Hymenoscyphus menthae, *H. macroguttatus* and *H. scutula*, a comparative taxonomic study emphasizing the value of spore guttulation and croziers

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Summary: The taxonomic value of spore guttulation (lipid pattern inside of mature ascospores) studied with the light microscope from fresh but also dried collections is illustrated mainly for the two species of *Hymenoscyphus* extensively treated here. Also, the value of croziers at the ascus base is emphasized. The high intraspecific consistency of these characters permits rapid recognition of these species in the living state: *H. menthae* with multiguttulate ascospores and simple-septate asci, *H. macroguttatus* (= *H. menthae s. auct.*) with spores containing a few large oil drops and asci arising from croziers. Further valuable characteristics in the genus *Hymenoscyphus* concern the shape of ascospores (homo- versus heteropolar), the presence of polar setulae on them, and the vacuolar guttules in the living paraphyses. The neglect of spore guttulation due to the current dominance of herbarium studies, and also the neglect of croziers resulted in much confusion and name changes in this group of fungi. The traditional delimitation of taxa within *Hymenoscyphus* according to the substrate (lignicolous, herbicolous, pteridicolous) is questioned because quite a few species turned out to be highly plurivorous.
The present type studies led to the following conclusions: (1) *Hymenoscyphus menthae* is an earlier synonym of *H. consobrinus*. (2) *H. pteridicola* Thind & Sharma is conspecific with *H. menthae s. auct.* and is replaced by the name *H. macroguttatus* because of the homonym *H. pteridicola* (Crouan) O. Kuntze. (3) *Helotium repandum* var. *rumicis*, *H. julianum*, and *H. stramineum* are later synonyms of *Hymenoscyphus menthae*. (4) *Helotium geiphilum* and *Hymenoscyphus vitellinus* are conspecific and hardly separable from the older *H. scutula*, whilst Svrček's interpretation of *H. vitellinus* mainly concerns *H. menthae*. (5) *Helotium scutula* var. *solani* might also be a synonym of *Hymenoscyphus scutula*, but type material could not be located. (6) The new species *H. sharmae* is described for collections from India (Himalaya) issued under the name *Helotium scutula* var. *solani*; it resembles *H. trichosporus* but differs in 4-spored asci. (7) A syntype of *Helotium hyalopes* in M contains a mixture of two similar species with scutuloid spores; possibly neither of them are synonymous with *Hymenoscyphus vitigenus*, a species described with homopolar spores and requiring restudy of the type.
Molecular data supports a close relationship between *H. menthae* and *H. repandus*, both having a yellow disc and homopolar ascospores, but the data suggests a strong separation from the bulk of *Hymenoscyphus s. str.*, which usually have heteropolar (scutuloid) but exceptionally also homopolar (*H. macroguttatus*) spores, and often whitish though also yellow apothecia.
Keywords: Ascomycota, *Helotiales*, vital taxonomy, lipid bodies, pleurorynchous.

Introduction

The genus *Hymenoscyphus* S.F. Gray in a restricted sense, with the exclusion of *Phaeohelotium* Kanouse and *Cudoniella* Sacc. as was accepted in Baral *et al.* (2013), comprises a large number of taxa which often exhibit only slight differences in their micromorphological characters, particularly when comparing treatments based on herbarium material. For this reason, taxonomic subgroups or dichotomous keys were often constructed based on the type of substrate (e.g., Dennis, 1956: 67, 1964; Thind & Sharma, 1980). A synoptic key by Lizoň (1992) includes various microscopic characters but neglects ascospore guttulation and croziers. A recently compiled checklist (Lizoň & Kučera, 2014) briefly mentions a total of 1180 taxa which have ever been combined in *Helotium* or *Hymenoscyphus*, and illustrates the excessive need for taxonomic work and careful type studies in this group of fungi.

