Fr. 8: 43. 1892. — *Auxarthron umbrinum* (Boud.) Orr & Plunkett in Can. J. Bot. 41: 1446. 1963.

*G. uncinatus* Eidam in Beitr. Biol. Pfl. 3: 292. 1880. — *Uncinocarpus uncinatus* (Eidam) Currah in Mycotaxon 24: 186. 1985.

*G. verrucosus* Eidam in Jber. schles. Ges. 64: 162. 1887 = *Amauroascus mutatus* (Quél.) Rammeloo in Bull. Jard. bot. nat. Belg. 52: 241. 1982.

*A. verrucosus* Orr & Kuehn in Mycologia 64: 62. 1972 = *G. aurantiacus* (Orr & al., 1976).

*G. verticillatus* A. L. Smith in Trans. Br. mycol. Soc. 1: 154. 1896. — *Actinodendron verticillatum* (A. L. Smith) Orr & Kuehn in Mycopath. Mycol. appl. 21: 211. 1963. Genus and species are doubtful; ascospores unknown.

*G. vinaceus* (Raiillo) Apinis in Mycol. Pap. 96: 9. 1964 = *Pseudogymnoascus roseus* Raiillo (Samson, 1972).



*A. volatilis-patellus* Orr & Kuehn in Mycologia 64: 61, 1972. — *Amauroascus volatilis-patellus* (Orr & Kuehn) Currah in Mycotaxon 24: 136, 1985.

*G. zuffianus* Morini in Mem. Accad. Sci. Inst. Bologna 4: 205, 1889. — *Auxarthron zuffianum* (Morini) Orr & Kuehn in Can. J. Bot. 41: 1445, 1963. Currah (1985) included in *Auxarthron* seven species. Their delimitation, however, is difficult and no key is given.

The author thanks Dr. K. A. Seifert for reading the manuscript and for useful suggestions.

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## MALLOCHIA, A NEW GENUS OF THE EUROTIALES

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*Pseudoarachnietus echinulatus* is classified in a new genus *Mallochia* of the Eurotiaceae. It also shows affinities to *Narasimhella* (Gymnoascaceae) and *Eleutherascus* (Ascodesmidaceae).

In 1976, Dr. Sultan Ahmad (Lahore, Pakistan) sent a number of samples of fungal material collected on decaying plant material. Specimens identified as *Chaetomium* spec. were incubated in moist chambers at 28°C. The isolated *Chaetomium* species are discussed elsewhere (von Arx & al., 1986). Among the other fungi which could be isolated was a cellulose decomposing ascomycete, which was identified as *Pseudoarachnietus echinulatus* Dutta & Ghosh. The isolate was compared with a subculture of the type (CBS 278.64) and with a culture received from Dr. G. F. Orr (ATCC 24534 = CBS 168.73).

The description of *P. echinulatus* given by Dutta & al. (1963) is rather inadequate. They described and depicted stalked asci and spherical, echinulate ascospores. In fact the asci develop from conjugating hyphal tips or from croziers and the ascospores are distinctly dorsiventrally flattened, with an equatorial furrow. Von Arx (1971) synonymized *Pseudoarachnietus* with *Arachnietus* and transferred *P. echinulatus* to *Amauroascus*. All typical species of this genus have spherical, reticulate or echinulate, pigmented ascospores. Consequently, *P. echinulatus* has to be classified in a separate genus, which is dedicated to our colleague Dr. D. Malloch (Toronto, Canada).

## MALLOCHIA v. Arx &amp; Samson, gen. nov.

Ascomata absunt; ascogonia in mycelio aëria oriunda, clavata vel contorta; asci singuli vel pauci proferunt, obovati vel subglobosi, tenui tunicati, plerumque octospori; ascosporae aseptatae, dorsiventrali compressae, bivolvatae, spinosae, cum 2 cristis aequatorialibus; paraphyses absunt; conidia absunt. — Typus: *Mallochia echinulata* (Dutta & Ghosh) v. Arx & Samson.

*Mallochia echinulata* (Dutta & Ghosh) v. Arx & Samson, comb. nov. — Figs. 1, 2

*Pseudoarachnietus echinulatus* Dutta & Ghosh in *Mycologia* 55: 775. 1963 (basionym). — *Amauroascus echinulatus* (Dutta & Ghosh). v. Arx in *Persoonia* 6: 375. 1971.

Colonies on cornmeal agar at 28°C with a daily growth rate of 2–3 mm, with a white or pale aerial mycelium, becoming yellow or pale ochraceous with age, without coloured exudates: expanding hyphae septate, rather thick-walled, hyaline, 4–6 µm broad, often

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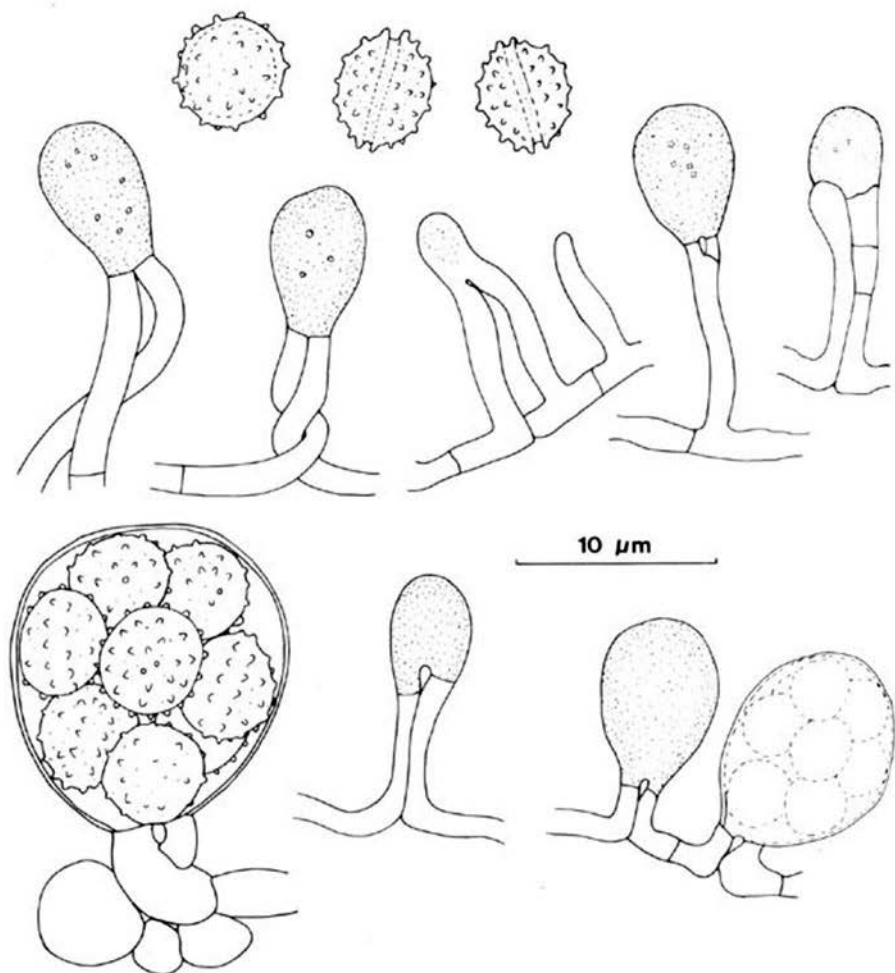


Fig. 1. *Mallochia echinulata*, initials, immature and mature asci, and ascospores (from CBS 139.86).

with some swollen cells; aerial hyphae septate, hyaline, 1.5–2.5  $\mu\text{m}$  broad; ascigerous initials formed in the aerial mycelium, composed of two erect, conjugating hyphae, occasionally twisted at the base, usually clavate, septate, or composed of a clavate cell surrounded by a septate coil; asci single or in small clusters, formed from conjugating hyphal tips or from croziers, spherical, obpyriform or obovate, with an attenuated and truncate base, with a rather persistent wall, usually 8-spored, 13–18  $\times$  10–14  $\mu\text{m}$ ; ascospores

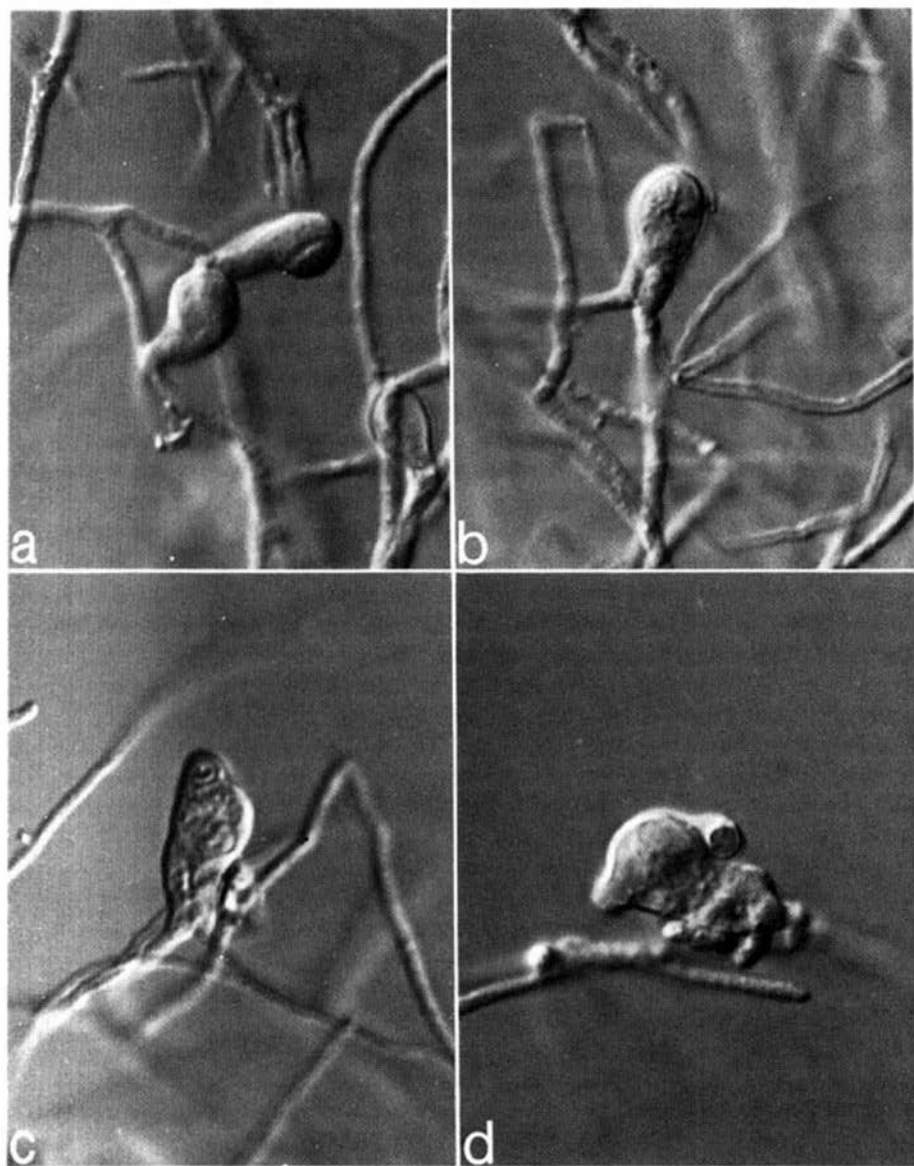


Fig. 2. *Mallochia echinulata* — a–d. Development of ascigerous initials  $\times 1400$ . Note the characteristic conjugating hyphae in Figs. b, c.

dorsiventrally flattened, bivalvate, roundish in face view, elliptical in lateral view, aseptate, with an equatorial furrow surrounded by two rims, covered with conical, blunt spines, hyaline or pale yellow when mature,  $5-6.5 \times 4-5 \mu\text{m}$ .

The description given above is based on a fresh isolate (CBS 139.86, ex plant debris, Lahore, Pakistan).

The ascospores of *Mallochia echinulata* are reminiscent of those of the Eurotiaceae, especially of species classified in *Emericella* and *Neosartorya* which include *Aspergillus* anamorphs. In these species, the asci develop in distinct asomata and usually are catenate and not formed from croziers. *Mallochia echinulata* shows also affinities to *Narasimhella* and *Eleutherascus*. In *Narasimhella poonensis* Thirumalachar & Mathur, the type species of the genus *Narasimhella*, the obovate asci also develop from croziers in a superficial mycelium, but the ascospores are unequally bivalvate and smooth, except some granulae often visible along the equatorial rim. *Eleutherascus lectardii* (Nicot) v. Arx, the type species of *Eleutherascus*, differs from *M. echinulata* by larger (about  $10 \mu\text{m}$  diam.), spherical, spiny ascospores without equatorial furrow or rim. Von Arx (1971) classified *Eleutherascus* in the Pezizales.

Currah (1985) synonymized *Narasimhella* with *Gymnascella*. Both genera, however, are not closely related. *Gymnascella aurantiaca* Peck, the type species of the genus *Gymnascella*, has discoid (not bivalvate), pigmented ascospores without equatorial furrows or thickenings, and the asci are spherical and do not develop from croziers, but by budding. *Gymnascella aurantiaca* is congeneric with *Gymnoascus reessii* Baranetzki, the type of *Gymnoascus*, which has similar asci and similar, slightly smaller ascospores. Peridial structures are unknown in *Narasimhella* species.

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THE NOMENCLATURE OF *RUSSULA* SPECIES AND THE SYDNEY RULES

R. SINGER\* &amp; R. MACHOL\*\*

A recent paper by Th. W. Kuyper & M. van Vuure shows general agreement with an earlier paper by Singer & Machol on many nomenclatural problems and on the number of *Russula* species affected by the new starting point rules. A few minor disagreements with regard to contradiction between Arts. 13.1 and 63 are mentioned, and those regarding *R. delica*, *R. nitida* and *R. atropurpurea* are explained. We conclude (contrary to Kuyper & van Vuure's conclusions) that their statements confirm that Art. 13.1 as it now stands is detrimental to stability in nomenclature of Basidiomycetes, and unsettling as well as burdensome to the working taxonomist, and should be changed according to Proposal 42 now before the Nomenclature Committee.

In a paper on the nomenclature of *Russula* species, Kuyper & van Vuure (1985)—hereafter K&V—have invited 'comments on the nomenclatural . . . conclusions arrived at in this paper.' In the majority of cases they agree with Singer & Machol (1983)—hereafter S&M. In one case where they disagree (*R. aurea* Pers.), we now concede that they are correct. In a few cases, taxonomical or nomenclatural interpretations differ slightly, a consequence not of oversight by either K&V or S&M, but of the difficulties arising from the new rules (Art. 13.1, Sect. 4 of the ICBN 1983). We would therefore have refrained from further comment, had K&V not chosen to draw conclusions with regard to the present rules that are not only in contrast to our proposals (Singer & al., 1984) but to K&V's own nomenclatural statements. They admit that the new Art. 13.1 (1983) causes 'temporary' instability of nomenclature. In fact, it also causes new, otherwise unnecessary library 'research', controversies such as the ones we have to deal with at present, new proposals to clarify the rules, and endless proposals to conserve and reject. All this not only makes the new rules less clear and more difficult than the ones that were accepted for 75 years, but also causes sterile extra work, expense, and publication. K&V recognize the necessity to check almost any name in *Russula* (and, of course, other genera) for newly appearing homonyms (such as *R. rosea* Qué.); they apparently recognize that since 1983 it has become impossible to 'reject the use of names which may cause error or ambiguity or throw science into confusion' (ICBN, Preamble); and they acknowledge the fact that most working mycologists are reluctant to accept the consequences of illegitimacy which has increased under the new rules.

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K&V (p. 454) say 'although (the new wording of Art. 13.1 d) will necessitate several name changes . . . we firmly (believe) that only by this procedure a correct and stable nomenclature of the agarics could be achieved.' They also assert 'It is our firm conviction that only this voluntary self-restraint can lead to a stable nomenclature.' Alas, the postulated self-restraint is quite rare; we could cite long lists of new names and new combinations on the basis of mostly quite shaky or, with a view to the ever-changing rules, quite ephemeral arguments. The lack of restraint of such authors seems to us matched by the lack of restraint of the rule-changers who, as in the case of Art. 13, did the voting first and the investigation of the consequences afterwards.

Having stated this, we believe that the discussion of each individual case in *Russula* is of secondary importance. Some comments are attached here not in a spirit of controversy, but in order to show that, under the new rules more than under the old ones, final nomenclatural decisions are dependent on many and often complicated considerations.

