

NOTES ON HYMENOSCYPHUS – II

On three non-fructicolous species of the 'fructigenus-group' with croziers

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Descriptions, illustrations, and keys are given of a small part of the 'fructigenus-group' of the ascomycete genus *Hymenoscyphus*. The species concerned are characterized by asci originating from croziers. *Hymenoscyphus scutuloides* and *H. fucatus* var. *badensis* are described as new, while the combination *H. fucatus* is validly published.

The taxonomic core of the genus *Hymenoscyphus* S.F. Gray is formed by a homogeneous group of species which have the same stipitate-cupulate habit, the same excipular structure, and almost the same shape of asci, ascospores, and paraphyses. This group, here called 'fructigenus-group'¹, comprises some dozens of lignicolous (incl. fructicolous), caulicolous, and foliicolous species, such as *H. albidus* (P. Karst.) W. Phill., *H. albopunctus* (Peck) Kuntze, *H. caudatus* (P. Karst.) Dennis, *H. fastidiosus* (Peck) Arendholz, the *H. fructigenus*-complex, *H. humuli* (Lasch) Dennis, *H. salicellus* (Fr.: Fr.) Dennis, *H. scutula* (Pers.: Fr.) W. Phill., and *H. serotinus* (Pers.: Fr.) W. Phill. Their exciple is composed of two layers: the inner layer (medulla) is a thin-walled *texturaorrecta*, the outer layer (cortex) is a mostly thin-walled *textura prismatica*. The excipular hyphae are running parallel with or oriented at a low angle to the excipular surface and they are not embedded in a gelatinous matrix. Characteristic of the 'fructigenus-group' are the ellipsoid-fusiform to obovoid-fusiform ascospores. Such spores show the upper half of an ellipsoidal to obovoidal body and the lower half of a fusiform one. The spores are in general approximately bilaterally symmetrical, owing to an abaxially angulate or even hooked apex, occasionally combined with some slight curving or single-sided flattening of the spore. This particular shape is nowadays often indicated as 'scutuloid'², a term introduced by Baral (in Baral & Kriegelsteiner, 1985: 120). As the torpedo shape is providing for an optimal discharge, some asymmetry causes the spores to rotate round their axis. This spinning can easily be seen under the microscope, at least in mounts of rehydrated material in ammonia 10%. Moreover, the spores of several species, e.g. *H. salicellus* and *H. scutula*, are provided at their ends with one or more hyaline, thread-like appendages, commonly indicated as 'cilia' but – because of their immovability and consistency – preferably called 'setulae' (bristles). Whether these appendages have a function in spinning, in attachment to substrata, or in any other process, is unknown (cf. Hawksworth, 1987: 186–187).

1) Also called 'scutula-stirpe' (Dennis, 1956: 66, 82; cf. White, 1944: 609, 613) or 'caudatus-group' (Dumont, 1981: 60), but preferably named 'fructigenus-group' because *H. fructigenus* (Bull.: Fr.) S.F. Gray, the type species of the genus, forms part of it.

2) From *H. scutula*, a member of the group.

As generally known, asci arise at the (provisional) end of ascogenous hyphae, from 2- or 3-celled structures called 'Dangeardian elements' (see e.g. Chadefaud, 1943). Within the inoperculate ascomycetes two main types of such structures have been found, viz. the pleurorhynchous type and the aporhynchous type (Berthet, 1964: 98 et seq.). In the pleurorhynchous type the snout of the elements is laterally turned off over an angle of about 180°. Hence such elements are hook-shaped and called 'crozier' (French 'crochet (ascogène)', German 'Haken', Latin 'uncus'). In the aporhynchous or (secondarily) hookless type the forming of a lateral snout is thought to be suppressed, so that the asci seem to be 'simple-septate' (as called by Huhtinen, 1990: 66–67). When the foremost binucleate cell or 'crook' of a crozier develops into an ascus, the terminal (uninucleate) cell³ may remain visible as a small by-pass arching over the septum between the ascus and the preceding cell⁴. A separate term for this small arch seems not to be in common use, at least in English literature. For that reason several authors have resorted to a circumscription as 'Asci originating/produced/arising from croziers' (e.g. White, 1943; Dumont, 1976; Korf & Lizoñ, 1994) or 'Asci aus Haken entstehend' (e.g. Arendholz, 1979), without making clear whether the arch remains visible. Some other authors have misapplied the term 'crozier' to the arch solely (e.g. Dennis, 1956: 76, 79; Haines, 1989⁵). However, a similar process of forming arches is well known from many basidiomycetous fungi, viz. in the development of hyphae of the secondary mycelium (incl. basidia). In these fungi, the anastomosing arch has, for more than a century, been called 'clamp-connection' or, shortly, 'clamp' (Fr. 'boucle' or 'anse d'anastomose', Germ. 'Schnalle', Lat. 'fibula'). Since there is general agreement on the homology of early development of basidia and asci, and on the homology of clamp forming in basidiomycetes and arch forming in ascomycetes (see e.g. Martens, 1932: 261; Moreau, 1950; Moreau, 1954: 1563; Berthet, 1964: 98, 99, 118; Arx, 1967: 183, 184; Boidin, 1971: 143, 144; Dörfelt, 1989: 47; cf. Gäumann & Dodge, 1928: 421, 422), it seems justified and – for correct interpretation – advisable to apply the term 'clamp(-connection)' to relevant ascomycetes too. Yet, in several dictionaries the 'clamp' is considered as a character unique to basidiomycetes (e.g. Hawksworth et al., 1983; Dörfelt, 1989). I would, however, advocate a less exclusive application of this term. Accordingly Moreau & Moreau (1922) and Berthet (1964: 118) have already used the term 'boucle' and von Arx (1967: 69 et seq.) the term 'Schnalle' for the ascomycete clamp.

Most species of the '*fructigenus*-group' contain asci which originate from aporhynchous Dangeardian elements. Hence they lack an anastomosing arch at their base. In this article attention is paid to three species whose asci arise from pleurorhynchous Dangeardian elements, alias croziers, and generally do show a basal anastomosing arch. The presence of croziers and arches respectively is, indeed, not the only character by which these three species are distinguished from others. If so, I would not have regarded them as separate species but as taxa of an infraspecific rank. Such is the case in e.g. *Phaeohelotium*

3) Also called 'tip' (e.g. Gäumann & Dodge, 1928: 130) or 'downward protuberance' (Huhtinen, 1990: 66–67).

4) Also called 'stipe' (Gäumann & Dodge, 1928: 130), 'stalk cell' (Huhtinen, 1990: 67) or 'pédoncule' (Martens, 1932: 259).

5) Haines (1989: 315) simultaneously introduced 'crozier' [gen. 'crozieris', pl. 'crozieres'] as a Latin term ('cum crozieribus'), but there is no need for such an objectionable neologism.

(*Hymenoscyphus imberbe* (Bull.: Fr.) Svrček, wherein two otherwise identical forms can be distinguished: one with croziers and another with aporhynch elements.

Since there was no fresh material available, the presented full-descriptions have been based on dried specimens which were rehydrated in ammonia 10%. Microscopical observation and measuring were carried out on hand-made sections and squash preparations supplied with a solution of 0.2% cotton blue in lactic acid.

Measurements of asci, ascospores and paraphyses (length of end cells) are based on samples taken at random, with the exception of extremes (between round brackets) which are based on select elements outside the sample(s) referred to. The number of samples (k) and the number of elements per sample (n) are indicated between square brackets, just as the calculated taxon averages (length, width, and length/width-ratio respectively) and standard deviations.