The two taxa are treated in detail here, *Hymenoscyphus menthae* (W. Phillips) Baral (= *H. consobrinus* (Boud.) Hengstm.), a species very common in Central Europe, and *H. macroguttatus* Baral, Declercq & Hengstm. (= *H. menthae s. auct.*), a less common species with a very similar distribution. Whenever fresh samples were available, spore guttulation was observed to be an absolutely constant character which allowed a rapid and unambiguous determination. *H. menthae* sharply differs by its multiguttulate spores (Figs 1–17, 26–30) from *H. macroguttatus* which has oligoguttulate spores with a few large guttules and some small ones (Figs 32–42, 47–50). Over the past 40 years, 57 collections of *H. menthae* and 18 of *H. macroguttatus* were studied and often also documented by me in the fresh, living state, and some further ones from herbarium material. Various other workers have made numerous collections of these two species and examined them mostly in the living state, and in an extraordinarily high number by B. Declercq in Belgium.

This striking difference in spore guttulation can often also be recognized in old herbarium material, if mature spores, preferably not yet released from the asci, are found which show the undistorted lipid pattern. In this way, the original pattern of spore guttulation could be verified in all of the type specimens examined in the present study. The frequent neglect of LBs in the literature as a result of studying herbarium material, together with the disregard of the ascus base, are the most important causes of confusion in this group. Spore guttulation and croziers were found to have a high diagnostic value in the genus, whereas a correlation with the substrate, even within the categories wood and bark, herbaceous stems, dicots vs. monocots, and stems of pteridophytes, was not observed in the species treated here.

Hymenoscyphus menthae and *H. macroguttatus* have oblong, homopolar spores of a very similar size, and are plurivorous though mainly caulicolous. Various earlier as well as more recent authors have confused them, and merged them even with the common, also plurivorous and somewhat variable *H. scutula* (Pers.: Fr.) W. Phillips, which is characterized by distinctly heteropolar spores which often possess prominent setulae at both ends (currently referred to as "cilia", but see Hengstmengel, 1996). Despite their homopolar spore shape, the two species treated here have actually been included in the scope of *H. scutula* as more or less doubtful forms or varieties (e.g., by Dennis, 1956), whereas Hengstmengel (1996) confirmed their independence in his careful study of herbarium material. Molecular data gained recently shows that the two species are not closely related to each other, and that *H. menthae* is not even related to *Hymenoscyphus s. str.* as represented by *H. scutula* and the type species *H. fructigenus* (Bull.) Gray. The latter two species are characterized by strongly heteropolar spores with a rounded to obtuse, more or less distinctly asymmetrical apex with a minute acute, oblique or lateral protrusion, and a tapered, more or less acute base. If setulae are present, they are usually inserted at the subapical protrusion

and the acute base. Often the spores are slightly curved, which causes a unilateral flattening or slightly concave outline at the side of the protrusion. This remarkable spore shape was termed "scutuloid" by me (in Baral & Krieglsteiner, 1985: 120), and is a rather unique character of the genus *Hymenoscyphus s. str.* (see also Baral & Bemmann, 2014). More or less scutuloid spores are illustrated in the present study in Figs 56–63.

To find a proper name for *H. menthae s. auct.* was a major problem. Although helpful, the revision of Velenovský's taxa of *Helotium* by Svrček (1985) neglects croziers, and reports eguttulate spores even though they were originally described as guttulate. The same kind of problem applies to the "Revision of the British *Helotiaceae*" by Dennis (1956), which includes many descriptions of types. Consequently, I have reexamined type material of W. Phillips, H. Rehm, J. Velenovský, and K.S. Thind & M.P. Sharma concerning taxa which appeared from the available descriptions to be similar to my two species with homopolar spores. All these types are figured in the present paper.