### 1. *Russula delica* vs. *R. exsucca*

The interpretation of *A. piperatus*  $\beta$  *exsuccus* Pers., Obs. 2: 41 as being typified by *Agaricus giganteus* Leyss. Fl. Hal. no. 1213 does not save the epithet *delica* under the Sydney rules. In the first place Persoon himself (1801: 429) dropped this quotation, retaining only Buxb Cent. 4 p. 1 t. 1 and his own original diagnosis; secondly if Leysser's taxon is indeed considered as a representation of *exsuccus*, it is either not identical with *Leucopaxillus giganteus* (Pers.) Sing. & Sm., or if it is identical, it is in contrast with the original description, since the lamellae are described as, 'sparsis, subdistantibus' while they are crowded to subclose in *L. giganteus*. According to Art. 7.8 and 7.17 (ICBN 1983: 7) a neotype has to be chosen to typify Persoon's and Fries's (ssp./var.) *exsuccus* and since according to Art. 8 (l.c.: 9) the type cannot be *A. giganteus* because it is in contrast with the protolog, and 'the type . . . of a . . . intraspecific taxon is a single specimen . . .' (Art. 9) it is proposed that the specimen F.M. 1030764, *Singer C 7671* (F), (as *Russula delica* Fr.) be the neotype of *A. piperatus*  $\beta$  *exsuccus* Pers. This is the only legitimate and honest procedure, considering that all *Russula* specialists tend to interpret *A. exsuccus* as a *Russula* of the *delica* group, most probably identical with *R. delica* Fr., and that var. *exsuccus* Fr. 1821 is sanctioned and based on Persoon (1801).

### 2. *Russula nitida*

*Russula nitida* (Pers. ex Fr.) Fr. and *Agaricus nitidus* Pers. ex Fr. (or Pers.: Fr.) are now (since 1983) undoubtedly superfluous names in the sense of Art. 63. As sanctioned name (1821) it should have been typified with *A. purpureus* Schaff. or *A. risigallinus* Batsch (Art. 7.11; 7.13). If the fungus is then called *R. purpurea* (Schaff.) Quél. (1897) it becomes a homonym of *R. purpurea* Gill. (1884). If it is called *R. risigallina* (Batsch) K&V it becomes a synonym of one of the species of the *R. lutea* group. The *R. nitida* in the sense of modern monographers, i.e. sensu Singer or sensu J. Schäffer, Romagnesi, etc. is therefore not available anymore. We (Singer & Machol, 1983) have considered it doubtful whether Art. 63 can supersede Art. 13.1 d, and we still believe that the rules are not at all explicit or clear about this. K&V think that they are. But the typification

of *R. nitida* according to Art. 7.11 can hardly be challenged. It is another question whether *A. nitidus* Pers. is a superfluous name. We interpret Persoon's words as expressing doubt merely whether *A. purpureus* Schaff. is a synonym of *A. nitidus* (var. *nitidus*) or var. *atropurpureus*, not as doubtful about its identity with the species *sensu lato*. The remark may indeed be interpreted differently. Yet it makes no difference whose interpretation is correct unless we admit K&V's new proposal to change Art. 7.17. A meaningful discussion of the consequences and acceptability of the Sydney rules cannot be made if we do not accept the rules as they are presented to us.

### 3. *Russula atropurpurea* vs. *R. krombholzii*

Neither of the names is directly linked with the Sydney rules but here again we face a complexity that has caused various conclusions which after a more detailed examination of the nomenclatural and taxonomical facts appear rather unwarranted.

When Krombholz described the species as *A. atropurpurea* he was not fully aware of its variability, and it was only after later specialists included a paler form or variety that certain synonymies became applicable. It is now believed probable or possible that this pallescent form is partly or entirely conspecific with *R. depallens* Pers. and/or Fr. as admitted by R. Maire, Singer, J. Schäffer and Romagnesi. Since *R. atropurpurea* (Krombh.) Britz. is but a later homonym of *R. atropurpurea* Peck, we have to consider calling the species *R. depallens* Pers.: Fr. inasmuch as this species is a sanctioned one (Fries, 1821: 58). The present rules make it tempting to designate a neotype in this sense, but Persoon's description (more than Fries's) contains a few data that contradict this interpretation so that it appears to be prudent to refrain from such typification. However, there is a species which almost certainly is the same as this pallescent form of *R. atropurpurea* (Krombh.) Britz., viz. *R. bresadolae* Schulzer in Hedwigia 24: 139. 1885. In our opinion there is no other interpretation possible, and Cooke's picture of *R. depallens* is certainly identical. It is however possible that the pallescent fungus is more than an occasional form or variety of the typically deep purple form(s) but even if such a possibility were considered, *R. krombholzii* Shaff. would still be antedated by *R. atropurpurina* (Sing.) Crawshay, Spore Orn. Russ.: 128. 1930. Just in order to be complete, we also mention the fact that *A. luteoviolaceus* Krombh. has been indicated as synonymous with *R. atropurpurea* (Krombh.) Britz. by Singer and Romagnesi, in both cases doubtfully. Our present opinion is that this species is specifically different from *R. atropurpurea* (Krombh.) Britz. Which then is the correct name of *R. atropurpurea* (Krombh.) Britz. non Peck? We do not have the final answer but it is not *R. krombholzii* Shaff., nor could it be *R. depallens* Fr. if Art. 7.17 is rescinded as K&V propose.

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## ON THE TYPIIFICATION OF SOME PERSOONIAN PYRENOMYCETE NAMES

L. HOLM\*

The original material of some Persoonian species belonging to the present day genera *Leptosphaeria* and *Lophiostoma* has been revised. Lectotypes are selected for *Sphaeria cristata* Pers., *S. crenata* (Pers.) Fr., *S. diminuens* Pers., and *S. dolium* Pers.

In connection with the author's studies on the taxonomy and nomenclature of certain pyrenomycete genera it was found desirable to lectotypify some Persoonian names. Thanks to the courtesy of the Mycology Department of the Rijksherbarium I have got the opportunity to examine the pertinent material preserved in Persoon's herbarium. The specimens are listed below with the original names and notes cited, as far as I have been able to read them, with some comments added.

***Sphaeria compressa* Pers., Syn. Meth. Fung. 54**

Fr., Syst. Myc. 2: 470. — *Lophiostoma compressum* Ces. & De Not. in Comm. Soc. critt. ital. 1: 219. 1863. — *Platystomum compressum* Trev. in Bull. Soc. R. Bot. Belg. 16: 16. 1877.

910.270-356. '*Sphaeria compressa*' (scr. Persoon). Quite immature.

910.270-358. '*Sphaeria compressa*'? (scr. Persoon). This is *L. compressum* sensu auct. and was appropriately selected as lectotype by Chesters & Bell (1970: 48).

***Sphaeria cristata* Pers., Syn. Meth. Fung. 54**

*Lophium cristatum* Crouan & Crouan, Fl. Finistère 29. 1867. — *Lophiella cristata* Sacc., in Michelia 1: 337. 1878.

*Sphaeria cristata* Pers. comprised two infraspecific taxa, viz.  $\alpha$  *Sphaeria crenata* and  $\beta$  *Sphaeria arundinis*. It seems reasonable to take *S. crenata* as the type variety, the more so as this name, not *S. cristata*, was sanctioned by Fries in Syst. Myc. 2: 469.

***Sphaeria crenata* (Pers.) Fr., Syst. Myc. 2: 469**

910.270-379. '*Sph. cristata*' (in Persoon's handwriting). This is *L. compressum*.

910.270-390. '*In cortice Populi fastigiatae Sphaeria*'? (scr. Mougeot). '*cristata* var. *dehiscens*'? (scr. Persoon). This is *L. compressum*, too.

910.270-391. '*Sph. cristata* var. *crenata*' (scr. Persoon). This is good material of *L. crenatum* as generally conceived, and is here proposed as lectotype for *Sphaeria crenata* (Pers.) Fr.

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910.270-392. 'Sphaeria cristata  $\beta$  media?' (scr. Persoon). *L. compressum* is present, well developed.

910.270-417. 'in caulibus umbelliferarum Sphaeria cristata??' (scr. Mougeot) 'var.' (scr. Persoon). This is typical and well developed *L. caulium* with the appendages still visible.

910.270-418. 'Sphaeria cristata' (scr. Persoon). This is *Navicella pileata*.

**Sphaeria cristata  $\beta$  arundinis** Pers., Syn. Meth. Fung. 56

*Sphaeria arundinis* (Pers.) Fr., Syst. Myc. 2: 510.

910.270-367. 'Sphaeria cristata  $\beta$  arundinis. S. fung. an Spec. distincta. erumpens. inquinans, ostiolo sphaerula . . . tiore' (scr. Persoon). The material is in poor condition but is apparently *L. semiliberum*.

910.270-374. 'Sphaeria cristata  $\beta$  arundinis Pers. S. 54: 103' (scr. Chaillet). This is *Leptosphaeria grandispora* Sacc. sensu Müller = *Massariosphaeria grandispora* Leuchtmann.

**Sphaeria dehiscens** Pers., Syn. Meth. Fung. 55

910.270-410. 'in ramulis Pruni Padi Sphaeria cristata? Pers.' (scr. Mougeot). 'dehiscens' (scr. Persoon). — Old stromata of a pyrenomycete, probably *Eutypella padi*.

910.270-610. 'Sphaeria dehiscens Pers. macrostoma C. 802a' (scr. Chaillet). This is *Navicella pileata*, as already suggested by Chesters & Bell (1970: 32).

910.270-635. 'Sphaeria dehiscens. Syn. fung. p. 55' (scr. Persoon). No identifiable fungus found.

As apparent from the protologue *S. dehiscens* must be considered an obligate synonym of *S. macrostoma* Tode. It has scarcely been used by subsequent authors.

**Sphaeria diminuens** Pers., Syn. Meth. Fung. 57

Fr., Syst. Myc. 2: 417. — *Lophiostoma diminuens* Ces. & De Not. in Comm. Soc. critt. ital. 1: 220. 1863. — *Lophidium diminuens* Sacc., Syll. 2: 714. 1883.

There are four specimens in the Leiden folder:

910.270-608. 'Sphaeria innata mihi . . . . diminuens' (in Persoon's handwriting). No identifiable fungus present.

910.270-615. 'Sphaeria diminuens? sphaerulis immersis, simplicibus, ostiolo crasso prominente.' This is *Lophiostoma compressum*, as already pointed out by Chesters & Bell.

910.270-616. ' . . . tiges mortes du framboisier' (?) (scr. Mougeot). 'Sphaeria diminuens' (det. Persoon). Very immature, according to Chesters & Bell (1970: 9) = '*Lophiostoma angustilabrum*'.

910.270-627. 'Sphaeria diminuens' (scr. Persoon). This is *Lophiostoma compressum*, as stated by Chesters & Bell (1970: 48). We think that this collection would be the appropriate lectotype for *Sphaeria diminuens* which will make this name a taxonomic synonym of *Sphaeria compressa*. The two names being of equal priority we select *S. compressa* (ICBN, Art. 57.2).

**Sphaeria libera** (Tode) Pers., Syn. Meth. Fung. 54

*Sphaeria macrostoma*  $\delta$  *libera* Tode, Fungi Meckl. 2: 13. 1791.

910.267-105. 'Sphaeria pileata Pers. - macrostoma a. C: 802a' (scr. Chaillet). 'Sph. libera?' (scr. Persoon). As stated by Chesters & Bell (1970: 32) this is *Navicella pileata*.

**Sphaeria macrostoma** Tode, Fungi Meckl. 2: 12. 1791

Persoon did not adopt this name in the Synopsis.

910.263-1128. 'Sphaeria macrostoma Tode Prope Parisios' (scr. Persoon). This matches the description of *L. compressum* var. *pseudomacrostromum* in Chesters & Bell (1970).

910.263-1130. 'Gallia. Sphaeria macrostoma Tode. Fries Syst. 2 p. 269' (scr. Persoon). This is *Navicella pileata*.

910.269-382. 'Sphaeria macrostoma Tode in ligno quercino' (scr. Persoon). As stated by Chesters & Bell (l.c.: 48), this is *L. compressum*.

**Sphaeria doliolum** Pers., Ic. Descr. 2: 39. 1798

*Leptosphaeria doliolum* (Pers.) Ces. & De Not., Comm. Soc. critt. ital. 1: 234. 1863.

As is apparent from the following account Persoon had a remarkable clear concept of the species. There are no less than 15 specimens in the *Sphaeria doliolum* folder in Persoon's herbarium.

910.270-490. 'Sphaeria Doliolum var. depressa affinis quoque Sphaeriae Lingam Tode' (scr. Persoon). This is well developed *Massaria anomia* (Fr.).

910.270-492. 'Sph. doliolum Pers.'. Material in poor condition but in all probability it is *L. doliolum* var. *conoidea* (Ces. & De Not.).

910.270-501. 'Sphaeria Doliolum' (scr. Persoon). This certainly is *L. doliolum* var. *conoidea*, though not in very good state.

910.270-515. 'Sphaeria Doliolum. Syn. fung.' (scr. Persoon). It is well developed *L. doliolum* var. *conoidea*!

910.270-519. 'Sphaeria Doliolum var. rimosa Fries 2. 509?' (scr. Persoon). An anamorph with bacterioid conidia.

910.270-526. 'Sphaeria Doliolum var.?' (scr. Persoon) 'in caulibus emortuis plantarum variarum' (scr. Desmazières). In bad condition but seems to be *L. doliolum* var. *conoidea*.

910.270-527. 'Sphaeria Doliolum Syn. ad caules exsicc. umbelliferarum vere' (scr. Persoon). Sundry spores have a longitudinal septum, but otherwise it is typical *L. doliolum* var. *conoidea*.

910.270-535. 'Sph. Doliolum? var. In Artemisia vulgaris' (scr. Persoon). In very poor condition, possibly *L. doliolum* var. *conoidea*.

910.270-536. 'Sphaeria doliolum. Tode.' (not Persoon's handwriting). This is *L. doliolum* var. *doliolum*.

910.270-537. 'Sphaeria-var. Sph. Dolioli? affinis quoque Sph. Herbarum' (scr. Persoon). This is well developed *L. doliolum* var. *conoidea*.

910.270-538. 'Sphaeria Doliolum affinis Sph. Herbarum. In caulibus siccis praesertim Angelicae sylvestris.' Beautiful var. *conoidea*!

910.270-609. 'Sphaeria an ab herbarum distincta', 'ad Doliolum accedit' (scr. Persoon). 'in caulibus herbarum' (scr. Mougeot). The material is too old, but the appearance is suggestive of *L. doliolum* var. *doliolum*.

910.270-650. 'Sphaeria Doliolum' (scr. Persoon). The host seems to be *Urtica*, and the fungus is well developed *L. doliolum* var. *doliolum*. This material seems to be an appropriate lectotype, and is here designated as such.

910.270-661. 'Sphaeria Doliolum' (scr. Persoon). 'in caule arido angelicae sylvestris. autumnno' (scr. Mougeot). This is beautiful var. *conoidea*.

910.270-683. 'Sphaeria Doliolum var. subdepressa' (scr. Persoon). 'in caulibus exsiccatis angelicae sylvestris. aestate Bellovaco'. Empty ascocarps but in all probability *L. doliolum* var. *conoidea*.

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## NOTULAE AD FLORAM AGARICINAM NEERLANDICAM—XII

Small, saprophytic *Volvariella* species in the Netherlands

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Characters used in current taxonomy of the genus *Volvariella* are discussed. Spore dimensions are a good additional character for distinguishing species. *Volvariella caesiostincta*, *V. hypopithys*, *V. murinella*, and *V. pusilla* are redescribed. *Volvariella murinella* f. *brevispora* is described and *V. taylori* is reduced to a variety of *V. pusilla*.

The genus *Volvariella* has been intensively studied during the last decades (e.g. Shaffer, 1957; Orton, 1974; Courtecuisse, 1984). During our investigations, however, we had problems in identifying small, saprophytic species of *Volvariella*, such as *V. murinella*, *V. hypopithys*, and *V. pusilla*. According to Orton (1974), the principal diagnostic features of this genus are the colour of the pileus and volva, the morphology of the volva (two-lobed versus four-lobed), the surface structure of the pileus and stipe, and the habitat. We carefully studied the material available from the Netherlands and tried to evaluate the characters used in current taxonomy of this genus.

## MORPHOLOGY OF SPORES, VOLVA AND SURFACE STRUCTURES

Our observations indicate that in *Volvariella* the colour of both pileus and volva is rather variable. But the dimensions of the spores seem to be a good additional character for delimitating species (Figs. 1, 2). *Volvariella murinella* is well characterized by narrow, elongate ellipsoid to subcylindrical spores,  $5.5\text{--}8.0 \times 3.0\text{--}4.5 \mu\text{m}$ ,  $Q\ 1.5\text{--}2.3$  (Fig. 1). In one collection, the colour of the pileus of this species ranges from entirely white with a pale grey-brown umbo to grey-brown with a brownish grey centre (*Bas* 6596, L). In the same collection the colour of the volva varies from white to ochraceous and was found 2- to 4-lobate.