KEY TO THE SPECIES TREATED

- 1a. Asci 72–90 μm long (average length < 87.0 μm). Ascospores 14–21 μm long (average length < 19.0 μm), with length/width-ratio of 3.4–5.9 (average ratio < 5.00), occasionally apiculate but not obviously setulose 3. *H. menthae*
 b. Asci 80–136 μm long (average length > 87.0 μm). Ascospores 18–36 μm long (average length > 19.0 μm), with length/width-ratio of 4.8–8.8 (average ratio > 5.00), mostly provided at the ends with obvious, up to 4.0 μm long setulae 2
 2a. Ascospores 18–27 \times 3–4 μm (average length < 24.0 μm , average width < 4.0 μm), with length/width-ratio of 5.1–7.7 (average ratio > 5.50); setulae 1.0–4.0 μm long
 2. *H. scutuloides*
 b. Ascospores 23–36 \times 4–6 μm (average length > 24.0 μm , average width > 4.0 μm); setulae 1.5–2.5 μm long 1. *H. fucatus*

1. *Hymenoscyphus fucatus* (W. Phill.) Baral & Hengstm., *comb. & stat. nov.*

Peziza fucata Cooke & W. Phill. in herb. [invalid: ined.]; in Cooke, *Grevillea* 4 (1876) 132, pl. 65, fig. 300 [invalid: nomen nudum; see also Carpenter, *Mem. New York Bot. Garden* 33 (1981) 214]. — *Hymenoscyphus fucatus* (Cooke & W. Phill.) Baral in Baral & Krieglsteiner, *Beih. Z. Mykol.* 6 (1985) 128 [as '(Phill.)'; invalid: nomen nudum].

Peziza scutula var. *fucata* W. Phill., *Elv. brit.* (3) (1877) n. 120 [invalid: nomen nudum]. — *Hymenoscypha scutula* var. *fucata* W. Phill., *Man. Brit. Discomyc.* (1887) 137 (basionym). — *Phialea scutula* var. *fucata* (W. Phill.) Sacc., *Syll. Fung.* 8 (1889) 266. — *Helotium scutula* var. *fucatum* (W. Phill.) Rehm in Rabenh. *Krypt.-Fl.* ed. 2, 1 (3) (1893) 793 [as var. '*fucata*']. — *Helotium scutula* forma *fucatum* (W. Phill.) Massee, *Brit. Fung.-fl.* 4 (1895) 254 [as forma '*fucata*'].

Helotium superbum Velen. in herb. et ms. 1923 [invalid: ined.] fide Svrček (1985: 159, 188). — *Helotium macrosporum* Velen., *Monogr. Discomyc. Bohem.* 1 (1934) 194 [illegitimate: later homonym]; non *Helotium macrosporum* Peck, *Ann. Rep. State Bot.* 26 (1874) 82.

Hymenoscyphus fucatus has relatively long and wide spores. Two other non-lignicolous species of the 'fructigenus-group', viz. *H. dearnessii* (Ellis & Everh.) Kuntze and *H. suspectus* (Nyl.) Hengstm., have ascospores which are similar in length, but narrower than those of *H. fucatus*, while their asci are narrower than those of *H. fucatus* and do not arise from croziers.

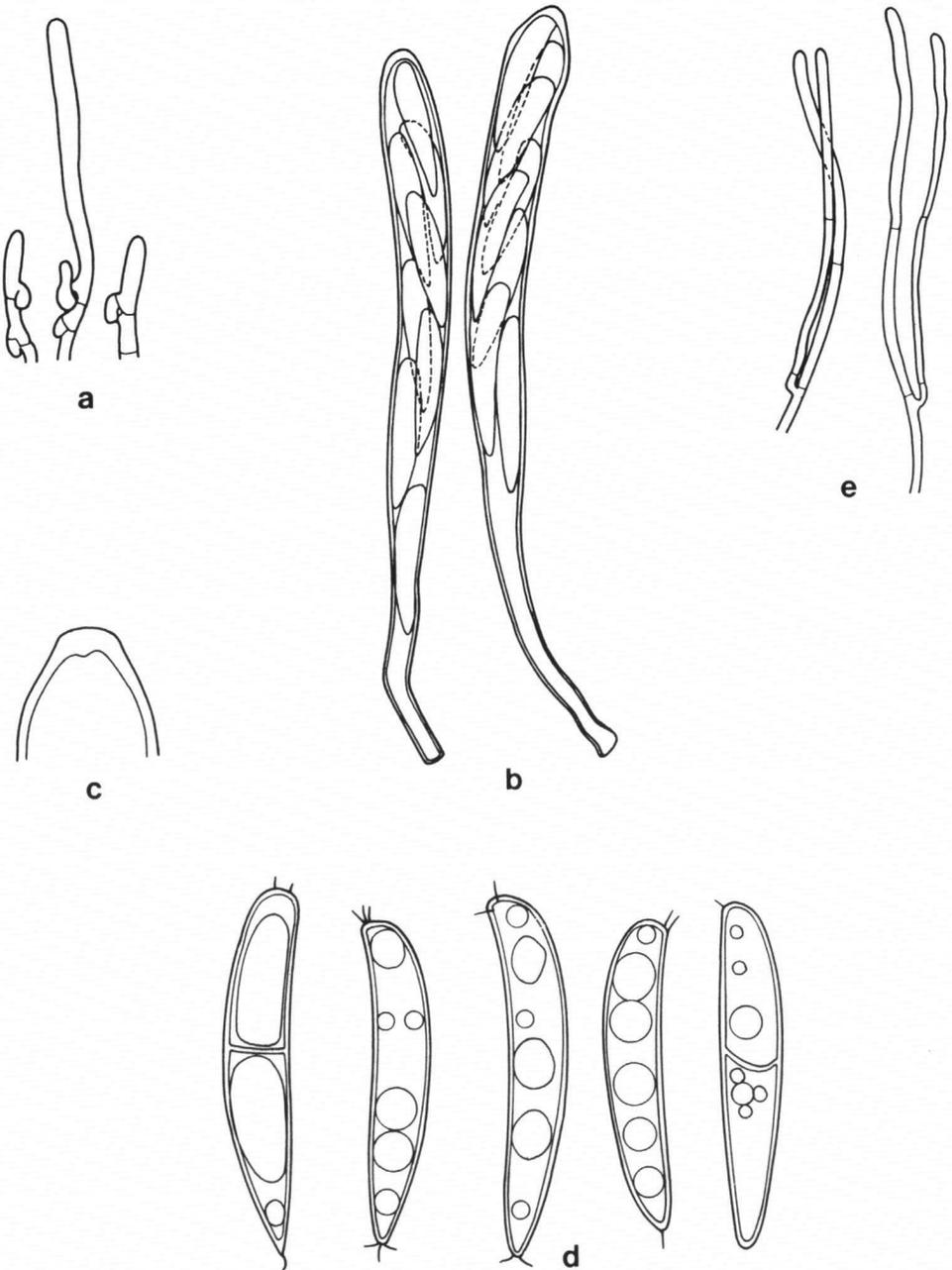


Fig. 1. *Hymenoscyphus fucatus* var. *fucatus* (from *Krieglsteiner*, 23 July 1986): a. young asci ($\times 750$), b. mature asci ($\times 750$), c. ascus apex ($\times 1500$), d. ascospores ($\times 1500$), e. paraphyses ($\times 750$).

For an extensive description, an enumeration of the examined collections and further comments, see under the distinguished varieties.

KEY TO THE VARIETIES

- a. Asci 83–101 × 9–11 μm. Ascospores 23–35 μm long (average length < 27.5 μm) and 4–5 μm wide b. *H. fucatus* var. *badensis*
 b. Asci 113–136 × 10–14 μm. Ascospores 24–36 μm long (average length > 27.4 μm) and 4–6 μm wide a. *H. fucatus* var. *fucatus*

1a. *Hymenoscyphus fucatus* var. *fucatus* — Fig. 1

Apothecial morphology — Apothecia stipitate-cupulate, up to about 1 mm high when rehydrated, loosely clustered, rarely mutually grown together at the base, erumpent through (locally blackened) epidermis or superficial on decorticated parts of the substratum; some dozens up to more than a hundred apothecia over a length of 10 cm of the substratal stem. Cupule saucer-shaped, up to 0.8 mm in diameter when rehydrated. Receptacle and stipe smooth to subpruinose. Stipe cylindrical to obconical, up to about 0.8 mm when rehydrated, about as long as the diameter of the cupule.