Abbreviations: CB = cotton blue in lactophenol, CR = congo red (in NH_4OH), CRB = cresyl blue (ca. 0.5% aqueous), H_2O = tap water, KOH = potassium hydroxide (5%), IKI = Lugol's solution (1% I2, 3% KI in tap water), MLZ = Melzer's reagent, NH_4OH = ammonium hydroxide (10%), BB = blue at low (~0.2%) and high (0.5–1%) iodine concentration (IKI), LB = lipid body (oil drop), VB = refractive vacuolar body; * = living state of a cell, † = dead state; → = from immature to mature; d.v. = document seen (usually macro- and microillustration), n.v. = no illustration or material seen, ø = unpreserved, sq. = DNA sequence, vs. = versus (as opposed to), MTB = German grid system (Messtischblatt), MB = MycoBank, MBT = Mycobank typification number. The numbers of examined samples in which the reported character was tested and observed are indicated between {} (numbers after the slash refer to uncertain identifications).

Mentioned official herbaria: GENT = Laboratory of Plant Systematics, Gent; HMAS = Institute of Microbiology, Academia Sinica, Beijing; K = Royal Botanic Gardens, Kew; KR = Staatliches Museum für Naturkunde, Karlsruhe; L = Naturalis Biodiversity Center, Leiden; M = Botanische Staatssammlung, München; PAN = Punjab university, Chandigarh; PRM = National Museum, Prague; REG = Regensburgische Botanische Gesellschaft; STU = Staatliches Museum für Naturkunde, Stuttgart; TAAM = Institute of Zoology and Botany, Tartu; TFC = Herbario Dept. de Biología Vegetal, Universidad de La Laguna, Tenerife, Spain), Z = Universität Zürich.

Private herbaria: A.P. = Adriana Ileana Pop (†, Cluj-Napoca). B.D. = Bernard Declercq (Wachtebeke, mainly in GENT), C.S. = C.M. Swart-Velthuyzen (Rales de Llanes), E.B. = Edward Batten (Wenhaston), E.R.D. = Enrique Rubio Dominguez (Avilés), H.B. = H.-O. Baral, H.E. = Heinz Engel (†, Weidhausen), H.H. = Hans Haas (†, Schnait, in STU), H.L. = Heinrich Lehmann (Kiel), J.H.P. = Jens H. Petersen (Tirstrup), J.P. = Jean-Pierre Prongué (†, Buchs), J.P.P. = Jean-Paul Priou (La Gacilly), K.S. = Klaus Siepe (Velen), L.K. = Lothar Krieglsteiner (Schwäbisch Gmünd), M.E. = Matthias Eckel (†, Taura), M.H. = Michel Hairaud (Poivendre de Marigny), M.K. = Maren Kamke (Felm), M.Y. = Marcus Yeo (Peterborough), N.V. = Nicolas Van Vooren (Lyon), P.B. = Paul Blank (†, Schaffhausen, presently in H.B.), P.R. = Peter Rönsch (Steigra), P.T. = Peter Thompson (Wolverhampton), R.T. = Rudolf Thate (†, Neustadt/Weinstr., in KR), S.H. = Stip Helleman (Boxmeer), T.L. = Till-R. Lohmeyer (Tittmoning), U.S. = Unto Söderholm (Tampere), V.K. = Volker Kummer (Potsdam).

Taxa with more or less homopolar, ellipsoid-fusoid ascospores (*H. menthae*, *H. macroguttatus*, *H. sharmae*)

Hymenoscyphus menthae (W. Phillips) Baral, *in* Baral & Krieglsteiner, *Beih. Z. Mykol.*, 6: 131 (1985) – Figs 1–31.

≡ *Helotium menthae* W. Phillips, Elv. Brit. no. 188 (1877), *nom. inval.*, Art. 38.1(a) (ICN, without diagnosis).

≡ *Helotium menthae* W. Phillips, *in* Phillips & Plowright, *Grevillea*, 10: 69 (1881).

≡ *Hymenoscyphus scutula* var. *menthae* (W. Phillips) W. Phillips, *Man. Brit. Discom.*: 137 (1887) [as "*Hymenoscypha*"].