The spores of *V. murinella* agree fairly well with those of *V. surrecta*, which measure  $5.0\text{--}7.0 \times 3.0\text{--}4.0 \mu\text{m}$ ,  $Q\ 1.5\text{--}2.0$ . The latter species, however, is characterized by its habitat on basidiocarps of *Clitocybe nebularis*.

The other *Volvariella* species with small basidiospores (less than  $9.0 \mu\text{m}$  long) have considerably broader spores, e.g. *V. pusilla*, *V. caesiostincta*, *V. hypopithys*, and *V. bombycina* (Fig. 2). *Volvariella bombycina* seems not closely related with the other species men-

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tioned, because of the large size of its basidiocarps, its habitat on trees, the peculiar morphology of its volva, which can be up to 75(–120) mm long and may enclose up to half the length of the stipe, and its different pileipellis, which is a trichodermium composed of creeping to ascending hyphae, made up of long and wide elements (c.  $1500 \times 40 \mu\text{m}$ ).

Among the remaining species, *V. hypopithys* is best characterized by its pale pileus and its entirely pubescent stipe. The volva is saccate, rather thick, whitish but soon becoming pale ochraceous-buff and 2- to 4-lobate.

The closely related *V. pusilla* differs mainly from *V. hypopithys* by the mature stipe being nearly glabrous. The stipe of young basidiocarps can be sparsely hairy as is also illustrated on Bulliard's (1787–1788) plate 330. The volva is saccate, thin, whitish or occasionally grey-brown and not or 2- to 4-lobate. Persoon (1799: pl. 4, figs. 4, 5) depicted *V. pusilla* with a distinctly radially striate pileus.

Specimens keyed out with Orton's key (1974) as *V. taylori* differ from *V. pusilla* only by slightly larger basidiocarps, a brown to ochraceous grey, irregularly 1- to 3-(5)-lobate volva and a pale buff-grey to grey centre of the pileus. Because the volva and the centre of the pileus of *V. pusilla* are occasionally brownish grey and because the margin of the pileus of *V. taylori* can be slightly striate, the two taxa are very close indeed and the latter species is reduced to a variety under *V. pusilla*. Our observations agree with the original description of *V. taylori* by Berkeley (1860: 140), in which the pileus is described as striato-rimose from the apex.

*Volvariella caesiotinctoria* is also related to *V. pusilla*, but differs from that species in its habitat on wood, a *Geranium robertianum*-like smell and an unpleasant, somewhat ad-

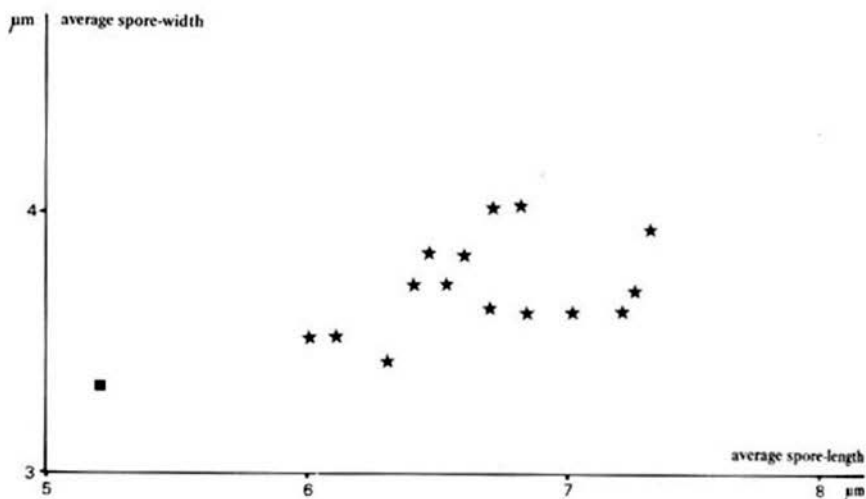


Fig. 1. Scatterdiagram of average spore-sizes of *Volvariella murinella f. murinella* (★) and *V. murinella f. brevispora* (■).

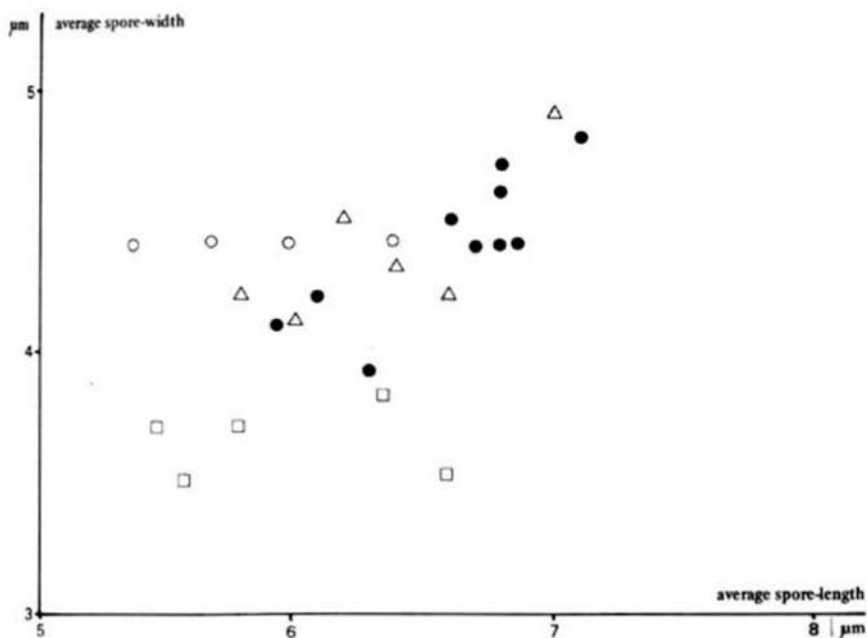


Fig. 2. Scatterdiagram of average spore-sizes of *Volvariella hypophitys* (●), *V. pusilla* var. *pusilla* (○), *V. pusilla* var. *taylora* (△), and *V. surrecta* (□).

stringent taste. The volva of *V. caesiotincta* is saccate, thin, greyish brown and 2- to 3-(5)-lobate and the centre of the pileus is rather dark grey-brown.

#### DESCRIPTIONS OF SOME SPECIES

##### *Volvariella caesiotincta* P. D. Orton—Fig. 3

*Volvariella caesiotincta* P. D. Orton in Bull. mens. Soc. linn. Lyon 43 (Num. spéc.): 319. 1974.

*Volvariella murinella* var. *umbonata* J. Lange, Fl. agar. dan. 5: 97. 1940.

Misapplied name.—*Volvariella murinella* sensu Kühn. & Romagn., Fl. anal. Champ. sup. 426. 1953.

Selected illustrations.—Bull. trimest. Soc. mycol. Fr. 43, Atl. pl. 21. 1927; J. Lange, Fl. agar. dan. 5, pl. 200B. 1940.

Selected descriptions.—Malençon & Bertault, Flore Champ. Maroc 1: 108. 1970 (as *Volvariella murinella* var. *umbonata* Lange); P. D. Orton in Bull. mens. Soc. linn. Lyon 43 (Num. spéc.): 319. 1974.

Basidiocarps medium-sized, solitary or in small groups. Pileus 30–60(–90) mm, convex to applanate, frequently with low broad umbo, pale greyish cream to grey-brown (Munsell 10 YR 8/2; 2.5 YR 6–7/2), with darker grey-brown centre, dry, densely felted





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Fig. 3. *Volvariella caesiostincta*. — Habit ( $\times 1$ ), spores ( $\times 1500$ ), and cheilocystidia ( $\times 1000$ ).

hairy at centre, appressed radially fibrillose near margin. Lamellae crowded, free, rather broadly ventricose, up to 10 mm wide, whitish when young, finally flesh-pink, with whitish flocculose edge. Stipe 35–80  $\times$  5–10 mm, cylindrical with a clavate base, up to c. 20 mm broad, solid, whitish but soon with a yellowish brown tinge, innately fibrillose-striate, entirely pubescent when young, mostly the greater part soon glabrous. Vohva membranous, saccate, up to 30 mm high, with 2–3(–5) lobes, greyish brown, with sub-tomentose felted outer surface. Context white, becoming pale dingy straw yellow. Smell faint to rather strong, reminiscent of *Geranium robertianum*. Taste rather strong, unpleasant, somewhat adstringent.

Spores 5.3–7.3(–7.8)  $\times$  3.5–4.8  $\mu\text{m}$ ,  $Q = 1.3$ –1.8(–20), ellipsoid to elongate, sometimes tending to elongate-ovoid. Basidia 20–35  $\times$  7–10  $\mu\text{m}$ , clavate, 4-spored. Cheilocystidia 35–85  $\times$  15–30  $\mu\text{m}$ , clavate, frequently with apical papilla or with finger-like appendages (up to c. 20  $\mu\text{m}$  long) or ventricose-lageniform. Pleurocystidia rather rare, 40–70  $\times$  10–35  $\mu\text{m}$ , clavate to ventricose lageniform. Hymenophoral trama made up of 5–20  $\mu\text{m}$  wide, cylindrical to subfusiform hyphae. Pileipellis a cutis, made up of hyphae consisting of cylindrical cells, 60–160  $\times$  10–30  $\mu\text{m}$ , with intracellular grey-brown pigment; hairs at centre of pileus slender cylindrical, up to 300  $\mu\text{m}$  long. Hairs at apex of stipe slender cylindrical, up to c. 200  $\mu\text{m}$  long.

Habitat & distribution.—Epixyloous, on decaying trunks of broad-leaved trees (e.g. *Fagus*); rare, in the Netherlands known from five localities.

Material examined.—NETHERLANDS: prov. Overijssel, Diepenveen, estate 'Nieuw Rande', 6 Aug. 1972, G. & H. Piepenbroek; prov. Noord-Holland: Bergen, 1 Aug. 1967, F. A. van der Bergh; isle of Texel, Oudeschild, 13 July 1983, M. Groenendaal; prov. Zeeland, Axel, Axelse Bos, 8 June 1981, A. de Meyer 285b; prov. Limburg: Linne, along Vlootbeek, 6 Sept. 1963, C. Ph. Verschueren; ditto, 13 July 1966, C. Ph. Verschueren (all in L).

*Volvariella caesiostincta* is closely related to *V. pusilla* var. *taylori*, from which it differs mainly by its epixyloous habitat. Less pronounced differences are its *Geranium robertianum*-like smell and unpleasant taste. As Orton (1974: 320) pointed out, the epixyloous *V. bombycina* differs by its more yellow, distinctly scaly pileus and by larger spores. We also found differences in the structure of the pileipellis of these two species. The cutis of *V. caesiostincta* consists of rather short, cylindrical cells, while that of *V. bombycina* is made up of very long (up to 1500  $\mu$ m) cells.

#### *Volvariella hypopithys* (Fr.) Shaffer—Fig. 4

*Agaricus hypopithys* Fr., Hymenomyc. eur.: 183. 1874. — *Volvaria hypopithys* (Fr.) P. Karst., Ryssl. Finl. Skand. Halfons Hattsvamp.: 251. 1879. — *Volvariella hypopithys* (Fr.) Mos., Blätter- und Bauchpilze. In Gams, Kl. Kryptog. Fl. 2: 110. 1953 (not val. publ.: no basionym mentioned). — *Volvariella hypopithys* (Fr.) Shaffer in Mycologia 49: 572. 1957.

*Volvaria plumulosa* Lasch ex Quéf. in Bull. Soc. bot. Fr. 24: 320. (1877) 1878. — *Volvariella plumulosa* (Lasch ex Quéf.) Sing. in Lilloa 22: 401. 1951.

*Agaricus pubescentipes* Peck in Rep. N. Y. St. Mus. nat. Hist. 29: 39. 1878. — *Volvaria pubescentipes* (Peck) Sacc. (as *V. pubipes*), Syll. Fung. 5: 658. 1887. — *Volvariopsis pubescentipes* (Peck) Murrill in N. Amer. Fl. 10: 141. 1917. — *Volvariella pubescentipes* (Peck) Singer in Lilloa 22: 401. 1951.

*Volvaria parvula* var. *biloba* Masee, Brit. Fung. Fl. 296. 1893. — *Volvaria pusilla* var. *biloba* (Masee) J. Lange, Fl. agar. dan. 2: 80. 1936.

Misapplied name.—*Volvariella pusilla* sensu Kühn. & Romagn., Fl. anal. Champ. sup.: 426. 1953.

Selected illustrations.—Dähnke & Dähnke, 700 Pilze: 267 (as *V. pusilla*). 1979; Konr. & M., Ic. sel. Fung. 1, pl. 17, fig. 1. 1928; J. Lange, Fl. agar. dan. 2, pl. 68D (as *V. pusilla* var. *biloba*). 1936; Michael, Hennig & Kreisel, Handb. Pilzfr. 3, pl. 38. 1979.

Selected descriptions.—Kühn. & Romagn. in Bull. trim. Soc. mycol. Fr. 72: 240. 1956; P. D. Orton in Trans. Br. mycol. Soc. 43: 384. 1960; Shaffer in Mycologia 49: 572. 1957.

Basidiocarps small to medium-sized. Pileus (10–)20–65 mm, at first hemispherical or conical, becoming plano-convex to plano-concave, with low broad umbo, with inflexed margin slightly exceeding lamellae, thin-fleshed to rather fleshy, white but centre soon becoming pale pinkish buff to pale buff (Mu. 10 YR 8/4), dry, shiny, radially fibrillose with tips of fibrils slightly ascending. Lamellae rather crowded, free, rather remote from stipe, ventricose, up to c. 6 mm broad, cream when young (Mu. 2.5 YR 8/2), finally pale flesh pink to flesh pink (Mu. 7.5 YR 7/4), with slightly paler, somewhat fimbriate edge. Stipe 30–65  $\times$  2–6(–10) mm, mostly somewhat broadening towards base, solid, whitish, but soon becoming pale isabella, entirely pubescent, innately longitudinally fibrillose. Volva saccate, rather thick, white but soon becoming pale ochraceous buff

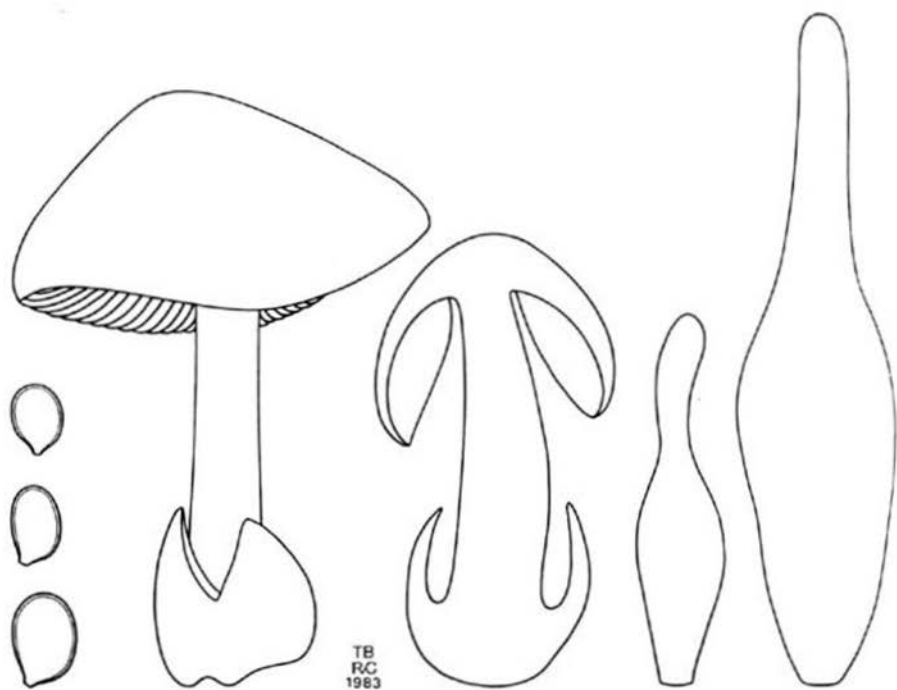


Fig. 4. *Volvariella hypopithys*. — Habit ( $\times 1$ ), spores ( $\times 1500$ ), and cheilocystidia ( $\times 1000$ ).

(Mu. 10 YR 6–7/4), 2- to 4-lobate, with felted outer surface. Context dull white to pale yellow, in stipe becoming pale brownish. Smell indistinct. Taste weak, slightly raphanoid or bitterish. Spore-print pinkish brown (Mu. 7.5 YR 6/4).