Anatomy — Asci [$k = 1$, $n = 10$] cylindric-obconical to cylindric-clavate, 113–136 μm long [average length ± standard deviation: 123.8 ± 8.2 μm], 10–12(–14) μm wide [average width ± standard deviation: 11.1 ± 0.7 μm], with length/width-ratio of 9.7–13.7 [average ratio ± standard deviation: 11.2 ± 1.2], 8-spored, originating from croziers; apex truncated conical; annulus turning medium blue in Melzer's reagent. Ascospores [$k = 2$, $n = 20$] obovoid-fusiform to ellipsoid-fusiform, sometimes almost cylindrical, straight to slightly curved, 24–36 μm long [29.1 ± 2.7 μm], 4–6 μm wide [5.0 ± 0.3 μm], with length/width-ratio of 4.8–7.2 [5.8 ± 0.6], 1-celled when mature, afterwards 2-celled, hyaline, thin-walled, smooth, provided with 1–2 large or about 4–6 medium-sized and occasionally some small guttules, obliquely biseriate, at apex and base mostly provided with 1–2 (–3) short, up to 1.5(–2.0) μm long, straight or slightly curved setulae; apex rounded to abaxially angulate, sometimes beaked; base (almost) acute, sometimes rather acute. Paraphyses [$k = 1$, $n = 10$] subcylindrical, 1.5–2.0 μm wide, at the top often slightly wider than at the bottom, hyaline, according to Baral (in litt.) provided with highly refractive guttules when fresh, with 3–5 septa in the uppermost 100 μm, forked about half-way (sometimes also in upper half); terminal cell 22–40 μm long [29.0 ± 6.0 μm], 0.9–1.5 times as long as the subterminal cell [1.3 ± 0.2], with rounded tip; subterminal cell 18–30 μm long [23.4 ± 4.6 μm]. Subhymenium up to about 60 μm thick, composed of branched and strongly winding hyphae, partly provided with anastomosing arches. Exciple 2-layered. Medulla a thin layer of textura porrecta with about 2–4 μm wide, thin-walled hyphae. Cortex consisting of textura prismatica; hyphae 4–10 μm wide but covering hyphae only 2–4 μm wide, thin-walled, running parallel with or oriented at a low angle to the excipular surface, not embedded in a gelatinous matrix; individual cells about 8–23 μm long.

Occurrence — Saprotrophic on stems of *Polygonum lapathifolium*, *P. robustius*, and possibly other herbs; July–September.

Collection examined. GERMANY: Baden-Württemberg, Schwäbisch-Hall, Teurershof, MTB 6824/3, in rush zone of a pond, on dead stem of *Polygonum lapathifolium*, 23 July 1986, L. Krieglsteiner s.n. (herb. Baral 3057).

The typical variety of *H. fucatus* has been fully redescribed and illustrated by White (1944: 609–613, figs. 25–30). According to him its asci measure $118\text{--}135 \times 12\text{--}15 \mu\text{m}$ and its ascospores $24\text{--}34 \times 5\text{--}6.8 \mu\text{m}$, at each end beset with one to several small, inconspicuous 'cilium-like processes'. It is noteworthy that these setulae have not been mentioned or depicted by Dennis (1956: 79, fig. 69G), who also examined an isotype-collection.

Hymenoscyphus fucatus has originally been found and collected in Shropshire, England, on dead stems of *Polygonum* lying in water.

A probable record in 1923 in the Czech Republic can be deduced from Svrček (1985: 159, 188, pl. IX, fig. 4). For, in his revision of the taxa described by Velenovský in the genus *Helotium*, he states that the lectotype collection of *Helotium macrosporum* Velen., found on stems of *Cicerbita alpina* in Bohemia, is identical with *H. scutula* var. *fucatus*. White (1944: 610–613) collected it in both 1936 and 1938 in the same locality in New York State, USA, on old stems of *Polygonum robustius* lying in a swamp. Pallo collected the species in 1975 on a herbaceous dicotyledon stem in the Western Caucasus, Russia (Vaasma et al., 1986: 26). Baral (in Baral & Krieglsteiner, 1985: 128) reported its occurrence in 1975 on stems of *Solidago* sp. in Baden-Württemberg, Germany (no herbarium material preserved). Blank has found *H. fucatus* sensu Baral in 1987 on a stem of *Solanum dulcamare* in Thayngen, Switzerland (not preserved; Baral in litt.). Weber (1992: 28, 122) has also examined a Swiss collection of it, found by Baral & Blank in 1990 on a dicotyledon stem in the canton Graubünden and determined by Baral (herb. Baral 4193). As to the last three records it has to be pointed out, however, that *H. fucatus* sensu Baral differs from the type in lacking arches at the ascus base (Baral in litt.; Weber, 1992: 121). Another alleged find was from Germany in 1989 on stems of *Aruncus silvester* in Bavaria, but the description and figures of this material show neither croziers or arches nor setulae (Engel, 1993: 5, 8; Engel & Hanff, 1993: 44).

A supposed record in the Netherlands (prov. Flevoland, Abbertbos, 10 Oct. 1981; herb. Swart-Velthuyzen 367) has turned out to represent typical *H. scutula*.

1b. *Hymenoscyphus fucatus* var. *badensis* Hengstm., var. nov. — Fig. 2

A varietate typica differt ascis minoribus, $83\text{--}101 \times 9\text{--}10 \mu\text{m}$, et ascosporis etiam paulo minoribus, $(23\text{--})25\text{--}31\text{--}(35) \mu\text{m}$ longis.

Apothecial morphology — Apothecia stipitate-cupulate, 0.4–1.5 mm high when rehydrated, scattered, erumpent through substratal epidermis; about 60 fruit-bodies on 6 cm long fragment of a leaf. Cupule cup- to saucer-shaped, 0.2–0.9 mm in diameter when rehydrated, with slightly raised to flat margin. Hymenium slightly concave to flat, light yellow when dried. Receptacle pale yellow when dried, subpruinose. Stipe cylindrical, up to 1.3 mm long when rehydrated, about as long as or longer than the diameter of the disc, 0.1–0.2 mm across, pale yellow when dried, subpruinose.

Anatomy — Asci [$k = 1$, $n = 10$] cylindric-clavate to obconical-clavate, $83\text{--}101 \mu\text{m}$ long [$91.0 \pm 5.9 \mu\text{m}$], $9\text{--}10 \mu\text{m}$ wide [$9.7 \pm 0.5 \mu\text{m}$], with length/width-ratio of 8.4–11.3 [9.5 ± 0.9], 8-spored, originating from croziers but anastomosing arches usually not

remaining visible at mature asci; apex more or less bullate and with thickened wall when immature, but slightly truncated conical and with hardly thickened wall when mature; annulus turning medium blue in Melzer's reagent. Ascospores [$k = 1$, $n = 20$] obovoid-fusiform to ellipsoid-fusiform, rarely subcylindrical, straight or slightly curved, bilaterally symmetrical, (23–)25–31(–35) μm long [$26.9 \pm 1.9 \mu\text{m}$], 4–5 μm wide [$4.6 \pm 0.2 \mu\text{m}$], with length/width-ratio of (5.1–)5.3–7.0(–8.8) [5.8 ± 0.5], 1-celled, hyaline, obliquely