≡ *Helotium scutula* var. *menthae* (W. Phillips) Rehm, *Rabenh. Krypt.-Fl.*, ed. 2, 1 (3): 793 (1893).

≡ *Helotium scutula* f. *menthae* (W. Phillips) Massee, *Brit. Fung.-fl.*, 4: 254 (1895).

≡ *Phialea scutula* var. *menthae* (W. Phillips) Sacc., *Syll. fung.*, 8: 266 (1889).

= *Hymenoscyphus consobrinus* (Boud.) Hengstm., *Persoonia*, 12: 489 (1985).

≡ *Helotium consobrinum* Boud., *Hist. class. Discom. Eur.*: 114 (1907).

≡ *Hymenoscyphus consobrinus* (Boud.) Arnolds, *Coolia*, 26 (suppl.): 313 (1984), *nom. inval.*, Art. 40.1, 41.5 (ICN, no basionym cited).

≡ *Hymenoscyphus consobrinus* (Boud.) Arnolds & Baral, *in* Baral & Krieglsteiner, *Beih. Z. Mykol.*, 6: 124 (1985), *nom. inval.*, Art. 41.3 (ICN, date spread 1905–10 given for basionym).

= *Helotium alismaceum* Velen., *Monogr. Discom. Bohem.*: 202, tab. 20, fig. 1 (1934).

≡ *Hymenoscyphus alismaceus* (Velen.) Svrček, *Sb. Nár. Mus. Praze* (B), 40: 133 (1985).

= *Helotium repandum* var. *rumicis* Velen., *Monogr. Discom. Bohem.*: 191 (1934).

= *Helotium julianum* Velen., *Novit. mycol.*: 185 (1940).

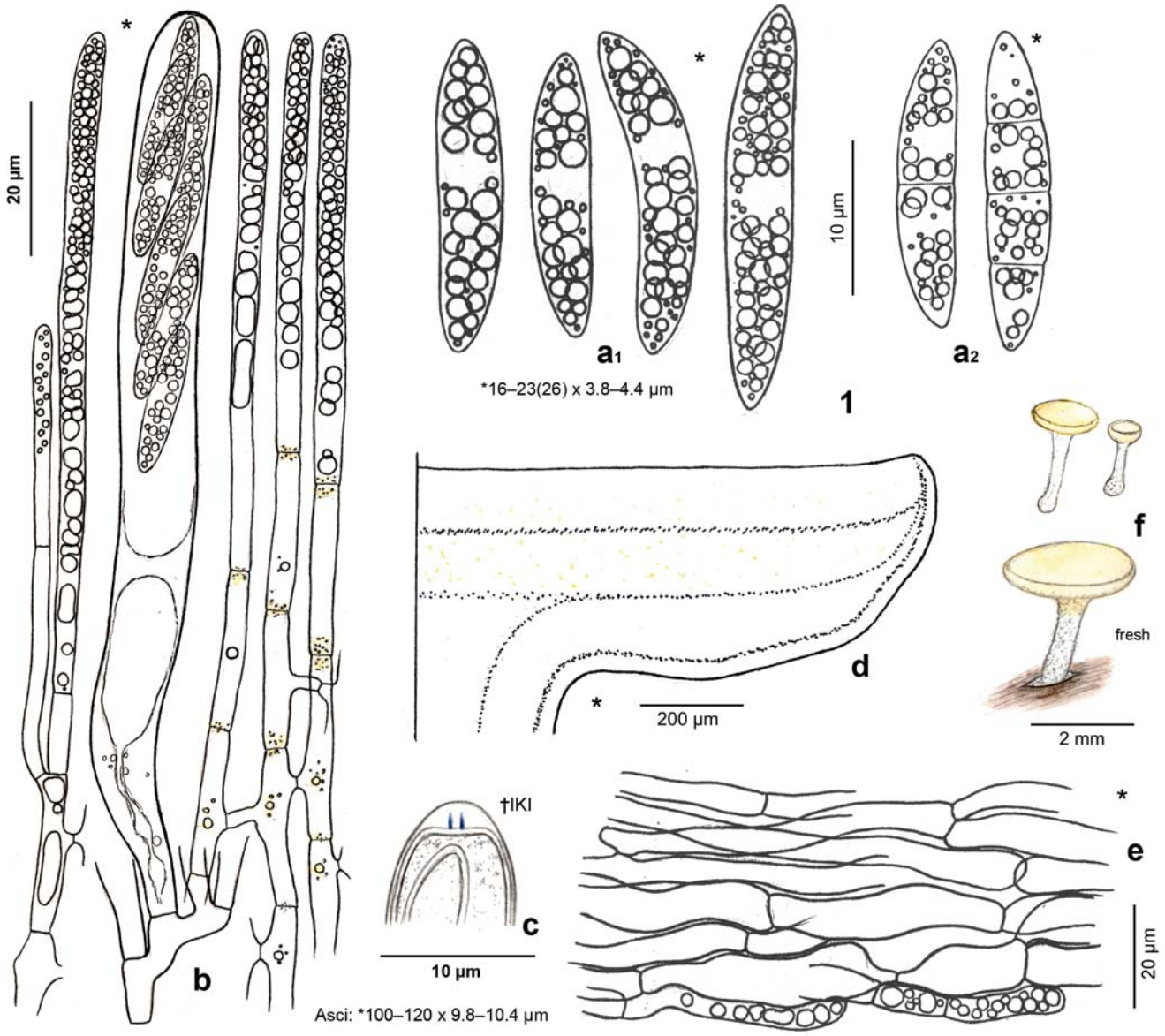
= *Helotium stramineum* Velen., Novit. mycol.: 185 (1940).