Spores (5.6–)6.2–7.8(–8.1)  $\times$  3.5–5.0  $\mu\text{m}$ , Q = 1.35–1.7(–2.0), ellipsoid to elongate. Basidia 20–30(–40)  $\times$  7–10  $\mu\text{m}$ , clavate, 4-spored. Cheilocystidia 40–110(–140)  $\times$  10–35  $\mu\text{m}$ , variable in shape, clavate, fusiform to sublageniform. Pleurocystidia similar to cheilocystidia. Hymenophoral trama made up of 5–30  $\mu\text{m}$  wide, thin-walled hyphae. Pileipellis a cutis made up of short-celled hyphae with cells measuring 50–170  $\times$  5–30  $\mu\text{m}$ , pigment absent. Hairs of stipe cylindrical, 100–450  $\times$  5–12  $\mu\text{m}$ .

Habitat & distribution.—Terrestrial in broad-leaved forests, on litter, on rich or rather rich soils; fairly frequent, seems to occur in all parts of the Netherlands.

Material examined.—NETHERLANDS: prov. Flevoland: Oostelijk Flevoland, Biddinghuizen, along Strandgaperweg, 8 Oct. 1981, C. Bas 7811; Dronten, Bremerbergbos, 10 Oct. 1980, J. Daams 80–13; Roggebotsbos, 24 Oct. 1976, Langevoord & Boezewinkel; prov. Gelderland: Nijmegen, Heilige Landstichting, 2 Oct. 1955, J. Kalf; Winterswijk, Bekendelle, 19 Oct. 1981, J. Schreurs 310; prov. Utrecht, Bunnik, Fort Rhijnauwen, 22 Oct. 1977, M. van Vuure; prov. Zeeland, Axel, Axelse Bos, 8 June 1981, A. de Meyer 302; prov. Limburg, St. Geertruid, Savelsbos, 5 Aug. 1981, J. Schreurs 596 (all in L).

*Volvariella pusilla* is closely related to *V. hypopithys*, but differs from it by a nearly glabrous stipe and generally somewhat smaller basidiocarps. White forms of *V. murinella* differ from *V. hypopithys* mainly by their narrow, elongate to subcylindrical spores (Figs. 1 and 2).

*Volvaria plumulosa* Lasch ex Quél. (1878: 320) seems conspecific with *V. hypopithys*. However, the original descriptions of *Agaricus plumulosus* Lasch could not be located. Oudemans (1867: 25) cited *A. plumulosus* Lasch as a synonym of *A. parvulus* var. *major*. If *Agaricus plumulosus* Lasch, which seems to turn up for the first time in synonymy of *Agaricus parvulus* in Fries (1838: 139), is somewhere validly published and if the original description of *A. plumulosus* should point to the fungus described here, then the epithet *plumulosa* would have priority.

### *Volvariella murinella* (Quél.) Mos. ex Courtecuisse

*Volvaria murinella* Quél. in C.r. Ass. franç. Av. Sci. (La Rochelle, 1882) 11: 391, 1883. — *Volvariella murinella* (Quél.) Mos., Blätter- und Bauchpilze. In Gams, Kl. Kryptog. Fl. 2: 110, 1953 (not val. publ.: no basionym mentioned). — *Volvariella murinella* (Quél.) Mos. ex Courtecuisse in Bull. Soc. mycol. Nord 34: 19, 1984.

Excluded. — *Volvariella murinella* sensu Kühn. & Romagn., Fl. anal. Champ. sup.: 426, 1953 (= *V. caesiincta*).

### *Volvariella murinella* forma *murinella*—Fig. 5

Selected illustrations.—J. Lange, Fl. agar. dan. 2, pl. 67B, 1936; Michael, Hennig & Kreisel, Handb. Pilzfr. 3, pl. 33, 1979; Quél. in C.r. Ass. franç. Av. Sci. (La Rochelle, 1882) 11, pl. 11, fig. 6, 1883.

Basidiocarps small, solitary. Pileus 10–55 mm, conico-convex, convex to applanate, frequently with low broad umbo, thin-fleshed, whitish grey to grey (Mu. 10 YR 7/2–3), with a darker grey-brown centre (Mu. 10 YR 4–5/3), dry, hairy at centre, radially silky fibrillose to subsquamulose towards margin. Lamellae crowded, free, rather remote from stipe, ventricose, thin to rather thick, pale when young, becoming flesh-pink, with slightly paler edge. Stipe 15–70 × 1–5 mm, with subbulbose base up to 10 mm broad, solid, whitish, shiny, entirely pubescent when young, but soon glabrous in lower part, innately longitudinally fibrillose. Volva thin, membranous, saccate, whitish, but soon sordid grey-brown, 2–4 lobate, with slightly felted outer surface. Context white to pale greyish, in the stipe slightly turning ochraceous yellow. Smell weak, faintly aromatic herbaceous (remining of *Pelargonium*). Taste unpleasant, somewhat sourish-acrid fungoid.

Spores 5.5–7.7(–8.3) × 3.0–4.4 μm, Q = 1.5–2.3, elongate ellipsoid to subcylindrical. Basidia 20–30(–35) × 7–10 μm, clavate, 4-spored. Cheilocystidia 40–100 × 10–30(–50) μm, variable in shape, clavate, fusiform or ventricose-lageniform. Pleurocystidia similar to cheilocystidia. Hymenophoral trama made up of thin-walled, c. 5–20 μm wide hyphae. Pileipellis a cutis made up of short-celled hyphae, 10–20(–35) μm wide, with intracellular grey-brown pigment; hairs at centre of pileus slender cylindrical, up to 230 μm long. Hairs on stipe slender cylindrical, up to c. 270 μm long.

Habitat & distribution.—Terrestrial on rich soils (e.g. loam, clay) in broad-leaved and coniferous forests and in grasslands: not common.

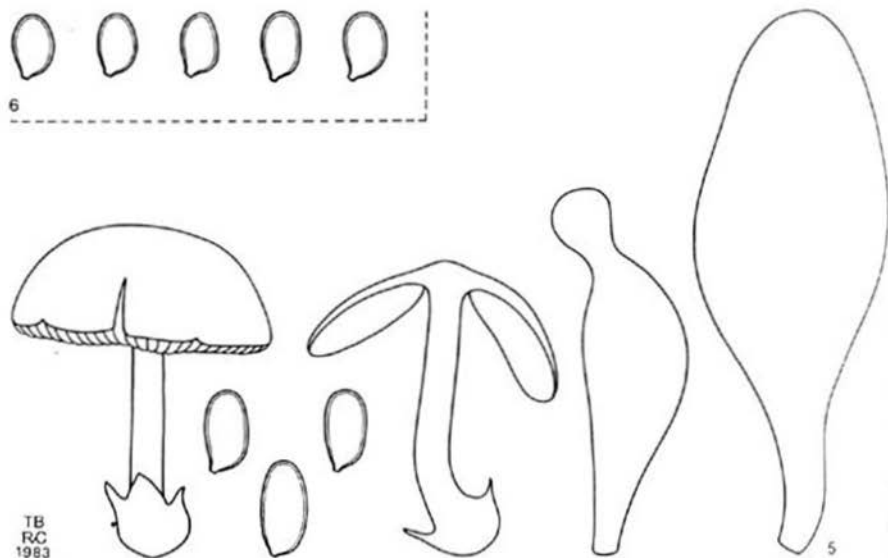


Fig. 5. *Volvariella murinella* f. *murinella*. — Habit ( $\times 1$ ), spores ( $\times 1500$ ), and cheilocystidia ( $\times 1000$ ).

Fig. 6. *Volvariella murinella* f. *brevispora*. — Spores ( $\times 1500$ ).

**Material examined.**—NETHERLANDS: prov. Overijssel, Deventer, estate 'Wijtenhorst', 15 Nov. 1970, G. & H. Piepenbroek; prov. Gelderland, Winterswijk, 20 Sept. 1975, J. Schreurs s.n.; prov. Utrecht, Bunnik, Rhijnauwen, 22 July 1954, C. Bas 533; prov. Zuid-Holland, Rockanje, Quackjeswater, 12 Nov. 1954, C. Bas 616; prov. Zeeland, Axel, Axelse bos, 26 May 1981, A. de Meyer 285; Krainingen, 21 Nov. 1982, H. Adema; prov. Limburg, St. Geertruid, Savelsbos, 13 Aug. 1980, J. Schreurs 434; ditto, 13 Sept. 1980, J. Schreurs 498; ditto, 24 Sept. 1981, J. Schreurs 641 (all in L).

*Volvariella murinella* is well characterized by narrow, elongate to subcylindrical spores (Fig. 1) and a generally pale volva. Typical specimens have a rather uniform greyish pileus. Some of the specimens studied differ by a nearly white pileus (e.g. Schreurs s.n., 20 Sept. 1975, L). This white variant of *V. murinella* differs from other white-capped *Volvariella* species (e.g. *V. hypopithys* and *V. pusilla*) mainly by its narrow spores (Fig. 1). *Volvariella cinerescens* (Bres.) Mos. seems closely related, but differs by a smooth surface of the pileus, which is distinctly translucently striate (Bresadola, 1929, pl. 82). Within the material studied we observed a short-spored form which is described below.

***Volvariella murinella* forma *brevispora* Boekhout, forma nov.**—Fig. 6

A *Volvariella murinella* f. *murinella* differt sporis brevioribus, ellipsoideis vel elongatis, 4.8–5.6  $\times$  2.9–3.6  $\mu$ m. — Holotypus: C. Bas 617, lectus in silva decidua solum arenosum occupante, prov. Zuid-Holland, Rockanje, Quackjeswater (L).

Pileus up to 50 mm, plano-convex with a low umbo, pale brownish grey with a slight olivaceous tinge, paler towards margin, distinctly radially fibrillose with centre subviscid and with edge fringed with fibrils. Lamellae free, ventricose, pale flesh pink with slightly paler flocculose edge. Stipe up to 70 × 6–9 mm, with clavate, up to 15 mm wide base, solid, white, shiny, glabrous, finely longitudinally fibrillose. Volva saccate, up to c. 27 mm high, white, irregularly lobed, with felted outer surface. Smell not reported. Taste not reported.

Spores 4.8–5.6 × 2.9–3.6  $\mu\text{m}$ , Q = 1.4–2.0, ellipsoid to elongate. Basidia 19–25 × 6–7  $\mu\text{m}$ , clavate, 4-spored. Cheilocystidia 45–65 × 12–20  $\mu\text{m}$ , clavate, subfusiform or ventricose lageniform. Pleurocystidia not observed. Pileipellis a cutis made up of short-celled hyphae up to 20  $\mu\text{m}$  wide.

Habitat & distribution.—Terrestrial, on sandy soil under broad-leaved trees (e.g. *Betula*, *Ligustrum*, and *Quercus*); very rare, up to now only known from the type locality.

Material examined.—NETHERLANDS, prov. Zuid-Holland, Rockanje, Quackjeswater, 12 Sept. 1954, C. Bas 617 (L).

*Volvariella murinella* f. *brevispora* is characterized by its small spores. The specimens differ slightly from typical *V. murinella* by their subviscid centre of the pileus.

*Volvariella smithii* Shaffer (1957: 568) seems closely related to *V. murinella* f. *brevispora* because of the small spores, the same size of the basidiocarps and the same colour of the pileus, but differs by its densely pubescent stipe and its ochraceous to pale cinnamon volva.

*Volvaria nauseosa* Romagn. (Romagnesi, 1937: 93) also has some resemblance to *V. murinella* f. *brevispora* because of its small spores (5.7–6.5 × 3.5–3.7  $\mu\text{m}$ ) and glabrous stipe. It differs, however, by the white fibrils covering the pileus (Romagnesi compared *V. nauseosa* to *V. hypopithys* and *V. pubipes*!) and the spore morphology. The spores of *V. nauseosa* have their largest width in the lower part (see Romagnesi, 1937, fig. 3, Sp2), while those of *V. murinella* f. *brevispora* are more ellipsoid and have their largest width in or near the middle. It remains uncertain whether the unpleasant smell of *V. nauseosa* differs from the up to now unknown smell of *V. murinella* f. *brevispora*.

### *Volvariella pusilla* (Pers.: Fr.) Sing.

*Amanita pusilla* Pers., Obs. mycol. 2: 36. 1799. — *Agaricus pusillus* Pers.: Fr., Syst. mycol. 1: 279. 1821. — *Volvariella pusilla* (Pers.: Fr.) Quél., Fl. mycol. 189. 1888. — *Volvariopsis pusilla* (Pers.: Fr.) Murrill in N. Am. Fl. 10: 141. 1917. — *Volvariella pusilla* (Pers.: Fr.) Sing. in Lilloa 22: 401. 1951.

*Agaricus parvulus* Weinm., Hymen. Gaster. Rossico: 238. 1836. — *Volvaria parvula* (Weinm.) Kumm., Führer Pilzk.: 99. 1871. — *Volvariella parvula* (Weinm.) Speg. in Boln Acad. nac. Ciénc. Córdoba 28: 309. 1926.

*Agaricus taylori* Berk., Outl. Brit. Fungol.: 140. 1860. — *Volvaria taylori* (Berk.) Gillet, Hyméno-mycètes: 386. 1878. — *Volvariella taylori* (Berk.) Sing. in Lilloa 22: 401. 1951.

(For further synonyms see Shaffer, 1957: 570.)

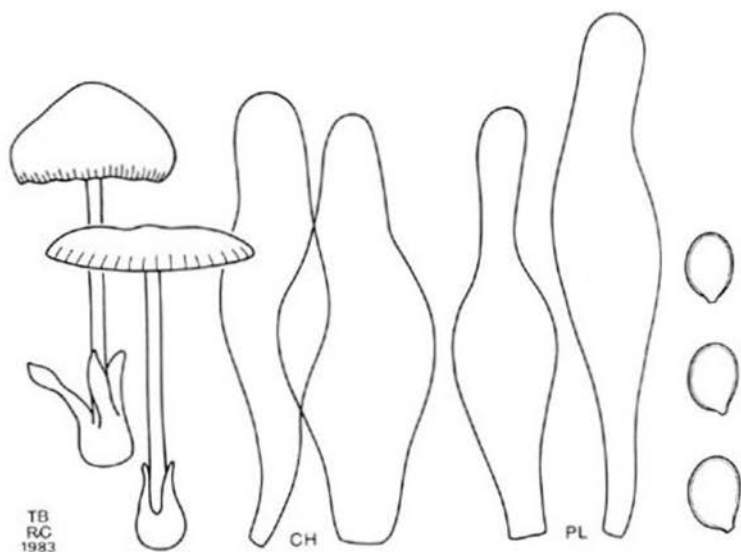


Fig. 7. *Volvariella pusilla* var. *pusilla*. — Habit ( $\times 1$ ), spores ( $\times 1500$ ), and cheilocystidia ( $\times 1000$ ).

### *Volvariella pusilla* var. *pusilla*—Fig. 7

*Amanita pusilla* Pers. — *Agaricus pusillus* Pers.: Fr. — *Volvaria pusilla* (Pers.: Fr.) Quél. — *Volvariopsis pusilla* (Pers.: Fr.) Murrill.

Selected illustrations.—Bresadola, *Iconogr. mycol.* 11, pl. 533, 1929; Konr. & M., *lc. sel. Fung.* 1, pl. 18, 1927; J. Lange, *Fl. agar. dan.* 2, pl. 68C, 1936; Michael, Hennig & Kreisel, *Handb. Pilzfr.* 3, pl. 35 (as *V. parvula*), 1979.

Selected descriptions.—Kühner & Romagn. in *Bull. trimest. Soc. mycol. Fr.* 72: 242, 1956; Shaffer in *Mycologia* 49: 570, 1957.

Basidiocarps small, solitary. Pileus 10–35 mm, at first convex, becoming plano-convex, subumbonate, white or occasionally silvery greyish (Mu. 10 YR 7–8/1), finally at the centre very pale beige (Mu. 10 YR 8/3–4), subviscid when very young, later appressedly silky-fibrillose, with radially sulcate margin. Lamellae crowded, free, up to c. 6 mm broad, ventricose, pale sordid pink (Mu. 75 YR 7/2) when young, later becoming brownish pink (Mu. 5 YR 6/6), with concolorous, minutely fimbriate edge. Stipe 15–40  $\times$  1.0–2.5 (–6.0) mm, with clavate base, solid, white, when very young with scattered hairs, but soon becoming glabrous. Volva saccate, whitish, sometimes becoming pale grey-brown, not or 2- to 4-lobate. Context white. Smell faint, sweet fungoid. Taste absent.

Spores 5.5–7.2  $\times$  4.1–5.5  $\mu\text{m}$ , Q = 1.2–1.5 (–1.65), broadly ellipsoid to ellipsoid. Basidia 20–30  $\times$  7–10  $\mu\text{m}$ , clavate, 4-spored. Cheilocystidia 45–85  $\times$  10–20  $\mu\text{m}$ , clavate, fusiform to ventricose-lageniform. Pleurocystidia similar to cheilocystidia. Hymenopho-

ral trama made up of c. 5–15  $\mu\text{m}$  broad hyphae. Pileipellis a cutis, made up of cylindrical hyphae, c. 10–20  $\mu\text{m}$  wide, with very pale intracellular pigment.