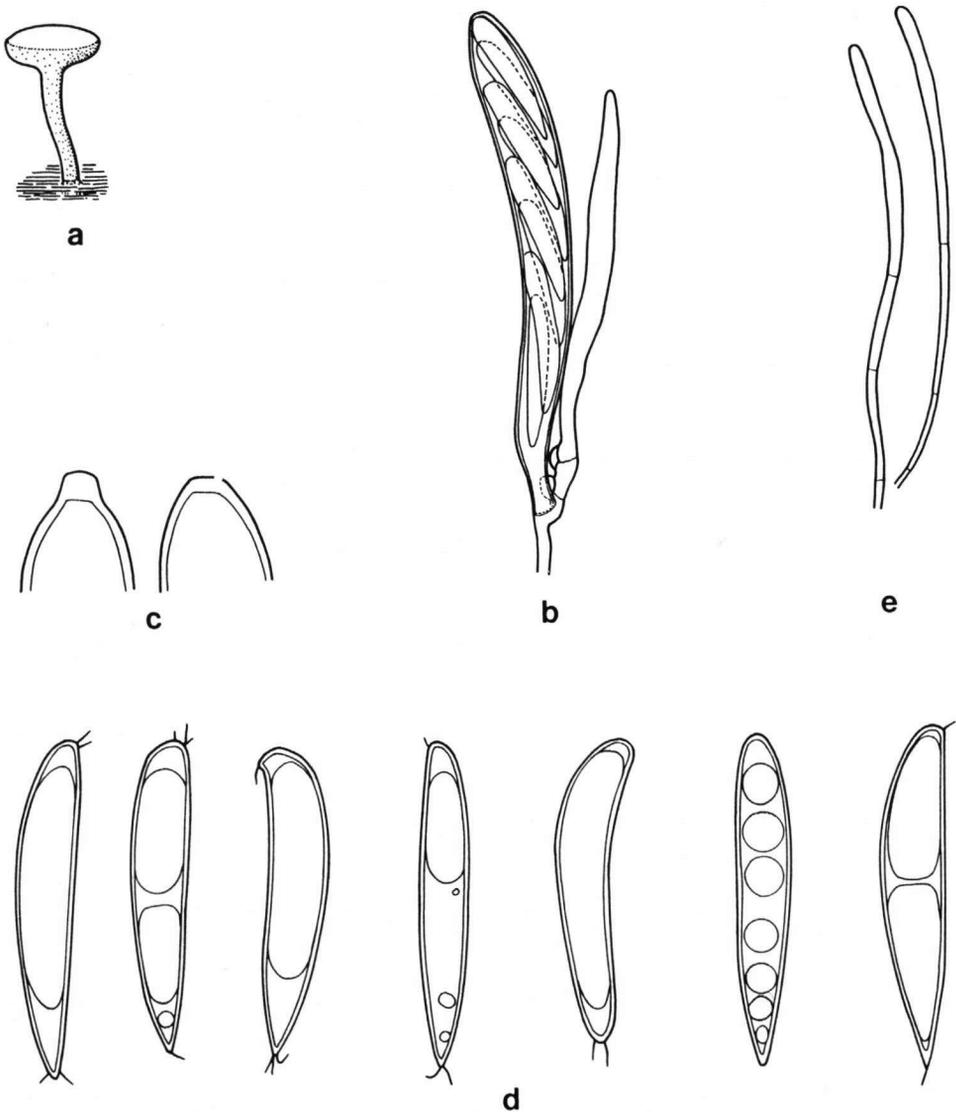


Fig. 2. *Hymenoscyphus fucatus* var. *badensis*, holotype: a. habit ($\times 20$), b. asci ($\times 750$), c. ascus apices in different stages ($\times 500$), d. ascospores ($\times 1500$), e. paraphyses ($\times 750$).

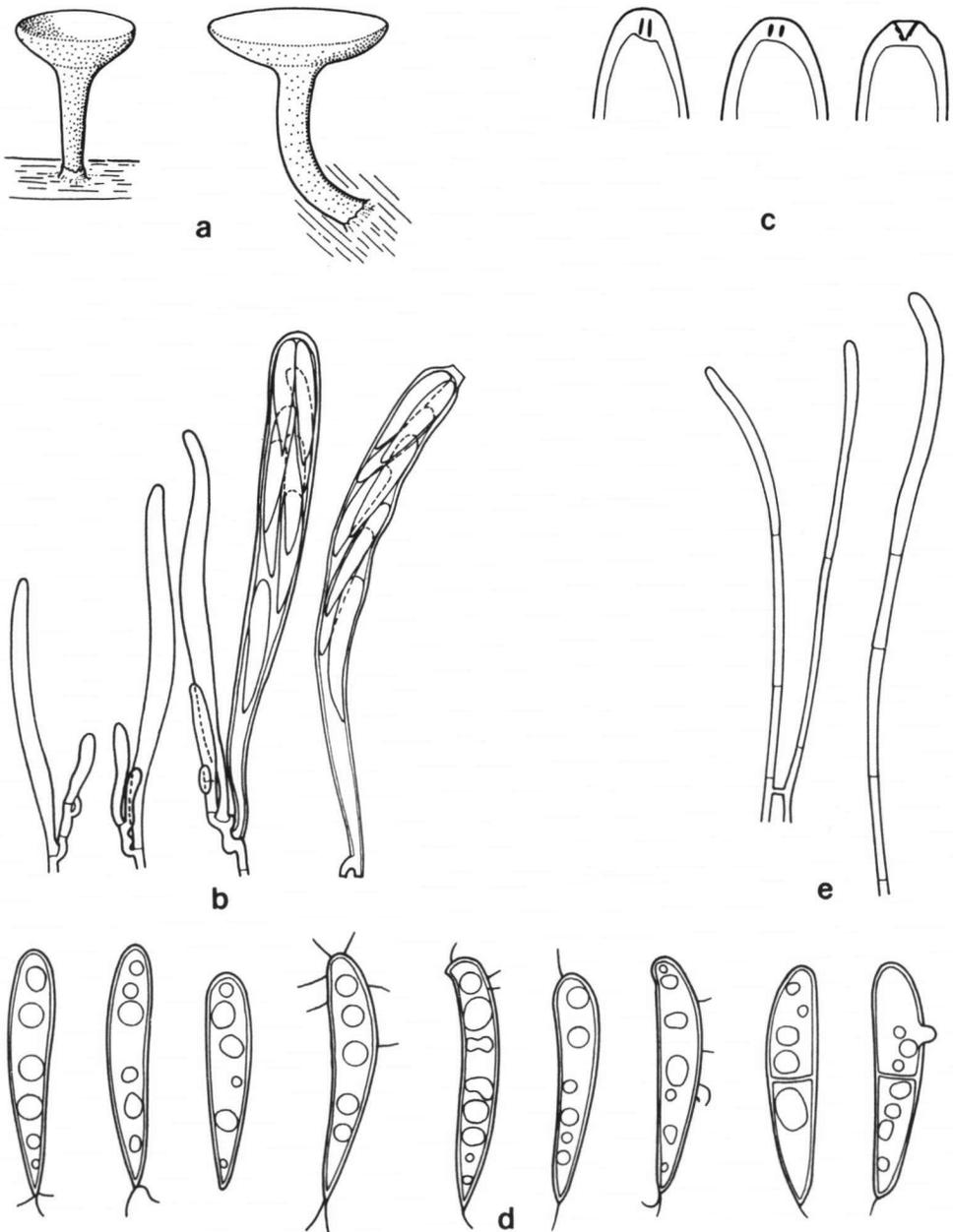


Fig. 3. *Hymenoscyphus scutuloides*, holotype: a. habit ($\times 20$), b. asci ($\times 750$), c. ascus apices (stained with iodine) in different stages ($\times 1500$), d. ascospores ($\times 1500$), e. paraphyses ($\times 750$).

biseriate, provided with 1–2 large and possibly one or a few small guttules when mature, afterwards with increasing number (up to about eight) of shrinking guttules and finally slightly granulose to optically empty, thin- and smooth-walled, at apex and base frequently (at least about 50% of the extremities) provided with 1–3 tiny setulae; apex blunt or rounded to abaxially angulate or sometimes laterally beaked (not hooked); base acute; setulae at most 2.5 μm long, extremely thin, mostly curved. Paraphyses [k = 1, n = 10] cylindric-obconical, about 1.0 μm wide near the base and up to 1.5–2.0 μm wide at the tip, rather scarce, hyaline, according to Baral (in litt.) with highly refractive guttules (only when fresh), provided with 2–3(–4) septa in the uppermost 80 μm , sometimes forked or anastomosing in the lower half; terminal cell 24–50(–60) μm long [$39.6 \pm 9.1 \mu\text{m}$], 1.0–2.8 times as long as the subterminal cell [1.8 ± 0.5], with rounded tip; subterminal cell 14–31 μm long [$22.5 \pm 5.0 \mu\text{m}$]. Subhymenium above the stipe up to about 25 μm thick, consisting of 2–3 μm wide, strongly branched and winding hyphae, partly provided with arches. Exciple 2-layered. Medulla up to about 10 μm thick, a *textura porrecta* with 1–2 μm wide, thin-walled hyphae. Cortex up to about 30 μm thick, a *textura prismatica*; hyphae about 5–10 μm wide and near the edge about 2–3 μm wide but covering hyphae only about 1–2 μm wide, thin-walled, almost parallel with the excipular surface, not embedded in a gelatinous matrix; individual cells about 11–24 μm long.

Occurrence — Saprotrophic on sedge-like leaf; October.

Collection examined. GERMANY: Baden-Württemberg, Weingartener Moor (Oberrheinebene), MTB 6916–17, 113 m, reed-land, on leaf of '*Carex*' (according to finder), 1 Oct. 1986, W. Winterhoff 86570 (holotype; herb. Baral).