Typification: *menthae*: England, Shropshire, Shrewsbury, stems of *Mentha*, undated (W. Phillips, Elv. Brit. No. 188, K(M) 52786, lectotype, designated here, MBT 202657); – *consobrinum*: France, Val d'Oise, Paris, Montmorency, undated (December), stems of *Rumex acetosa*, collector unknown (not requested); – *alismaceum*: Czechia, Mnichovice, Hubáčkov, stems of *Alisma plantago-aquatica*, 30.VIII.1926, J. Velenovský (PRM 147258, lectotype); – *repandum* var. *rumicis*: Mnichovice, Stráncice, *Rumex crispus*, X.1927, J. Velenovský (PRM 148523, lectotype); – *julianum*: Mnichovice, Tehov, culm of indet. *Poaceae*, 11.VII.1938, J. Velenovský (PRM 148152, holotype); – *stramineum*: Mnichovice, Hrusice, culms of *Triticum aestivum*, VI.1939, J. Velenovský (PRM 48072, holotype).

Etymology: *menthae*, *alismaceus*, *rumicis* after the host genus; *consobrinus* being a cousin (of *H. virgultorum* and *H. scutula*); *julianus* collected in July; *stramineus* growing on straw.

Misapplication: *H. menthae s.* Baral & Krieglsteiner (1985: 131), Hengtsmengel (1996), Zhang & Zhuang (2002) = *H. macroguttatus*, *H. menthae s.* Zhao & Hosoya (2014) = *Hymenoscyphus sp.*; *H. vitellinus s.* Svrček (1985), Matheis (1976) = *H. menthae*, except for the type of *H. geiphilum* (= *H. scutula*).