**Habitat & distribution.**—Terrestrial in broad-leaved forests on clayey soil, also in greenhouses; rare, only known from Amsterdam (Amsterdamse Bos), Loenen (estate 'Valburg'), and greenhouses in Kortenhoef.

**Material examined.**—NETHERLANDS: prov. Gelderland, Loenen estate 'Valburg', 23 Aug. 1980, *J. Wisman* s.n.; prov. Utrecht: Kortenhoef, 9 Oct. 1970, *J. Daams* 70–36; ditto 26 May 1971, *J. Daams* 384; ditto, 16 Jan. 1973, *J. Daams* 780 (all in L).

This species is closely related to *V. hypopithys*, which differs mainly by its distinctly and completely pubescent stipe. In very young basidiocarps of *V. pusilla*, however, the stipe can also be sparsely hairy. Bulliard's (1787–1788) plate 330 shows that *V. pusilla* can be slightly pruinose at the apex of the stipe. His plate also indicates that the basidiocarps vary from small to rather small. This is also reported by Berkeley (1860: 140), who described *V. pusilla* as 'very variable in size, from a few lines to 2 inches'. Plate 4, figures 4 and 5 of Persoon (1799) illustrate a distinctly radially striated pileus.

Shaffer (1962: 563) reduced *V. argentina* Speng. (type of the genus) to the synonymy of *V. pusilla*.

***Volvariella pusilla* var. *taylori* (Berk.) Boekhout, *comb. nov.***

*Agaricus taylori* Berk., Outl. Brit. Fungol.: 140. 1860 (basionym). — *Volvaria taylori* (Berk.) Gillet. — *Volvariella taylori* (Berk.) Sing.

Misapplied names.—*Volvaria parvula* sensu Kühn. & Romagn., Fl. anal. Champ. sup.: 426. 1953; in Bull. trimest. Soc. mycol. Fr. 72: 244. 1956.

*Volvaria plumulosa* sensu Lange, Fl. agar. dan. 2: 79. 1936.

Selected illustrations.—Bresadola, Iconogr. mycol. 11, pl. 527. 1929; J. Lange, Fl. agar. dan. 2, pl. 68A (as *V. plumulosa*), pl. 68F (as *V. taylori*). 1936; Michael, Hennig & Kreisler, Handb. Pilzfr. 3, pl. 34. 1979.

Selected descriptions.—Kühn. & Romagn. in Bull. trimest. Soc. mycol. Fr. 72: 244. 1956; Shaffer in Mycologia 49: 565. 1957.

Basidiocarps small to medium, solitary or in small groups. Pileus (20–)30–50 mm, conical, plano-conical or convex, finally somewhat undulating, with margin inflexed when young, at centre pale buffy grey to grey (Mu. 10 YR 7/3–4, 8/2–3, 5/3), paler towards margin, radially silky fibrillose, with margin fibrillose fringed when young and not or only vaguely and short-striate. Lamellae crowded to fairly distant, free, sometimes rather remote from stipe, ventricose, up to 8 mm wide, pale to brownish pink (Mu. 5 YR 7/4–6), with nearly concolorous, entire edge. Stipe (10–)30–70  $\times$  (2.0–)4.0–7.0 mm, not or somewhat broadening towards base, up to 7–11 mm, solid, white but soon with ochraceous to buff tinge, very minutely downy at apex (under lens), glabrous below. Volva saccate, up to c. 13 mm high, brown to ochraceous grey (Mu. 10 YR 5–6–7/4, 6/3), somewhat paler towards base, irregularly lobate with 1–3(–5) lobes, with subfelted outer surface. Context white, becoming pale buff in base of stipe. Smell indistinct. Taste weak, fungoid.

Spores 5.5–7.6(–8.3)  $\times$  3.6–4.9(–5.5)  $\mu\text{m}$ , Q = 1.3–1.8, ellipsoid. Basidia 25–35(–45)  $\times$  7–10  $\mu\text{m}$ , clavate, 4-spored. Cheilocystidia 40–70  $\times$  10–30(–40)  $\mu\text{m}$ , clavate



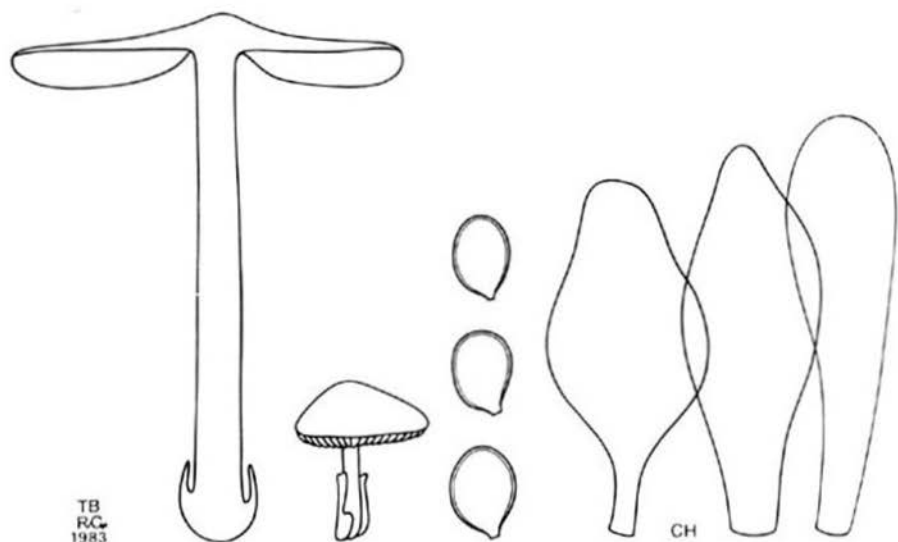


Fig. 8. *Volvariella pusilla* var. *taylori*. — Habit ( $\times 1$ ), spores ( $\times 1500$ ), and cheilocystidia ( $\times 1000$ ).

to ventricose lageniform. Pleurocystidia similar to cheilocystidia. Hymenophoral trama consisting of 10–20  $\mu\text{m}$  broad, thin-walled hyphae. Pileipellis a cutis made up of 1–20  $\mu\text{m}$  broad hyphae, with intracellular grey-brown pigment.

**Habitat & distribution.**—Terrestrial in grasslands on clayey soil (*F. A. van der Bergh* s.n., 12 June 1972 was collected in a dune area, but there the soil was artificially raised with clay). Occasionally also gathered from a cellar. Rather rare, known from Bergen (N.-H.), Drimmelen, 's-Gravenhage, Leiden, Olst, and Texel.

**Material examined.**—NETHERLANDS: prov. Overijssel, Olst, Hengforder Waarden, 5 Oct. 1975, *G. & H. Piepenbroek* 975; ditto, 19 Sept. 1976, *G. & H. Piepenbroek* 999; prov. Noord-Holland: Petten, near Reactor Centre Nederland, 12 June 1972, *F. A. van der Bergh* s.n.; Texel, Waddijk, 5 Sept. 1982, *M. Groenendaal* s.n.; prov. Zuid-Holland: 's-Gravenhage, estate 'Clingendael', 12 Aug. 1963, *M. A. Donk*; Leiden, 15 Aug. 1966, *R. A. Maas Geesteranus* 14832; prov. Noord-Brabant, Drimmelen, 10 July 1956, *H. Rijkhoek* s.n. (all in L).

No authentic material of *Agaricus taylori* is present in the Kew herbarium. We regard our specimens identical with Berkeley's fungus.

Dutch specimens of *Volvariella pusilla* var. *taylori* differ from the typical variety of *V. pusilla* by a brown to grey volva, slightly larger basidiocarps and a more brown-grey centre of the pileus.

Typical *V. pusilla* has a pileus with a striate margin, while striation has been claimed to be absent in *V. taylori* (compare for example Bresadola, 1929, pl. 527 (= *V. taylori*)).

and pl. 533 (= *V. pusilla*). Berkeley (1860: 140), however, described the pileus of *A. taylori* as 'striato-rimose from the apex'. The original descriptions of *Agaricus taylori* Berk. and *Amanita pusilla* Pers. are compared in Table I.

Table I. Original descriptions of *Amanita pusilla* and *Agaricus taylori*

Am. pusilla Pers. (1799: 36–37)	Ag. taylori Berk. (1860: 140)
Pileus 0.5 unc. latus, disco planus, incarnato-albido, margine reflexus, circa umbonem, qui brevis et obtusus, depressus, pilis sericeis adpressis et obtusus, fragilis, et subliquescent quasi, ob lamellas transparentes, colore subincarnatus.	Pileus thin, conical, obtuse, livid, striato rimose from the apex.
Stipes semiunciam ad unciam altus, cylindricus, candidus, pellucidus.	Stem pale, solid, nearly equal.
Volva radicalis caliciformis, persistens, ut plurimum quadrifidus: lobis erectis, apice subincurvis, 2 lin. magnis, externe sericeus.	Volva lobed, brown, small.
Lamellae inter se distantes, liberae s. stipiti vix annexae.	Gills uneven, broad in front, attenuated behind, rose-coloured.

The original description of *Ag. taylori* closely agrees with that of *Am. pusilla*. The only differences found are the livid, conical, obtuse pileus, the brown volva, and the uneven lamellae in the former. We noted a great variability concerning the first character. The pileus of *V. pusilla* var. *taylori* varies from conical, plano-conical to convex and finally becomes undulate. The lamellae in both species are similar. Thus, the colour of the pileus and volva and the slightly larger basidiocarps remain as the main differentiating characters. It is important to note that Bulliard's (1787–1788) plate 330 and Cooke's (1883) plate 300 of *V. pusilla* show a yellowish brown outer surface of the volva. Kühner & Romagnesi (1956, l.c.) described the volva of *V. pusilla* as 'brun ou gris brun à l'extérieur', while that of *V. taylori* (as *V. parvula*) is described as follows: 'Volve au début nettement brune ou brun-grisâtre, mais souvent pâlisant'. This is in agreement with our observations on the colour of the volva of *V. pusilla*, which can vary from whitish to grey-brown. According to most authors the pileus of *V. taylori* is somewhat darker if compared with the pileus of *V. pusilla* (Table II).

Table II. Descriptions of the colour of the pileus of *V. pusilla* and *V. taylori*

<i>V. pusilla</i>	<i>V. taylori</i>	Source
White, somewhat tinged with yellow or brown.	Livid.	(Berkeley, 1860)
White.	Dingy whitish (somewhat darker, livid argillaceous at the disc).	(J. Lange, 1936)
D'un blanc pur, même au centre seulement à la fin légèrement jauni ou sali à cet endroit, mais ne présentant pas de teinte grise.	D'abord blanc de neige, mais déjà avec le centre légèrement touché de gris brunâtre très dilué, puis cette teinte se précise et s'entend de plus en plus jusqu'à devenir brunâtre, mais le bord demeure très longtemps blanc et ce n'est que sur les exemplaires vétustes que toute la surface est paille brunâtre sale.	(Kühner & Romagnesi, 1956)
White, occasionally tinged with grey, especially on the disc.	Grey with avellaneous areas or greyish avellaneous overall.	(Shaffer, 1957)
White, sometimes tinged ivory or pale cream when old (in key).	Paler or darker grey, grey olivaceous hazel, sometimes creamy or pale buff at centre.	(Orton, 1974)
White, occasionally silvery greyish, finally at centre pale beige (Mu. 10 YR 8/3-4).	Centre pale buffy grey to brown-grey, paler towards margin (Mu. 10 YR 7/3-4, 8/2-3, 5/3).	(our observations)

The colour of the pileus of *V. pusilla* thus ranges from white to cream, beige, yellowish, or greyish. Whereas in *V. taylori* it varies from white, greyish, avellaneous to livid. There is hardly a discontinuous range of variation in the colour of the pileus of these two taxa. *Volvariella taylori* represents a more pigmented form of *V. pusilla*. Because of these great similarities between the two taxa, we reduce *V. taylori* to a variety of *V. pusilla*.

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**Ultrastructure of the ascus top and the ascospore wall in  
*Fimaria* and *Pseudombrophila* (Pezizales, Ascomycotina)**

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Morphological and developmental studies on the ascus top and the ascospore wall of *Fimaria theioleuca*, *F. cervaria*, *Pseudombrophila obliquerrimosa*, and *P. deerata* were carried out with light and electron microscopy. Ascus tops are found with roughly delimited ascostomes and opercula, without indentations, preformed weakened zones, or subapical rings. Dehiscence of the ascus takes place in an eroded, slightly thinner zone of the outer layer and next to a corresponding wrinkled region in the inner layer. This corresponds with the structure and dehiscence mechanism found in genera of Pyronemataceae studied thus far. During ascospore development in all species at first a smooth electron-dense secondary wall is formed. In *F. theioleuca* and *F. cervaria* this layer is permanent, but in *P. obliquerrimosa* and *P. deerata* it usually breaks up to form an ornamentation. The presence of smooth and rough ascospores in the same species is explained by assuming a common process of development followed by a further final ripening in the rough-spored ones. The presence of two types of septa is recorded from excipular cells and paraphyses of *F. theioleuca*.

In view of the preparation of a taxonomic revision of the genera *Fimaria* Vel. and *Pseudombrophila* Boud. but the almost complete absence of knowledge about the fine structure of the species of these genera, a study on the ultrastructure of asci, ascospore walls, and septa has been undertaken.

The comparative structural study of the dehiscence mechanism of operculate Ascomycetes started with the aid of light microscopy. Especially investigations by Boedijn (1933), Chadefaud (1942, 1944, 1946), and Le Gal (1946a, 1946b) of living and revived material yielded the first beginnings of understanding of the structure of this mechanism. As subject of these first investigations especially representatives of the family Sarcoscyphaceae were chosen. Here relatively thick walls were found in the top of the asci characterized by a very strong, but unequal, swelling of the different parts in water and other media.

Especially many of the post-mortem observations on revived exsiccata and on material conserved in liquid have led to wrong interpretations of the structure and the mechanism of the ascus dehiscence. Boedijn's (l.c.) observations on living asci of *Cookeina sulcipes* (Berk.) O. K. are contrasting examples of lasting value. The strongly asymmetrical structure of the ascus top with an eccentrically oriented operculum in this species which was also studied by Le Gal (1946a), make it difficult to homologize the structural details described with those observed in symmetrical asci.

The ultrastructure of the ascus top has now been investigated in more than 40 genera of Pezizales (e.g. Schrantz, 1970; Wells, 1972; van Brummelen, 1974, 1975, 1978;

Samuelson, 1975, 1978a–d; Hung, 1977; Bellemère, 1977; Samuelson & Kimbrough, 1978; Kimbrough & Benny, 1978; Samuelson & al., 1980).

Based on the fine structure of the ascus top in the Pezizales van Brummelen (1978) distinguished eight principal types of asci, while Samuelson (1978d) even concluded that 'no two genera share an identical apical apparatus.' Although the latter conclusion would seem to be somewhat extreme, comparative study of the structure of the ascus top can certainly help in determining taxonomic affinities at familial and sometimes even at generic level.

The structure of the ascospore wall and of its ornamentation in Pezizales have been the subject of extensive studies by Le Gal (1947) with light microscopy and by Merkus (1973, 1974, 1975, 1976) with electron microscopy. They, however, did not study species of the genera under consideration here.

In *Fimaria* and *Pseudombrophila* there occur taxa with smooth as well as with ornamented ascospores. In some taxa this character seems to be inconstant. Here smooth and rough ascospores can be found in the same, apparently homogeneous, collection. The ultrastructure of the ascospore wall may give an explanation for this phenomenon.

#### MATERIAL AND METHODS

For the present study fresh material was collected in the Netherlands, France, and Italy. The following list gives more details about the specimens and their origins. *Fimaria theioleuca* (Roll.) Brumm. — *van Brummelen* s.n., on sheep dung, Elspeet, Gelderland, the Netherlands, 7 XII 1972 (L); *Fimaria cervaria* (Phill. apud J. Stevenson) Brumm. — *van Brummelen* s.n., on hare dung, Vogelenzang, North Holland, the Netherlands, 4 VII 1974 (L); *Pseudombrophila deerata* (P. Karst.) Seaver — *Donadini*, on sheep dung, Aubagne, Bouche du Rhône, France, 25 IV 1981 (L); *Pseudombrophila obliquerrimosa* Harmaja — *Lucchini & van Brummelen* 6263, on rotten vegetable debris mixed with cow dung, near Selva di Trissino, Veneto, Italy, 2 V 1981 (L).