The asci of this variety are significantly smaller than those of the var. *fucatus*. Moreover, the ascospores tend to be smaller, and their average length is significantly smaller than that of the typical variety. The difference in spore size is even more convincing if we look at the dimensions of turgescient spores as found by Baral, viz. 23–30(–33) \times 4.5–5.5 μm in the latter collection versus (28–)30–38(–40) \times 5.5–7 μm in the collection of var. *fucatus* (Baral in litt.).

2. *Hymenoscyphus scutuloides* Hengstm., *spec. nov.* — Figs. 3, 4

?*Hymenoscyphus scutula* (Pers.: Fr.) W. Phill. sensu Breitenbach & Kränzlin, *Pilze Schweiz* 1 (1981) 170–171, pro parte.

Apothecia stipitato-cupulata, erumpentia, stipite longitudine diametrum cupulae circiter aequanti vel paulo superanti. Asci (80–)85–102(–105) \times 8–9(–10) μm , inoperculati, octospori, ex uncis orti; apex plus minusve truncate conicus, annulo iodo medie caerulescente. Ascosporae irregulariter obovoideo-fusiformes ut in *Hymenoscypho scutula*, (18–)20–27 \times 3–4 μm , maturitate continuae, demum (uni-) septatae, hyalinae, guttulate, in asci parte inferiore uniseriatae, sursum oblique biseriatae, parietibus tenuibus laevibusque, ad apicem basemque vulgo 1–3(–4) setis filiformibus plerumque 1–3 μm longis instructae; apex obtusus vel rotundatus usque lateraliter angulatus vel paulo uncutus, interdum sat acutus; basis acuta vel subacuta. Paraphyses cylindratae vel cylindrato-obconicae, longitudine ascos aequantes, inferne 1.0–2.0 μm , superne 2.0–3.0 μm latae, septatae, in dimidio inferiore aliquando furcatae vel anastomosantes. Excipulum bistratum. Medulla e *textura porrecta* constans. Cortex e *textura prismatica* constans, hyphis parallelis vel sub angulo parvo ad paginam excipuli currentibus, in gelatina haud inclusis, parietibus tenuibus vel paulo incrassatis.

Occurrit ad caules emortuos herbarum et Rubi sp.; mensibus Augusti–Septembris.

Holotypus: 'Netherlands, Winterswijk, 20 Sept. 1953, R. A. Maas Geesteranus 9510' (L).

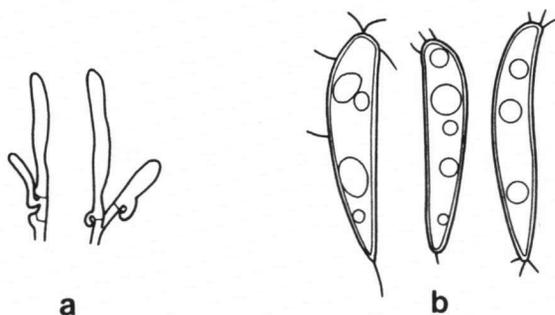


Fig. 4. *Hymenoscyphus scutuloides* (from Huijsman 55.H-99), a. young asci ($\times 750$), b. ascospores ($\times 1500$).

Apothecial morphology — Apothecia stipitate-cupulate, up to 2 mm high when rehydrated, concolorous light yellow when dry, scattered, erumpent through substratal epidermis; up to more than a hundred fruit-bodies over a length of 10 cm of the substratal stem. Cupule cup- to saucer-shaped, up to 1.5 mm in diameter when rehydrated, with slightly raised to entirely plane margin. Hymenium concave to flat. Receptacle smooth to subpruinose, occasionally slightly radially fibrous. Stipe cylindrical to obconical, up to 1.5 mm long, about as long as or slightly longer than the diameter of the cupule, up to 0.3 mm across, smooth to subpruinose, at the base sometimes surrounded by a small collaret of epidermal tissue.

Anatomy — Asci [$k = 1$, $n = 10$] obconical to cylindric-obconical, (80–)85–102 (–105) μm long [$96.0 \pm 4.9 \mu\text{m}$], 8–9(–10) μm wide [$8.6 \pm 0.5 \mu\text{m}$], with length/width-ratio of 9.6–12.9 [11.2 ± 1.0], 8-spored, originating from croziers and the resulting anastomosing arches at the base of the asci generally remaining visible; apex more or less truncated conical, thick-walled around the pore; annulus turning medium blue in Melzer's reagent, especially in the central part. Ascospores [$k = 1$, $n = 20$] bilaterally symmetrical (asymmetrical in side-view), obovoid-fusiform, flattened on one side or slightly curved, (18–)20–27 μm long [$21.7 \pm 1.5 \mu\text{m}$], 3–4 μm wide [$3.6 \pm 0.3 \mu\text{m}$], with length/width-ratio of 5.1–7.7 [6.1 ± 0.7], 1-celled, a few (older ones) 2-celled, hyaline, guttulate, in the lower part of the ascus uniseriate and upwards passing into obliquely biseriate, thin-walled, smooth, at apex and base mostly provided with 1–3(–4) setulae; apex blunt or rounded to oblique-angulate or slightly hooked, occasionally rather acute; base acute or subacute; setulae filiform, 1.0–3.0(–4.0) μm long, sometimes also adhering at the flanks of the spore; germination observed in 2-celled spores, laterally from the upper cell. Paraphyses [$k = 1$, $n = 10$] cylindrical or upwards slightly widening, equalling the asci, below 1.0–2.0 μm and above 2.0–3.0 μm wide, provided with 2–4 septa in the uppermost 100 μm , occasionally forked or anastomosing in the lower half, somewhat granulose, partly staining blue with cotton blue; terminal cell 20–58 μm long [$38.0 \pm 11.5 \mu\text{m}$], 0.7–4.9 times as long as the subterminal cell [2.3 ± 1.3], with rounded tip; subterminal cell 11–35 μm long [$20.0 \pm 7.8 \mu\text{m}$]. Subhymenium in the central part up to about 50 μm thick. Exciple 2-layered. Medulla near the stipe up to about 20 μm thick, composed of parallel, radially running, 2–4 μm wide, thin-walled hyphae (textura porrecta). Cortex

about 60 µm thick, inclusive of outer covering layer, a *textura prismatica*; hyphae parallel with or oriented at a low angle to the excipular surface, not embedded in a gelatinous matrix, with thin or slightly thickened walls (up to about 1.0 µm), 5–9 µm wide but covering hyphae thin-walled and only about 3 µm wide; separate cells about 5–30 µm long.

Occurrence — Saprotrophic on herbaceous stems and on canes of *Rubus* sp.; August–September.

Collections examined. NETHERLANDS: prov. Gelderland, Winterswijk, Bekendelle, on dead herbaceous stem, 20 Sept. 1953, R.A. Maas *Geesteranus* 9510 (holotype; L). — SWITZERLAND: canton Luzern, Schüpfheim, on dead cane of *Rubus* sp., 21 Aug. 1955, H. S. C. Huijsman 55.H-99 (L).

An indication of the shape and colour of the apothecia in fresh condition is given in notes accompanying the Swiss collection, which state: [apothecia] ‘young deeply cup-shaped, later on more flat, but long time remaining cup-shaped, lastly flat; colour very light cream-lemon; disc slightly darker than rest.’

The type collection, originally identified as ‘*Helotium scutula* (Pers. ex Fr.) Karst.’, has been examined by Dr. K.P. Dumont (New York Botanical Garden) in March 1981, but was not annotated by him.

As already expressed by its name, *H. scutuloides* shows a great resemblance to *H. scutula*. The latter species, however, has larger asci (120–142 × 9–11 µm) which do not originate from croziers, while its spores are slightly broader (4–5 µm) and usually possess only one setula at each end. In view of the forementioned resemblance it is quite possible that *H. scutula* in the sense of some authors includes *H. scutuloides* as well. This seems to be the case in Breitenbach & Kränzlin (1981: 170–171, No. 190). Their description and figures of *H. scutula* are mainly based on a collection, found on herbaceous stems in the Swiss canton Luzern (compare examined collection!) and probably representing *H. scutuloides*. The presence of anastomosing arches at the base of the asci is not mentioned, but suggested by their fig. 190B. Perhaps *H. scutuloides* also has been found by Berthet (1964: 40–41, 101) on dead stems of *Solidago canadensis* in France, for the relevant collection of ‘*H. scutula*’ is described to be of the pleurohynchous type.