Apothecia ± gregarious, solitary but sometimes fasciculate, stipitate, erumpent from minute cavities beneath the epidermis, or superficial on epidermis-free areas; disc fresh 0.8–2.5(–4) mm diam., pale to bright yellowish-ochraceous to egg-yellow {>60}, rarely milky-white to cream {7}, slightly concave to flat, never convex, round, exterior glabrous; stipe (0.6–)1–3(–8) mm long, (0.15–)0.2–0.45(–0.5) mm wide, cylindrical, straight to flexuous, entirely white, rarely upper part ochraceous, at least partly with a slightly bulbose base {~15}, base or complete stipe finely pubescent; hymenium changing to rosaceous-brownish with age, yellow pigment fading in herbarium specimens. **Asci** *90–120(–130) × 8.5–10.5(–12) µm {7}, †70–110(–120) × (6.7–)7.3–9(–10.7) µm {9}, 8-spored, spores (*) obliquely biseriate, (†) biseriate or ± uniseriate below, *pars sporifera* *(40–)45–55(–60) µm {5}, †72–90 µm {3}, projecting *5–15 µm beyond paraphyses; apex of dead asci slightly to strongly conico-truncate, apical dome †1.6–1.8 → 1.5–1.6 µm thick, apical ring in IKI medium to strongly blue (BB) {25}, rarely weakly so {type of *Helotium julianum*}, occupying only 1/2–2/3 {12} or up to 5/6 of the dome {2},



H.B. 5873a: Germany, Tübingen, Pfrondorf, stem of *Solanum dulcamara*

Fig. 1. *Hymenoscyphus menthae*. – a. ascospores (a1 mature, a2 overmature), containing refractive guttules (LBs); b. mature ascus and paraphyses, the latter containing refractive vacuolar guttules (VBs); c. apex of nearly mature ascus in IKI, with euamyloid apical ring; d. median section of receptacle; e. do., ectal excipulum at lower flanks, with cortical hyphae containing refractive guttules (VBs); f. fresh apothecia. – Living state (except for c).

Hymenoscyphus-type, ring also visible in KOH without iodine; base with ± long stalk, arising from simple septa {43}, immature asci during meiosis densely filled with 0.3–0.5 µm large LBs which fuse in dead asci to form one large pale yellowish-chlorinaceous body. **Ascospores** *((13–))(15–)17–22(–26) × ((2.8–))3.5–4.2(–4.5) µm {26}, †(14–)16–22(–26.5) × (2.6–)3.2–4(–4.5) µm {19}, always non-septate within living mature asci, cylindric-fusoid-naviculate, without median constriction, consistently homopolar {>110}: both ends distinctly tapered to an obtuse or acute tip, never scutuloid, ± straight but mostly some slightly curved at centre or towards one end, recently discharged living spores ensheathed in a thin membrane that slips off the spore {1} (Fig. 29, not seen in other fresh collections), entirely without polar setulae {>110}; living mature spores consistently multiguttulate: densely filled with small (0.7–1.3(–1.5) µm) and minute (0.3–0.5 µm) refractive LBs except for the globose central nucleus (very high lipid content) {>90}, old herbarium specimens still with some or most spores multiguttulate {13}, or all spores with 1–4 large refractive aggregations {5}, wall surface lilac in CRB {1} or unstained {1}; aged spores (free or in dead asci) often with one median septum {7} or up to 3 septa {3}, remaining hyaline and smooth, rarely turning pale to light brown, scarcely increasing in size (*18.5–24 × 3.7–4.5 µm). **Paraphyses** cylindrical, straight, rounded at apex, terminal cell *40–84 {2} × (2.3–)2.5–3.5(–4) µm {5}, †(20–)29–65 × 1.7–2.7 µm {3}, lower cells *10–24 × 2.5–3.5 µm {1}, †14–28 × 1.7–2.5 µm {2}; VBs multiguttulate, rather strongly refractive {>60}, hyaline, ± restricted to terminal cell, in upper part small guttules in 2–3 rows, downwards larger, globose to short-cylindrical, uniseriate, extending (22–)30–50 µm {3} or 50–95 µm {2} from tip, slowly staining turquoise in CRB, IKI–, disappearing in dead cells, plasma then sometimes pale amber (†H_2O); abundant minute yellow-orange LBs near septa; rarely dichotomously branched near base or upper part but frequently anastomosing below. **Medullary excipulum** hyaline, of rather loose *textura intricata*, hyphae *2–8 µm wide {1}, eguttulate, delimited from ectal excipulum by a ca. 100 µm thick parallel layer of *t. porrecta*, individual cells *80–140 × 2–5 µm {1}. **Subhymenium** ca. 50–120 µm thick, of upwards oriented loose *t. porrecta*, cells with abundant anastomoses, with or without yellow-orange LBs. **Ectal excipulum** hyaline, of (*) rather thin-walled *textura pris-*