Living isolated asci or bundles of gently spread out asci were observed in water or in a weakly hypotonic solution of glucose in distilled water. The slides were studied with phase contrast and Normarski's interference contrast optics.

For light microscopy asci and ascospores were stained with e.g. Congo red, trypan blue, and methyl blue. For critical observations monochromatic light was used of a wavelength equal to that of the maximum absorption value of the stain used. Also, sections 0.2–0.5  $\mu\text{m}$  thick of material embedded in epoxy resin and stained with toluidine blue proved to be of value.

For electron microscopy, small squares of the hymenium of apothecia at different stages of ripening were cut and fixed.

One part of the material was fixed for 3 hours in 1% glutaraldehyde buffered at pH 7.2 with 0.2M cacodylate at 4°C. Another part was fixed for 1 hour in 1–1.5%  $\text{KMnO}_4$  in distilled water. All material was post-fixed for 1 hour in 1% buffered  $\text{OsO}_4$  at 4°C.

Fixed material was dehydrated in an ethanol graded series and embedded in Epon. During dehydration the material was stained for 5 minutes in a solution of 1% uranyl

acetate. Longitudinal median sections of asci were cut with a diamond-knife on an LKB Ultratome III. The grids were normally contrasted with Reynold's lead citrate and uranyl acetate, and occasionally also with barium permanganate. The ultrathin sections were viewed with an Philips EM 300 electron microscope.

## OBSERVATIONS

### The ascus top

In the species under observation, structural differentiation in the top of the ascus can only be observed in mature asci shortly before the moment of spore discharge. At this stage minor changes in the osmotic pressure of the medium may easily cause the discharge.

In mature undehisced asci the upper ripe ascospore is located in the top just under or against the apical wall. Since the endospore of mature ascospores in Pezizales becomes resistant to fixation, embedding, and thin sectioning, it is often difficult to study ascospores and apices of asci properly at the ripest stage. Consequently the study of the ascus top is especially based on ripening asci, on mature asci where the spores have accidentally been retracted from the top, and on dehisced asci.

Since ample material of *Fimaria theioleuca* from cultures was available, the structure of the ascus of this species is described and illustrated in the first place.

The shape of the asci is cylindrical with a rounded tip,  $150-200 \times 13-15 \mu\text{m}$ .

In the young ascus and during early ascospore formation, the ascus wall appears to be still undifferentiated, thicker throughout the lateral face of the ascus and thinner at the tip (Fig. 1A).

At the inner face of the lateral wall no protuberances are found in the apical or subapical region of the ascus.

In the apical epiplasm, also called acroplasm (Chadefaud, 1942), an apical funnel continuing as a tract downwards to the first ascospore can be found (Fig. 3A). Sometimes the tract can be followed further downwards along the lower ascospores. These structures can best be detected with phase contrast or interference contrast optics.

In  $0.2-0.5 \mu\text{m}$  thick sections the apical and subapical regions of the ascus wall stain strongly with toluidine blue, especially after dehiscence.

Also electron microscope observations of asci at different stages of development did not reveal a subapical ring or protuberances other than lomasomes at the inner face of the ascus wall.

In young asci of permanganate- $\text{OsO}_4$ -fixed material the wall at the immediate region of the tip is  $150-170 \text{ nm}$  thick, subapically the ascus wall reaches a thickness of  $200-500 \text{ nm}$ . At the outside of the ascus a thin electron-dense periascus is present from the beginning.

During the ripening of the ascospores an inner layer becomes discernible over the full length of the ascus. This layer is not contrasting much in electron-density with the outer layer, but it is marked by a contrasting boundary line. The formation of the inner

layer is completed at the moment of spore maturity. In the apical region, or the future operculum, the inner and outer layers are then of about the same thickness, both 100–120 nm, as well in glutaraldehyde-OsO<sub>4</sub> as in permanganate-OsO<sub>4</sub>-fixed material. In the subapical region there is a considerable but gradual change in the thickness of the ascus wall and in both of its layers. The ascus wall thickens from 240–270 nm closely behind the tip to 460–520 nm more downwards. This is due to changes in the thickness of the outer layer which increases from 170–200 nm in the upper part to 450–500 nm in the lower part of the subapical region. Over the same distance the inner layer reduces in thickness from 70–100 nm near the tip to only 20–25 nm lower down.

In the outer layer of the lateral wall, at some distance behind the apex, two strata can be distinguished: an outer stratum 310–344 nm thick and an inner stratum 120–155 nm thick (Fig. 2B).

Even at full maturity no trace of an indentation or a preformed weakened zone demarcates the place of the future operculum. The only indication of the formation of an operculum at the top of the ascus is the presence, at a short distance behind the tip, of a zone with a slightly thinner ascus wall and with some irregular erosion at the surface of the outer layer, corresponding with a region of wrinkling of the inner layer (Fig. 1B).

The operculum opens forcibly by a fracture in this zone of the outer layer and by a fracture in the inner layer next to the wrinkled region. As a result of this fracture, the margins of the ascostome (Seaver, 1928) and the operculum look rather irregular and rough, while in the operculum the outer layer usually overlaps the inner one (Fig. 1D, 2A, C, D).

Abbreviations used in figures. — AS, ascostome; AW, ascus wall; CM, condensed material; E, epiplasm; EN, endospore; EP, epispore; ER, endoplasmic reticulum; F, fracturing line; FU, funnel; IL, inner layer; IM, investing membrane; M, mitochondrion; N, nucleus; O, operculum; OL, outer layer; P, periascus; PM, plasma membrane or plasmalemma; PW, primary spore wall; S, ascospore; SP, sporoplasm; SW, secondary wall; T, tract or funiculus; WZ, weakened zone.

The scale markers in all figures equal approximately 0.5  $\mu$ m.

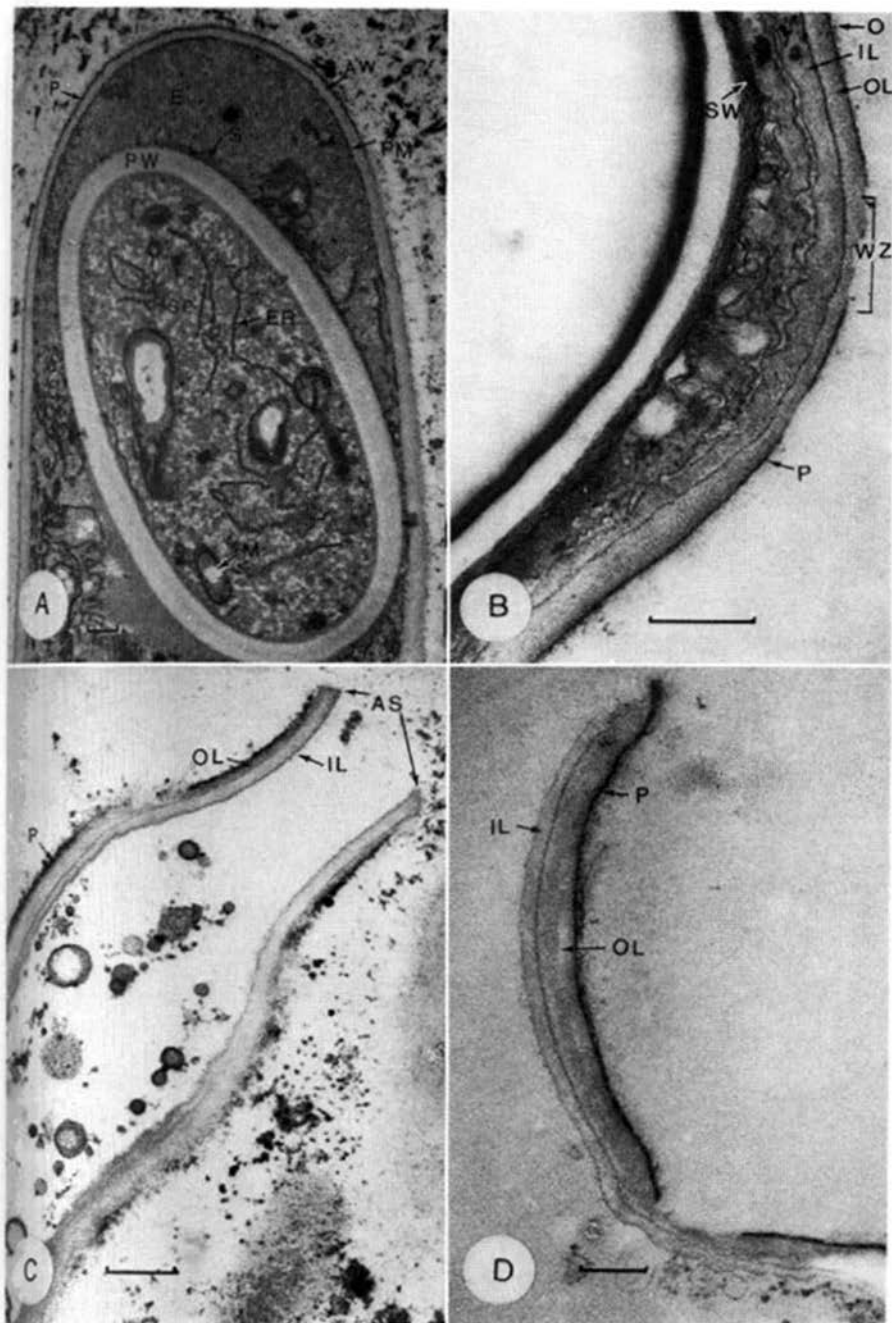
Fig. 1. *Fimaria theioleuca*, electron micrographs of ripening and emptied asci. — A. Median section of the distal portion of ripening ascus, fixed in 1% KMnO<sub>4</sub> and 1% OsO<sub>4</sub>. — B. Detail of apex of almost mature ascus just before dehiscence, with empty space of fallen out uppermost ascospore, fixed in 1% glutaraldehyde and 1% OsO<sub>4</sub>. — C. Apex of emptied ascus without operculum, fixed in 1% KMnO<sub>4</sub> and 1% OsO<sub>4</sub>. — D. Operculum of emptied ascus, fixed in 1% OsO<sub>4</sub>.

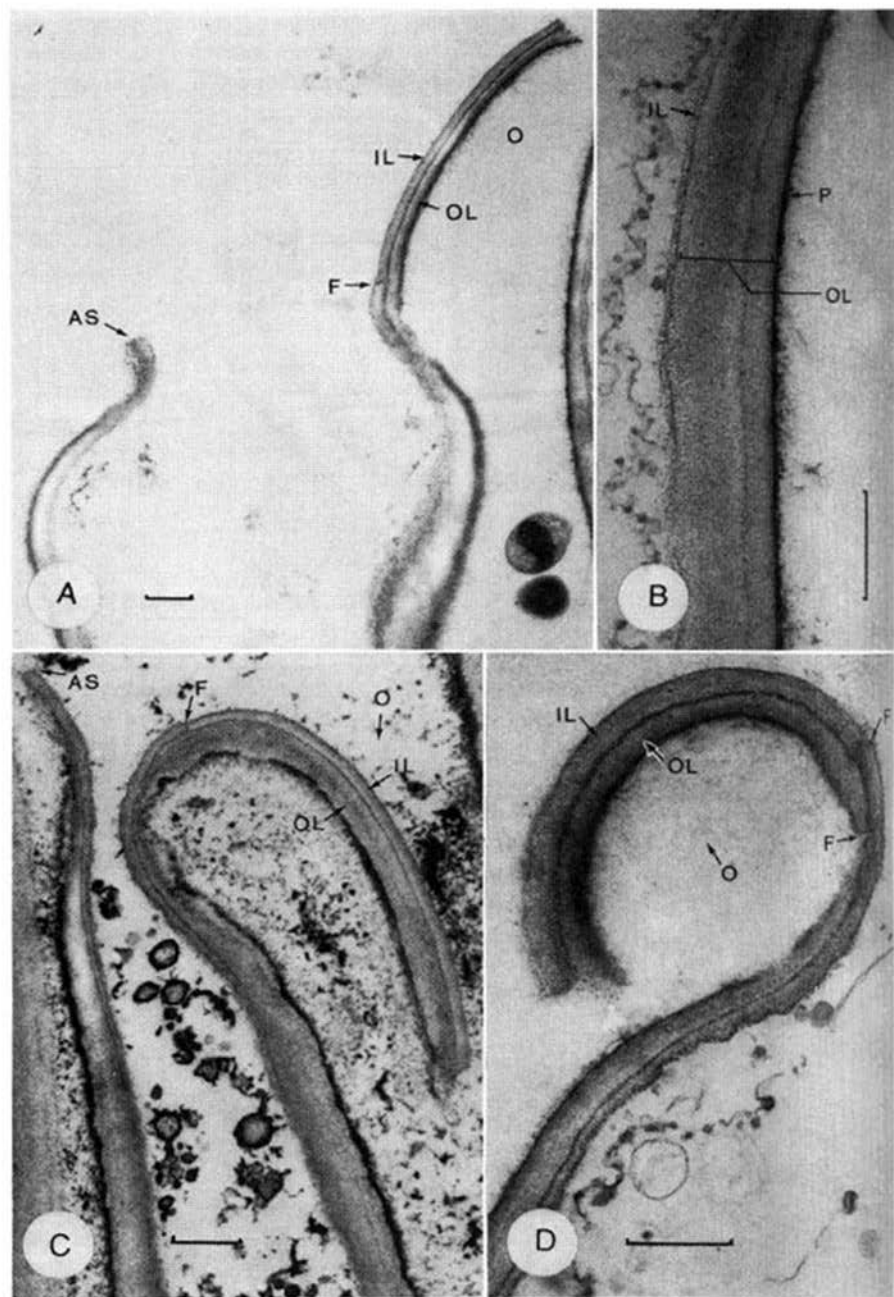
Fig. 2. *Fimaria theioleuca*, electron micrographs of emptied asci. — A. Median section of apex of emptied ascus with operculum, fixed in 1% glutaraldehyde and 1% OsO<sub>4</sub>. — B. Transverse section of lateral wall, fixed in 1% glutaraldehyde and 1% OsO<sub>4</sub>. — C. As A but fixed in 1% KMnO<sub>4</sub> and 1% OsO<sub>4</sub>. — D. Detail of operculum, fixed in 1% glutaraldehyde and 1% OsO<sub>4</sub>.

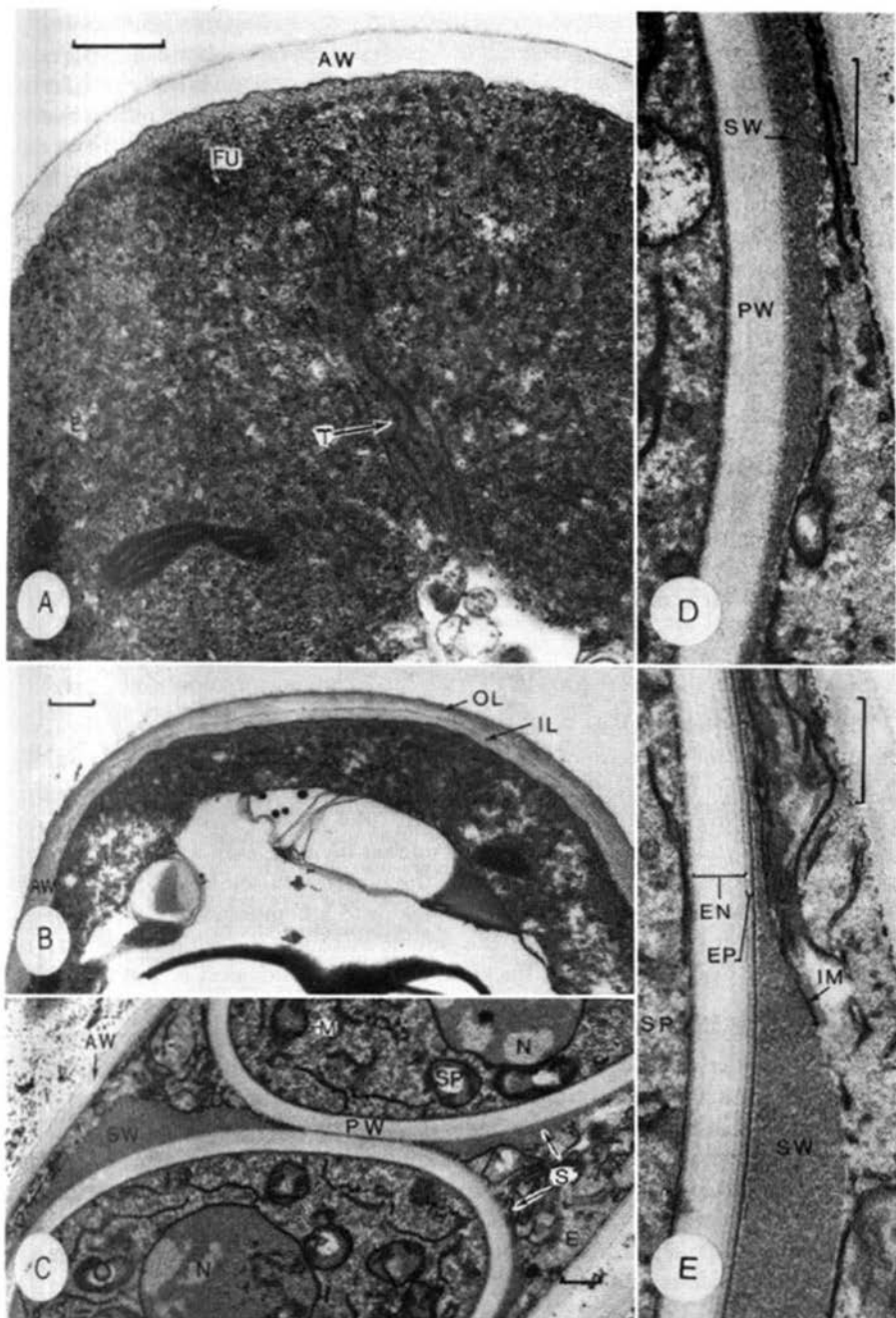
Fig. 3A, B. *Pseudobrophila obliquerrimosa*, electron micrographs of ripening asci, fixed in 1% glutaraldehyde and 1% OsO<sub>4</sub>. — A. Detail of apical epiplasm, showing tubular structure of tract. — B. Operculum region.