A related species, also resembling *H. scutula* and with asci said to be produced from ‘tiny’ croziers, has been described by Dumont & Carpenter (1982: 582–587, figs. 5, 6) under the name *H. ‘affin. scutululus’*. This species, however, found on various substrates in the neotropics, has obviously pigmented paraphyses and covering hyphae, while its spores are only 2–3(–4) µm wide, short-setulose at the base and shaped like those of *H. serotinus*.

3. *Hymenoscyphus menthae* (W. Phill.) Baral — Fig. 5

Helotium menthae W. Phill., *Elv. brit.* (4) (1881) n. 188 [invalid: nomen nudum]; W. Phill. in W. Phill. & Plowr., *Grevillea* 10 (1881) 69. (basionym). — *Hymenoscypha scutula* var. *menthae* (W. Phill.) W. Phill., *Man. Brit. Discomyc.* (1887) 137. — *Phialea scutula* var. *menthae* (W. Phill.) Sacc., *Syll. Fung.* 8 (1889) 266. — *Helotium scutula* var. *menthae* (W. Phill.) Rehm in Rabenh. *Krypt.-Fl.* ed. 2, 1 (3) (1893) 793. — *Helotium scutula* forma *menthae* (W. Phill.) Masec, *Brit. Fung.-fl.* 4 (1895) 254. — *Hymenoscyphus menthae* (W. Phill.) Baral in Baral & Krieglsteiner, *Beih. Z. Mykol.* 6 (1985) 131 [bibliographic error of citation of basionym].

Misapplied? *Helotium scutula* var. *solani* (P. Karst.) P. Karst. sensu Dennis (1956: 78).

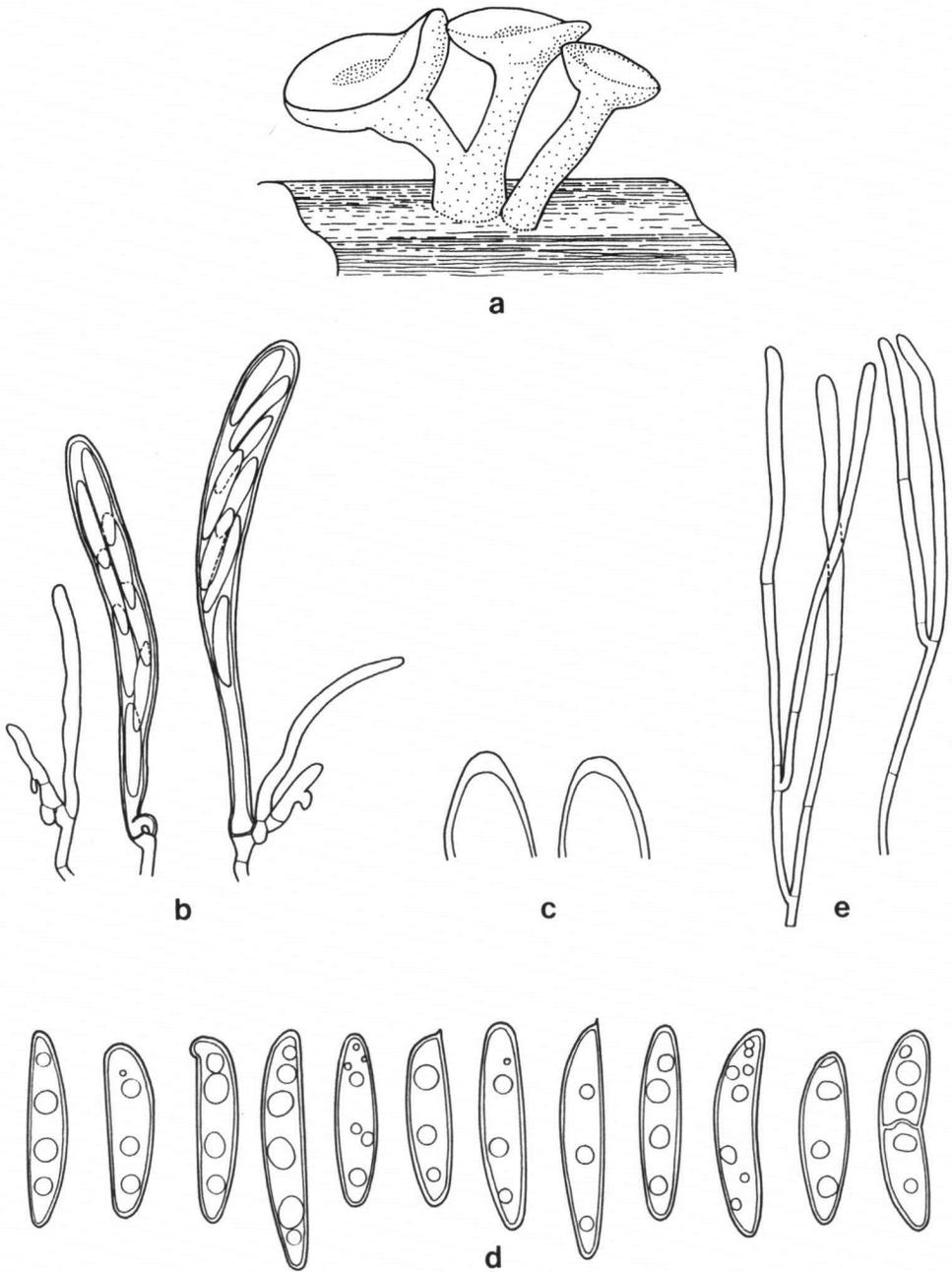


Fig. 5. *Hymenoscyphus menthae* (from Maas Geesteranus 9046), a. habit ($\times 20$), b. asci ($\times 750$), c. ascus apices ($\times 1500$), d. ascospores ($\times 1500$), e. paraphyses ($\times 750$).

Apothecial morphology — Apothecia stipitate-cupulate, variable in size, up to 6 mm high when rehydrated, concolorous light ochraceous yellow when dry, scattered, gregarious or clustered, rarely mutually grown together along whole length of the stipe, erumpent through substratal epidermis or superficial on decorticated parts, scanty to very numerous (up to more than a thousand specimens over a length of 10 cm of the substratal stem). Cupule cup- to saucer-shaped, up to more than 1.5 mm in diameter when rehydrated, when young with more or less raised margin. Hymenium concave to flat, young orange-yellow when fresh. Receptacle concolorous with hymenium, smooth to subpruinose. Stipe cylindrical to obconical, up to about 5×0.6 mm when rehydrated, about as long as or (much) longer than the diameter of the cupule, more or less pruinose, at the base occasionally surrounded by a small, often dark-coloured collaret of epidermal tissue.

Anatomy — Asci [$k = 1$, $n = 10$] (cylindric-)obconical to cylindric-clavate, (72–)76–90 μm long [$82.8 \pm 5.1 \mu\text{m}$], 7–9 μm wide [$8.3 \pm 0.5 \mu\text{m}$], with length/width-ratio of (8.4–)9.1–11.1(–11.6) [10.0 ± 0.7], 8-spored, originating from croziers of which the arches remain visible at the base of the asci; apex more or less truncated conical, thick-walled around the pore; annulus turning blue in Melzer's reagent, especially in the middle part. Ascospores [$k = 1$, $n = 20$] axially to bilaterally symmetrical (in the latter case asymmetrical in side-view), fusiform-ellipsoidal, ellipsoidal, obovoidal or ellipsoid-fusiform to obovoid-fusiform, straight to slightly curved, 14–21 μm long [$16.5 \pm 1.7 \mu\text{m}$], 3–4(–5) μm wide [$3.7 \pm 0.2 \mu\text{m}$], with length/width-ratio of (3.4–)3.6–5.5(–5.9) [4.4 ± 0.5], 1-celled, only a few 2-celled, hyaline, guttulate, obliquely biseriata, thin-walled, smooth, without obvious setulae but occasionally apiculate at apex or base; apex blunt or rounded to oblique-angulate, occasionally rather acute; base blunt to subacute. Paraphyses [$k = 1$, $n = 10$] obconical, equalling the asci, below 1.0–2.0 μm and above 2.0–3.0 μm wide, provided with (1–)2–4 septa in the uppermost 80 μm , often with one or two furcations in the lower half; terminal cell (26–)31–50(–65) μm long [$41.3 \pm 6.2 \mu\text{m}$], 1.2–2.5 times as long as the subterminal cell [1.7 ± 0.4], with rounded tip; subterminal cell 18–31 μm long [$24.3 \pm 3.7 \mu\text{m}$]. Subhymenium in the central part up to about 65 μm thick. Exciple 2-layered. Medulla not sharply defined from subhymenium and cortex, near the stipe about 35–50 μm thick, consisting of textura porrecta with 2–4 μm wide, thin-walled hyphae. Cortex about 40–60 μm thick, a textura prismatica, without clearly differentiated covering layer; hyphae 4–13 μm wide, parallel with or oriented at a low angle (at most 45°) to the excipular surface, not embedded in a gelatinous matrix, with thin or slightly thickened walls; separate cells about 8–40 μm long.