Figs. 3C–E. *Fimaria theioleuca*, electron micrographs of ascospore development, fixed in 1% KMnO<sub>4</sub> and 1% OsO<sub>4</sub>. — C, D. Development of the secondary wall. — E. Id., also showing development of the endospore and the epispore.









After the violent discharge of the ascospores the operculum remains attached to the rest of the ascus by a narrow hinge. In the species studied, the place of the hinge seems to be fully arbitrary. Even in the hinge the lines of fissuring can often be recognized in one or both layers (Fig. 2A, C, D). While the layer of the operculum remains more or less constant in thickness, 85–140 nm, the outer layer may swell up to double its original size, from 120 to 280 nm.

In the subapical region, somewhat behind the ascostome, often a zone of irregular swelling and very low electron-density can be distinguished in the wall (Figs. 2A, C). In this zone it is difficult to trace the boundary lines between layers and strata. It corresponds exactly with the sites of optimal staining with e.g. toluidine blue in light microscopy.

Also with electron microscopy a funnel and a tract can be distinguished in the apical part of the epiplasm; both consist of subparallel anastomosing electron-dense tubules 14–17 nm wide (Fig. 3A). In the top of the ascus the tract reaches a diameter of 270–350 nm.

The asci of *Fimaria cervaria*, *Pseudombrophila deerata*, and *P. obliquerosa* have also been studied in detail, showing that, apart from some minor differences in the dimensions of the asci, there are no significant differences between the four species in the structure of the ascus top and the mechanism of spore liberation.

#### The ascospore wall

The ultrastructure of these species of *Fimaria* and *Pseudombrophila*, with respect to the development of the ascospores, closely accords with the general process as described by earlier students of representatives of this group of fungi (e.g. Hawker, 1965; Bracker, 1967; Reeves, 1967; Wells, 1972; Merkus, 1973, 1974, 1975, 1976).

In the very young ascus, directly after nuclear division, each nucleus becomes surrounded by a double membrane separating the nuclei with some sporoplasm from the epiplasm. The wall of a young ascospore develops as a homogeneous electron-transparent substance between both parts of this double ascospore delimiting membrane. This primary wall is of rather constant thickness and remains the most constant part of the ascospore wall.

On further ripening an extra layer, the secondary wall, develops between the primary wall and the outer spore delimiting membrane. The aspect of this new wall material is slightly granular and more electron-dense than that of the primary wall.

At first the substance of the secondary wall is homogeneous, but during further development more electron-dense material condenses and accumulates locally in this matrix. The continuous addition of new wall material results in the formation of a distinct ornamentation pattern over the ascospore.

Where new material is formed the outer investing membrane is lifted up. In the end this membrane is often indistinct or fragmentary.

Simultaneously with the formation of the secondary wall, differentiation of the primary wall takes place. In the outer zone of the primary wall a more electron-dense band is formed. On further ripening of the ascospores two or more electron-dense layers become visible. The whole complex of thin layers is called the episporium. The remaining inner part of the primary wall is called the endospore. At times, especially after post-staining with uranyl and lead salts, also a sublayering of the endospore can be made visible (cf. Figs. 4 B–D, 5 B, C).

During ripening of the ascospores the epiplasm and the sporoplasm undergo changes. Especially in the end the epiplasm disintegrates almost completely, losing its original organelles, forming a few very large vacuoles, and remaining only as a thin layer just inside the ascoplasmalemma and in the tip.

In the sporoplasm the organelles remain present and increase in size and electron-density. Oil-drops are not formed.

#### *Fimaria theioleuca*—Figs. 3C–E, 4

In material fixed both in permanganate-OsO<sub>4</sub> and in glutaraldehyde-OsO<sub>4</sub>, the primary wall is of rather constant thickness (290–310 nm). The investing membrane separates along the whole surface of the primary wall and a secondary wall of strongly varying thickness with fairly electron-dense contents develops. The investing membrane may run rather irregularly. Often the secondary wall thickens considerably (up to 500 or even 1100 nm) and large homogeneous electron-dense masses are formed on the primary wall (Figs. 3C, E, 4A, B).

During the development of the secondary wall an episporium of about 60 nm thick and an endospore of 180–225 nm thick are formed (Figs. 3E, 4A–F). In the episporium usually two electron-dense layers can be observed, whereas the endospore may show four or five zones of slightly higher electron-density alternating with more electron-transparent ones. Simultaneously with changes in the epiplasm and the sporoplasm the secondary wall modifies. Within the secondary wall, on the outside of the episporium, a rather sharply delimited layer with increased electron-density is formed (Fig. 4B). Gradually this layer grows to form a layer 120–250 nm thick, while the rest of the secondary wall disappears gradually. At maturity a very fine fibrillar structure can be recognized in this layer. Sometimes remnants of the investing membrane can be found on its outside (Fig. 4E). The mature ascospores are smooth.

With light microscopy the secondary wall of mature ascospores stains intensely with methyl blue, showing a thin uninterrupted smooth layer.

#### *Fimaria cervaria*—Figs. 5F–J

At first the ascospores in this species develop in the same way as in *F. theioleuca*. In the permanganate-OsO<sub>4</sub>-fixed material, the primary wall is homogeneously electron-transparent, 330–370 nm thick. The investing membrane separates from the primary wall and the secondary wall is formed in between, consisting of homogeneous and fairly electron-dense material. The process of secondary wall formation proceeds along the whole primary wall. Locally the secondary wall thickens enormously, up to 1300 or

sometimes even 1700 nm. At the same time an episporium (40–60 nm thick) and an endospore (290–310 nm thick) develop and changes in the epiplasm and the sporoplasm take place. The episporium shows two thin electron-dense layers, the endospore remains homogeneous.

In the homogeneous matrix of the secondary wall locally and close to the surface of the episporium areas of slightly higher electron-density appear (Fig. 5G). Gradually these areas become more electron-dense and grow together to form a continuous layer with a wavy outer boundary, 90–336 nm thick (Figs. 5F, H). During further maturation an electron-dense layer of constant thickness (165–200 nm) with a fine fibrillar structure is formed, while the rest of the secondary wall and most of the epiplasm disappear; the mature spores are smooth (Fig. 5J).

Also with light microscopy, after staining with methyl blue or with interference contrast optics, the thin secondary wall in mature spores shows as an uninterrupted and smooth layer.

#### *Pseudombrophila obliquerrimosa*—Figs. 5A–E

The glutaraldehyde-OsO<sub>4</sub>-fixed material of this species has especially been studied during the last stages of spore development. The early development is the same as in *Fimaria theioleuca* and *F. cervaria*. The primary wall is 380–400 nm thick and has the normal aspect. Separation of the investing membrane from the primary wall has made formation of the secondary wall possible; this is composed of homogeneous and fairly electron-dense material. In the following development a two- or multi-layered episporium (65–70 nm thick) and a sublayered endospore (290–330 nm thick) differentiate within the primary wall. At the same time the secondary wall material concentrates as a continuous, rather uniform layer (120–230 nm thick) of electron-dense material on the episporium (Figs. 5A, B). Together with the main part of the epiplasm, the rest of the secondary wall disappears.

During the last stage of maturation the surface of the rather uniform secondary wall breaks up to form a series of more or less oblique ridges over the surface of the spore

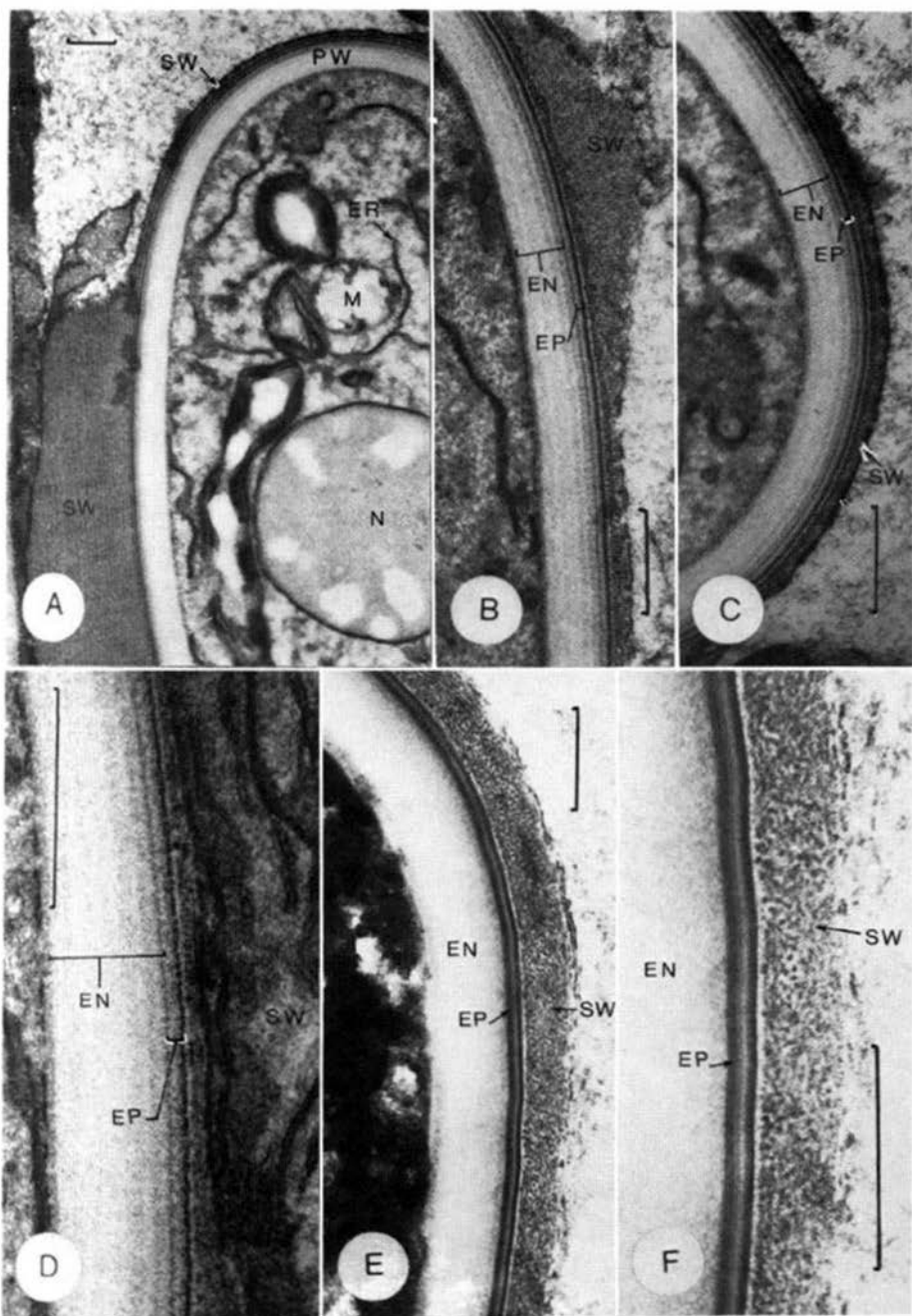
Fig. 4. *Fimaria theioleuca*, electron micrographs of ascospore development, fixed in 1% KMnO<sub>4</sub> and 1% OsO<sub>4</sub>. — A–C. Condensation of secondary wall material. — D. Detail of condensed material. — E–F. Advanced state of ascospore development.

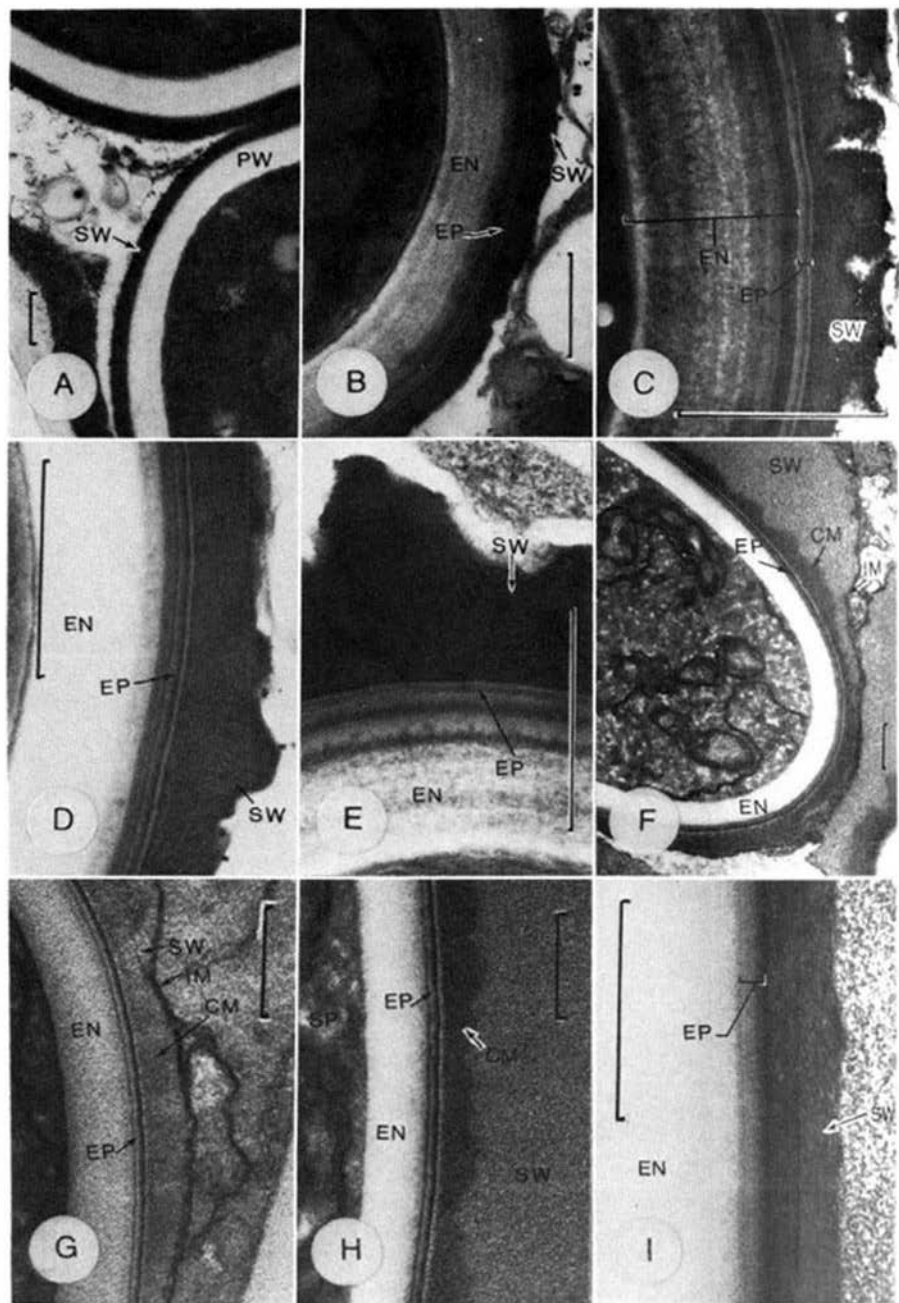
Figs. 5A–E. *Pseudombrophila obliquerrimosa*, electron micrographs of ascospore development, fixed in 1% glutaraldehyde and 1% OsO<sub>4</sub>. — A. Development of the secondary wall. — B, C, D, also showing development of the endospore and the episporium. — D, E. Advanced state in development of ornamentation, showing the fibrillar structure of secondary wall material.

Figs. 5F–J. *Fimaria cervaria*, electron micrographs of ascospore development, fixed in 1% KMnO<sub>4</sub> and 1% OsO<sub>4</sub>. — F–H. Development of the endospore and the episporium and condensation of secondary wall material. — I. Advanced state of ascospore development, showing a smooth layer of secondary wall material.

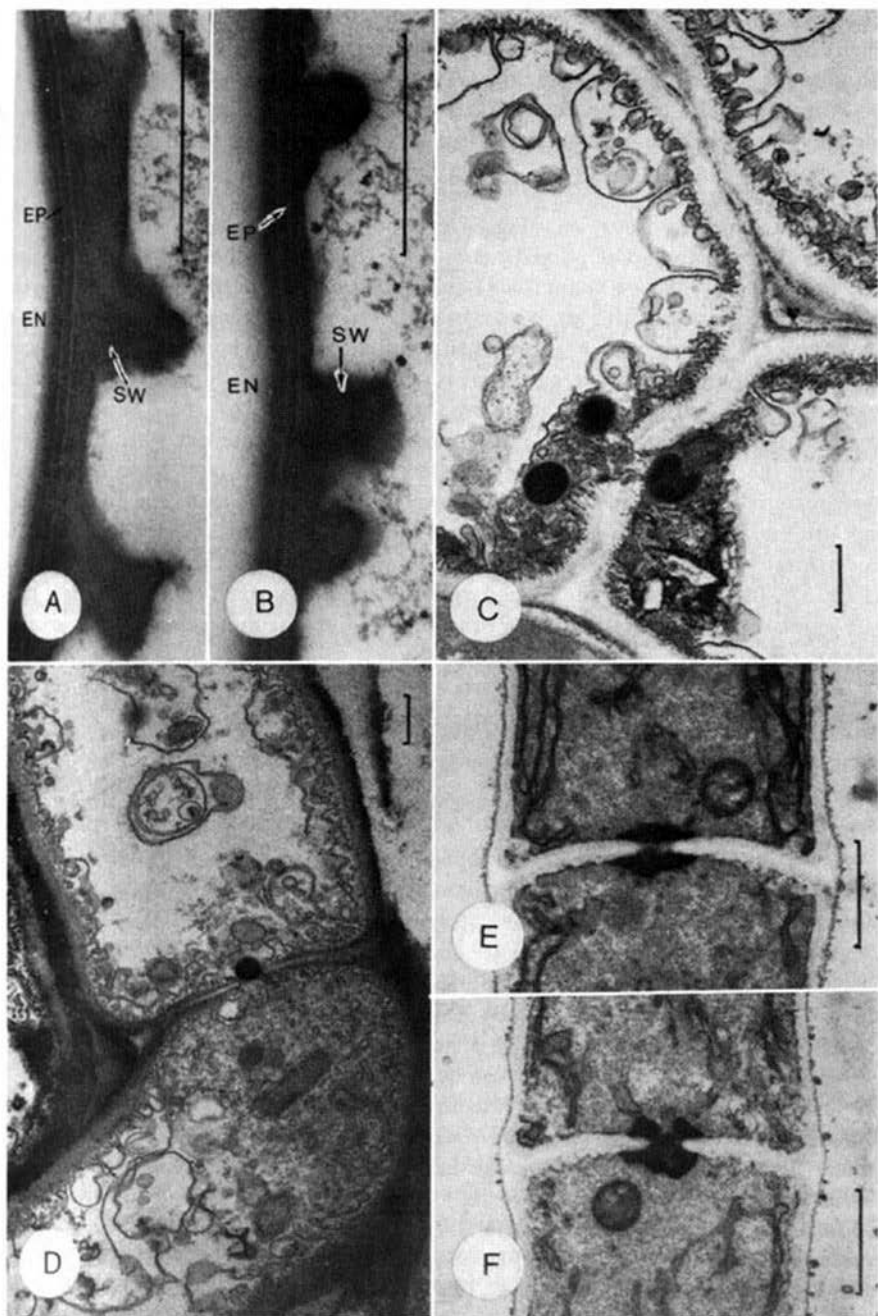
Figs. 6A, B. *Pseudombrophila deerata*, electron micrographs of an advanced state of ascospore development, fixed in 1% glutaraldehyde and 1% OsO<sub>4</sub>.

Figs. 6C–F. *Fimaria theioleuca*, electron micrographs of septa. — C, D. Septa of excipular cells, fixed in 1% glutaraldehyde and 1% OsO<sub>4</sub>. — E, F. Plugged septa in paraphyses, fixed in 1% KMnO<sub>4</sub> and 1% OsO<sub>4</sub>.









(Fig. 5C). In the mature spores an ornamentation of irregular ridges (130–490 nm high) of a fine fibrous structure and with an irregularly eroded surface can be observed. Usually the furrows between the ridges do not reach the base of the secondary wall.

With light microscopy and methyl blue staining the ornamentation, consisting of occasionally anastomosing oblique striae, can be observed in the major part of the mature ascospores.

#### *Pseudombrophila deerata*—Figs. 6A, B

The glutaraldehyde-OsO<sub>4</sub>-fixed material of this species shows that the structure of the primary wall (380–400 nm thick), the epiplasm, and the sporoplasm resemble those in the other species of this study. At an early stage an episporium (55–60 nm thick) and an endospore (330 nm thick) arise. At first the endospore is homogeneous and electron-transparent. Later the outer part increases in electron-density and forms a complete extra layer (25–30 nm thick) adjoining the episporium (Figs. 6A, B). The secondary wall material is fairly electron-dense and homogeneous at the moment when it is deposited between the primary wall and the investing membrane. At later stages the secondary wall material partly condenses on the episporium as a homogeneous and compact, rather smooth electron-dense layer (35–100 nm thick). Finally this layer often breaks up to form local protrusions or warts (160–280 nm high) over the surface of the ascospore (Figs. 5A, B). The rest of the secondary wall disappears together with the main part of the epiplasm. The structure of the ornamentation is not quite clear and the surface is irregularly eroded and somewhat fibrous.

With light microscopy the fine warts can just be observed under optimal conditions with methyl blue staining or with interference contrast optics.

#### The septa

Especially in *Fimaria theioleuca* septa have been studied. In glutaraldehyde-OsO<sub>4</sub>-fixed material, cells of the cortical part of the excipulum show strongly thickened cell walls and septa with a simple septal plate; each with a single central pore.

Apparently the thickened walls are densely clothed at their inner side with protuberances that are often densely and minutely diverticulate. Also the septum may be thickened in the same way (Figs. 6C, D). One or more spherical, electron-dense Woronin bodies accompany the septum. The diameter of the Woronin bodies is larger than the septal pores and often one of them can be found to occlude the poral opening.

This is considered the 'typical' ascomycete septal type by Gull (1978). It has been described from a great number of Ascomycetes and their anamorphs. Even in cells where the main part of the cytoplasm has already disappeared, Woronin bodies can be found active at the septal pores (Fig. 6C).

In permanganate-OsO<sub>4</sub>-fixed material of the same species septa have been studied in the paraphyses. Here also septal plates with a central pore are formed, but no accompanying Woronin bodies are found. The septal pore is closed by a tightly fitting electron-dense plug (Figs. 6E, F). In a section grazing the edge of the septal pore (Fig. 6E)

electron-dense flattened sides can be observed at each side of the pore. No central opening in the plug is found.

The septal plug in the paraphyses of *Fimaria theioleuca* resembles that of *Chaetomium brasiliensis* Batista & Pontual (Rosing, 1981), *Chaetomidium arxii* Benny (Benny & Samuelson, 1980), and *Neurospora crassa* Shear & B. Dodge (Trinci & Collinge, 1973). It is called the 'solid pulley-shaped plug' by Rosing (l.c.) or 'diabolo-shaped plug' by Chadefaud (1973).

#### DISCUSSION

The structure of the ascus top in the species of *Fimaria* and *Pseudombrophila* studied is very similar. This structure is summarised in a diagrammatic scheme (Fig. 7).

This type of ascus top with a rather roughly delimited operculum and ascostome, without internal indentation or a prominent ring shows great affinity to the 'Octospora type' of van Brummelen (1978) or with the 'apical apparatuses' described by Samuelson (1978b) for representatives of the 'Otidea-Aleuria complex'. This type is known from species of the genera *Pyronema*, *Anthracobia*, *Aleuria*, *Otidea*, *Coprobria*, *Cheilymenia*, *Scutellinia*, *Octospora*, *Sowerbyella*, *Jafnea*, *Humaria*, and *Sphaerosporella*; all genera belonging to the family Pyronemataceae. So the structure of the ascus top in *Fimaria* and *Pseudombrophila* underlines a close affinity with the members of this family.

In several species with this type of ascus a subapical swelling can be observed at the inner side of the wall at some distance behind the tip. This swelling has the shape of a more or less constant and regular ring. It is composed of material of the rather thin inner ascal layer and additional material precipitated from the surrounding ascoplasm, as may be concluded from the observed local concentration of endoplasmatic reticulum and the activity of lomasomes.

These rings differ clearly from the thick ring found in the subapical ascal wall in species of *Ascozonus*, which is composed of material of deeper wall layers (cf. van Brummelen, 1974; Samuelson, 1978b). The ring in *Ascozonus* is of a different origin and not homologous with the subapical ring found in some genera of the Pyronemataceae as suggested by Samuelson (l.c.).

The strong change in affinity of the operculum and the ascal walls in the subapical region to stains like toluidine blue may be due to local physical changes in the ascal wall at the moment of the forcible discharge of the spores. The walls in this region are strongly overstretched and deformed during dehiscence and often swollen afterwards.

The structure in the asci of several species of Pezizales, described as 'bourrelet sous-apical' by Chadefaud (1942, 1946), corresponds exactly with this area of swelling. From his descriptions it is clear that this 'bourrelet' is rather inconstant and often unequally developed at both sides of the ascus top. Sometimes after strong swelling the constituent layers or strata become partly loose one from the other. This agrees well with earlier observations on representatives of the 'Octospora type' (van Brummelen, 1978), where this cleavage of the ascal wall is often observed in the swollen region near the ascostome.

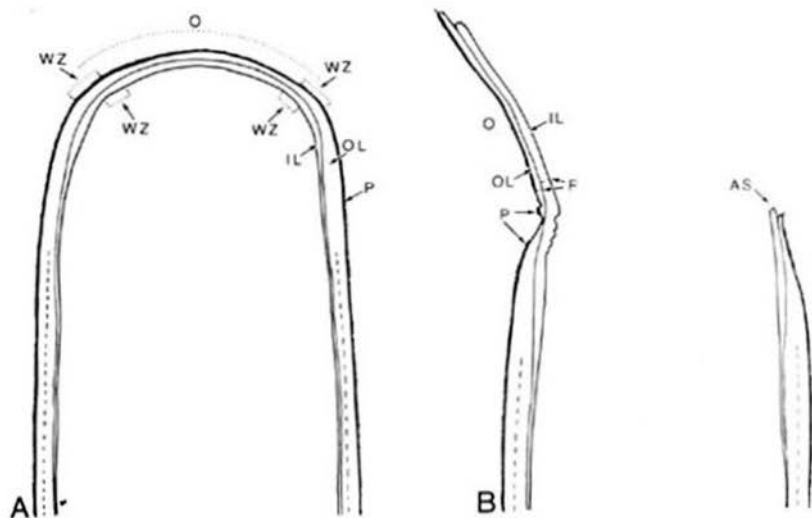


Fig. 7. Diagrammatic sections of ascus tops, as seen with electron microscopy. — A. Almost mature ascus. — B. Ascus after spore discharge.

The 'projecting border' described by Boedijn (1933) as part of the ascus top of *Cookeina sulcipes* (fam. Sarcoscyphaceae) relates to the same structure. In the Sarcoscyphaceae this subapical region is particularly obvious, because of the very strong swelling of the inner layer of the ascus wall. The strongly eccentrically placed operculum in species of *Cookeina* and some related genera make a comparison with symmetrical forms difficult (cf. Eckblad, 1968, 1972; van Brummelen, 1975; Samuelson, 1975; Samuelson & al., 1980).

For the same subapical region of the ascus Samuelson (1975) introduced the term 'suboperculum', defining 'the area of the ascus wall immediately below the line of dehiscence in which transitions in the wall layers are notable.' The upper boundary is well defined by the (future) ascostome, but the lower boundary is more variable, since the transition in wall layers is often rather gradual at the proximal side, especially when a subapical ring is not present.

The term 'suboperculum' for a certain part of the ascus wall is unfortunate, since the same term was more or less implied by Le Gal's (1946a, 1946b) introduction of the 'Suboperculés' for discomycetes with a certain type of operculum. Fully parallel with Le Gal's terminology, Chadefaud (1946) introduced simultaneously his 'para-opercule' for the same operculum model. Moreover the suboperculum of Samuelson is not restricted to the suboperculates of Le Gal, as he might have expected at first (cf. Samuelson, 1975; Samuelson & al. 1980). To prevent further confusion the terms 'subapical region', or 'projecting border' can better be used.

With regard to the development of the ascospore wall, considerable agreement is found between the species studied. The development of the primary wall and its differentiation into an episporium and an endospore reveal a strong resemblance to the general process described in other Pezizales (e.g. Wells, 1972; Merkus, 1973, 1974, 1975, 1976). The perceptibility of the sublayering of the episporium and the endospore depends much upon the methods of fixation and staining used.

A secondary wall of strongly varying thickness is always formed between the primary wall and the investing membrane. In *Fimaria cervaria* local areas of condensed secondary wall material are formed before this concentrates as a uniform smooth layer on the episporium. In the other species studied this local condensation is not observed and the secondary wall material seems to concentrate directly as a smooth layer.

In all cases a uniform smooth layer of electron-dense material is formed that on further ripening shows more or less clearly a fine fibrous structure. During final maturation the outer surface of the smooth layer may break up to form a pattern of ornamentation in all or, at least, a part of the spores. Since this ornamentation arises secondarily from a smooth layer, there is no fundamental difference between both types of spores. The formation of rough or ornamented ascospores in *Pseudombrophila obliquerrimosa* and *P. deerata* can be considered as a process of final ripening that is not always completed before their discharge.

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K. Esser. *Kryptogamen. Cyanobakterien, Algen, Pilze, Flechten. Praktikum und Lehrbuch*. 2. Aufl. (Springer-Verlag, Berlin, Heidelberg, New York, Tokyo. 1986.) Pp. XXII + 566, 310 Text-figs. Price: DM 98.-.

The first edition of this book was published in 1976. In this second, revised edition especially the chapter on Deuteromycetes has been changed and extended with more examples. The book is an introduction into the field of thallophyta, intended to be used as a guide for more extensive ('classical') university courses on this group of cryptogams.

It is well-illustrated with many drawings, photomicrographs, and schemes of life-cycles. In the theoretical part the principles of reproduction cycles are discussed. The part on technical methods gives a selection of cultural methods and microscopical staining procedures. The major part of the book is devoted to practical information on the main classes, orders, and families of the thallophyta. Appropriate objects are listed, certain tasks for students are set, and information is given on the structures to be observed.

P. Konrad & A. Maublanc. *Icones selectae Fungorum. Vol. III*. (Reprint edition. Libreria editrice Giovanna Biella, Saronno (It.). 1986.) Hundred Col. Pls. and accompanying text-pages. Price: Lire 110.000.

The third volume of the very well-done and attractively bound reprint edition of the 'classical' mycological iconography of Konrad & Maublanc. For more details see *Persoonia* 13: 134. 1986.

J. Rammeloo (Editor). *Icones mycologicae*. Jardin Botanique National de Belgique. Meise. Price: Ser. 1, 4, and 6 B. Frs. 800.-; ser. 2, 3, and 5 B. Frs. 600.-.

This work is delivered since 1982 in a number of series, of which six have been published till now. Each series consists of a varying number (16–20) of loose-leafed plates with accompanying descriptions and legends. Each plate with text has his own author.

The first series (1–18, 1982) contains 13 *Russula*'s by L. Imler. The second (19–34, 1983) and the third series (35–54, 1984) contain respectively 13 and 18 Myxomycetes (Trichiales) by J. Rammeloo. The fourth series (55–74, 1984) contains 6 myxo's by J. Rammeloo and 8 agarics (Boletaceae) by L. Imler. The fifth series (75–92, 1985) contains 8 *Galerina*'s by A. de Haan. The sixth series (93–110, 1986) contains 10 agarics by L. Imler, and 3 agarics and 5 myxo's by J. Rammeloo.

The plates are of high quality and well printed. They show scanning electron micrographs (SEM) of the myxo's and coloured habit drawings with line drawings and sometimes SEM-graphs of the agarics.