Occurrence — Saprotrophic on stems of *Polygonum cuspidatum* and other herbs and on canes of *Rubus* sp.; September–October.

Collections examined. NETHERLANDS: prov. Drente, Ruinen, Wijken van Eleveld, on dead cane of *Rubus* sp., 2 Oct. 1983, L. Jalink & M. M. Nauta 229 (WBS); prov. Utrecht, Baarn, Lage-Vuursche, on dead herbaceous stems, 1 Sept. 1957, J. Daams 306 (L); prov. Zuid-Holland, Warmond, estate 'Huys te Warmont', on dead stems of *Polygonum cuspidatum*, 24 Sept. 1952, R. A. Maas Geesteranus 9046 (L).

With the understanding that in relevant literature nothing is said about the presence or absence of croziers, the above description agrees well with the original description by Phillips (in Phillips & Plowright, 1881: 69) and with the description and figures of an authentic collection of *Helotium menthae* in herb. Cooke, as given by Dennis (1956: 78, fig. 71E). According to Dennis (1956: 78) the latter material, at the time sent by Phillips to

Cooke, is 'evidently the type collection' but this seems inconsistent with the fact that *Helotium menthae* is formally based on *Elvellacei britannici* 188. At the same place Dennis has put *Helotium (Hymenoscypha) scutula* var. *menthae* '(Phill.) Boud.' into the synonymy of *Helotium scutula* 'var. *solani* Karst. ... 1870'.⁶ I doubt whether this is justified. Firstly, the asci of var. *menthae* are up to 90 µm long, whereas the ascus of var. *solani*, as depicted by Dennis (1956: fig. 71B) from material in herb. Karsten, is more than 110 µm long. Secondly, the annulus of var. *menthae* always turns blue in iodine, whereas var. *solani* has 'thecae ... apice iodo non tinctae' (Karsten, 1870: 234). Afterwards Dennis has possibly abandoned the forementioned synonymy, for, in his rearrangement of the genus *Hymenoscyphus* (Dennis, 1964: 73–78) he does mention *H. scutula* var. *menthae* whereas var. *solani*, whose varietal epithet has priority in case of synonymy, has been omitted. In my opinion var. *solani* sensu Karsten is quite similar to, if not identical with *H. consobrinus* (Boud.) Hengstm., also because of its 'fusoid-elongate' spores which are generally uniseptate according to Dennis (1956: fig. 71B).

Assuming that all of the British collections mentioned by Dennis (1956: 78) represent 'var. *menthae*' sensu stricto, then this taxon has been recorded in Great Britain on stems of *Mentha sativa* [= *M. × verticillata*], *Teucrium scorodonia*, *Solanum tuberosum*, *Campanula latifolia* and *Polygonum* sp. (cf. Dennis, 1978: 136). The record on *Solanum tuberosum* seems also to have been referred to in Ellis & Ellis (1985: 425–426, pl. 161, fig. 1672). Kirk & Spooner (1984: 532) have reported on two findings of *H. 'scutululus'* var. *solani* in 1980 on *Urtica dioica* and unidentified herbaceous stems on Arran, Scotland. Dr. B.M. Spooner (in litt.) has kindly informed me, that 'the interpretation followed in the Arran account is that of Dennis (1956), as figured (fig. 71B) from Karsten's material' [of var. *solani* s.str.!]. He added, that the Arran collection 'may differ from var. *solani* as described by Dennis [p. 78; i.e. var. *menthae* s.str.!] in having a rather white-tomentose stipe base [characteristic of *H. consobrinus*, as already mentioned by Dennis (1956: 79)] and in being on *Urtica*.' All in all, at least the Arran collection seems to show more resemblance to *H. consobrinus* than to *H. menthae* as described in this article.

Baral (in Baral & Krieglsteiner, 1985: 131–132) reported several findings of *H. menthae* in Baden-Württemberg, Germany, viz. on *Polygonum cuspidatum* and *?piperatum*, *Scrophularia nodosa*, *Lysimachia vulgaris*, *Lycopus europaeus* and *Rubus idaeus*. Strangely enough, according to Baral (in litt.) *H. menthae* always has a white hymenium, whereas Phillips (1887: 137) speaks of a bright yellow disc. In 1914 and 1917 '*Helotium scutula* var. *menthae*' was found by P. Vogel in Mark Brandenburg, Germany, on stems of *Mentha piperita* and has been distributed within two German exsiccata series, viz. Sydow's *Mycotheca germanica* (as No. 1350) and Vogel's *Flora der Mark* (s.n.) respectively. However, the examined two copies of each of these exsiccata (L) all represent var. *scutula*. Exactly the same misapplication occurs in Petrak's *Flora Bohemiae et Moraviae exsiccata*, II. Serie, I. Abteilung, Lfg. 5, Nr. 243, collected by F. Petrak in 1911 on

⁶) *Helotium scutula* subsp. [!] *solani* P. Karst., *Symb. Mycol. fenn.* [1] (1870) 234 = *Helotium scutula* var. *solani* (P. Karst.) P. Karst., *Mycol. fenn.* 1 (1871) 111 = *Helotium scutula* forma *solani* (P. Karst.) Rehm in Rabenh., *Krypt.-Fl.* ed. 2, 1 (3) (1893) 793 [invalid: unintentional stat. nov.; only (erroneous) citation of Karsten's 'f. *Solani*' from 1871] = *Hymenoscyphus scutula* var. *solani* (P. Karst.) S. Ahmad, *Ascomyc. Pakistan* 1 (1978) 207 [neither by Thind & Sharma, *Nova Hedwigia* 32 (1980) 128, nor by Kirk & Spooner, *Kew Bull.* 38 (1984) 532, validly published as comb. nov. (both without basionym); superfluous combination by Korf & Zhuang, *Mycotaxon* 22 (1985) 500].

Mentha longifolia (examined specimen: L; cf. Samuels, 1985: 46). It is evident, that Vogel and Petrak wrongly used the substrate as an essential distinguishing feature. Likewise Oudemans (1890: 315) at first thought to deal with *H. scutula* var. *menthae* when he examined a *Hymenoscyphus* found in 1889 on stems of *Mentha aquatica* in the botanical garden of Amsterdam. Examination of authentic specimens of var. *menthae*, however, gave him certainty that the fungus of Phillips differed from his one, not only by the absence of cilium-like appendages, but also by the size and shape of the spores and the quantity of guttules.

From the Netherlands only the three indicated collections could be ascribed to *H. menthae*. Yet I examined several collections labelled as *Helotium/Hymenoscyphus scutula* var. *menthae* or var. *solani* (herb. Swart-Velthuyzen 210, 357; L ex herb. Ernste 937/82, 949/82), but these all belong to *H. consobrinus*, just like two Belgian collections originally determined as *Helotium scutula* var. *menthae* (herb. Swart-Velthuyzen 272; herb. Batten 839) and a Belgian collection of '*Helotium scutula* f. *solani*' (BR coll. V. Mouton).

Outside (Western) Europe *H. menthae* probably only has been recorded under the name '*H. scutula* var. *solani*' in the sense of Dennis (1956: 78). Ahmad (1978: 207–208) has collected this taxon in 1953 and 1959 in Pakistan. Thind & Sharma (1980: 128–129, figs. 3, 4) found it 'growing luxuriantly on *Polygonum* stems [i. a. *P. amplexicaule*] in the North-Western Himalayas', India. Korf collected it in 1981 on unidentified stems and on *Polygonum cuspidatum* in Sichuan, China (Korf & Zhuang, 1985: 500). According to Lizoñ (1992: 45), however, the latter collection represents (the typical variety of) *H. scutula*. Furthermore, Thind & Sharma (1980: 129) mentioned the occurrence of *H. 'scutula* var. *solani*' in i. a. North America, but without giving any reference although this taxon has not been listed by Farr et al. (1989).

It need not be said that only a careful re-examination of relevant collections can give more certainty about the real occurrence and distribution of this little known species.

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REFERENCES

- Ahmad, S. 1978. Ascomycetes of Pakistan. Part 1. Lahore. (Biol. Soc. Pakistan, Monograph 7.)
Arendholz, W. R. 1979. Morphologisch-taxonomische Untersuchungen an blattbewohnenden Ascomyceten aus der Ordnung der Helotiales. Hamburg.
Arx, J. A. von. 1967. Pilzkunde. Ein kurzer Abriss der Mykologie unter besonderer Berücksichtigung der Pilze in Reinkultur. Lehre.
Baral, H. O. & G. J. Krieglsteiner. 1985. Bausteine zu einer Askomyzeten-Flora der Bundesrepublik Deutschland: In Süddeutschland gefundene Inoperculate Discomycyten mit taxonomischen, ökologischen, chorologischen Hinweisen und einer Farbtafel. Beih. Z. Mykol. 6: 1–160.
Berthet, P. 1964. Essai biotaxinomique sur les Discomycètes. Lyon.

- Boidin, J. 1971. Nuclear behavior in the mycelium and the evolution of the Basidiomycetes. In: R. H. Petersen (ed.), *Evolution in the higher Basidiomycetes, An international symposium*: 129–148. Knoxville.
- Breitenbach, J. & F. Kränzlin. 1981. *Pilze der Schweiz. Beitr. Kenntn. Pilzfl. Schweiz. Band 1: Ascomyceten (Schlauchpilze)*. Luzern.
- Chadefaud, M. 1943. Sur les divers types d'éléments dangeardiens des Ascomycètes, et sur la formation des asques chez la Pézize *Pustularia catinus*. *Rev. scient.* 81: 77–80.
- Dennis, R. W. G. 1956. A revision of the British Helotiaceae in the herbarium of the Royal Botanic Gardens, Kew, with notes on related European species. *Mycol. Papers* 62.
- Dennis, R. W. G. 1964. Remarks on the genus *Hymenoscyphus* S.F. Gray, with observations on sundry species referred by Saccardo and others to the genera *Helotium*, *Pezizella* or *Phialea*. *Persoonia* 3: 29–80.
- Dennis, R. W. G. 1978. *British Ascomycetes. Revised edition*. Vaduz.
- Dörfelt, H. (ed.). 1989. *Lexikon der Mykologie*. Stuttgart and New York.
- Dumont, K.P. 1976. Sclerotiniaceae XI. On *Moellerodiscus* (= *Ciboriopsis*). *Mycologia* 68: 233–267.
- Dumont, K.P. 1981. Leotiaceae III. Notes on selected temperate species referred to *Helotium* and *Hymenoscyphus*. *Mycotaxon* 13: 59–84.
- Dumont, K.P. & S.E. Carpenter. 1982. Los hongos de Colombia VII. Leotiaceae IV. *Hymenoscyphus caudatus* and related species from Colombia and adjacent regions. *Caldasia* 13: 567–602.
- Ellis, M.B. & J.P. Ellis. 1985. *Microfungi on land plants, An identification handbook*. London and Sydney.
- Engel, H. 1993. Pilzneufunde in Nordwestoberfranken 1989, I. Teil. Auflistung, Kurzbeschreibungen, Hinweise. *Pilzfl. Nordwestoberfrankens* 14/15: 3–24.
- Engel, H. & B. Hanff. 1993. Pilzneufunde in Nordwestoberfranken 1989/1990, II. Teil. Ascomyceten. *Pilzfl. Nordwestoberfrankens* 14/15: 39–50.
- Farr, D.F., G.F. Bills, G.P. Chamuris & A.Y. Rossman. 1989. *Fungi on plants and plant products in the United States*. St. Paul, Minnesota.
- Gäumann, E. A. & C. W. Dodge. 1928. *Comparative morphology of fungi*. New York and London.
- Haines, J.H. 1989. Studies in the Hyaloscyphaceae IV: *Fuscolachnum*, a new genus for *Dasyscyphus pteridis*. *Mem. New York Bot. Garden* 49: 315–325.
- Hawksworth, D.L. 1987. The evolution and adaptation of sexual reproductive structures in the Ascomycotina. In: A.D.M. Rayner, C.M. Brasier & D. Moore (eds.), *Evolutionary biology of the fungi*: 179–189. Cambridge etc.
- Hawksworth, D.L., B.C. Sutton & G.C. Ainsworth. 1983. *Ainsworth & Bisby's dictionary of the fungi*. Seventh edition. Kew, Surrey.
- Huhtinen, S. 1990. A monograph of *Hyaloscypha* and allied genera. *Karstenia* 29: 45–252.
- Karsten, P.A. 1870. *Symbolae ad Mycologiam fennicam* [1]. *Notis. Sällsk. Fauna Fl. fenn. Förh.* 11: 211–268.
- Kirk, P.M. & B.M. Spooner. 1984. An account of the Fungi of Arran, Gigha and Kintyre. *Kew Bull.* 38: 503–597.
- Korf, R.P. & P. Lizoň. 1994. *Lambertellinia scutuloides* (Sclerotiniaceae), a new genus and species for a Discomycete previously confused with *Hymenoscyphus caudatus*. *Mycotaxon* 50: 167–174.
- Korf, R.P. & W.-Y. Zhuang. 1985. Some new species and new records of Discomycetes in China. *Mycotaxon* 22: 483–514.
- Lizoň, P. 1992. The genus *Hymenoscyphus* (Helotiales) in Slovakia, Czechoslovakia. *Mycotaxon* 45: 11–59.
- Martens, P. 1932. L'origine du «crochet» et de l'«anse d'anastomose» chez les Champignons supérieurs. *Bull. Soc. mycol. Fr.* 48: 259–281.
- Moreau, F. 1950. Le mycélium secondaire chez les Ascomycètes. *Bull. Soc. mycol. Fr.* 66: 114–118.
- Moreau, F. 1954. *Les Champignons*. Tome 2. Paris.
- Moreau, F. & Mme. 1922. Le mycélium à boucles chez les Ascomycètes. *C.R. Acad. Sci., Paris*, 174: 1072–1074.
- Oudemans, C.A.J.A. 1890. Micromycètes nouveaux. *Versl. Meded. Kon. Akad. Wetensch., Afd. Natuurkunde*, 3e reeks, 7: 312–327.

- Phillips, W. 1887. A manual of the British Discomycetes. London.
- Phillips, W. & C.B. Plowright. 1881. New and rare British fungi. *Grevillea* 10: 65–74.
- Samuels, G.J. 1985. An annotated index to the mycological writings of Franz Petrak. Vol. 4, H–L. Wellington.
- Svrček, M. 1985. A taxonomic revision of inoperculate Discomycetes described by J. Velenovský in the genus *Helotium*, preserved in National Museum, Prague. *Sb. nár. Muz. Praze* 40 B: 129–215 ('1984').
- Thind, K.S. & M.P. Sharma. 1980. The genus *Hymenoscyphus* S.F. Gray in India. *Nova Hedwigia* 32: 121–132.
- Vaasma, M., K. Kalamees & A. Raitviir. 1986. Macrofungi of the Caucasian State Nature Reserve. Tallinn.
- Weber, E. 1992. Untersuchungen zu Fortpflanzung und Ploidie verschiedener Ascomyceten. Berlin and Stuttgart. *Bibliothca mycol.* 140.
- White, W.L. 1943. Studies in the genus *Helotium*, III. History and diagnosis of certain European and North American foliicolous species. *Farlowia* 1: 135–170.
- White, W.L. 1944. Studies in the genus *Helotium*, IV. Some miscellaneous species. *Farlowia* 1: 599–617.