Tab. 1 – Phenology of *Hymenoscyphus menthae*, depending on the geographical region (atlantic: England, Benelux, western parts of France, northern parts of Germany). Exact collection data for Denmark were not available.

	Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
(sub)contin. Europe	0	0	1	2	10	13	11	23	5	12	10	4	2	2	0	0	0	0
(sub)atlantic Europe	2	2	19	44	28	27	31	17	22	29	30	28	23	14	7	0	1	

matica-porrecta from base to margin, oriented at an angle of ca. 0–20(–40)° to the surface, ca. 30–50 µm thick near base of receptacle, cells at flanks *(13–)18–40(–60)((–85)) {5} × (5–)7–10(–12)((–18)) µm {6}, †10–25 × 4–8 µm {2}, slightly gelatinized in KOH (common walls 0.6–0.9 µm thick); inner cells 65–100 × 4–10 µm, indistinctly delimited from medullary excipulum; cortical hyphae one-layered, 4–6.5(–8) µm wide {1}, undulating, filled with refractive VBs (multiguttulate), forming a network in surface view, frequent at margin and flanks, also present on stipe; receptacle hairless, stipe with short guttulate cylindrical hairs.

Cultural characteristics: the ascospores showed a high rate of germination on malt extract agar, producing an always hyaline mycelium with somewhat mealy appearance (Weber, 1992: 61).

Habitat: on previous year's herbaceous or woody substrates lying on the moist ground (hygric), predominantly in damp places (swamps, ditches or ruts in woods, bank-communities along rivulets and brooks, small lakes, reed and sedge dominated marshes, moist meadows or forb communities), also in gardens and horticultures remote from water (but substrate lying on moist ground); mainly on **herbaceous dicotyledons:** on rather rotten stems (sometimes roots, rarely inflorescences) of *Agrimonia eupatoria* {1}, *Angelica sylvestris* {1/1}, *Anthemis nobilis* {1}, *Apiaceae* indet. {3}, *Caltha palustris* {5}, *Chamaenerion angustifolium* {1}, *Cirsium* sp. {4}, *Coreopsis verticillata* {1}, *Epilobium* sp. {1}, *E. hirsutum* {2}, *Eupatorium cannabinum* {1}, *Fallopia japonica* {4}, *Filipendula ulmaria* {1}, ?*Galeopsis bifida* {1}, *Impatiens glandulifera* {4}, *I. nolitangere* {3}, ?*Lamiaceae* {1}, *Lamium galeobdolon* {2}, *Lycopus europaeus* {4}, *Lysimachia vulgaris* {4}, *Lythrum salicaria* {1}, *Mentha* sp. {2/1}, *M. aquatic*a {1}, *M.* × *verticillata* {1}, *Peucedanum palustre* {1}, *Polygonum* sp. {1}, ?*Potentilla palustris* {1}, *Ranunculus aconitifolius* {1}, *Rubus fruticosus* {1}, *R. idaeus* {3/1}, *Rumex* sp. {4/2}, *R. acetosa* {1}, *R. crispus* {1}, *Sambucus ebulus* {3}, *Saponaria officinalis* {1}, *Senecio fuchsii* {1}, *Solanum dulcamara* {4/1}, *Solidago* ?*canadensis* {1}, *Thalictrum dipterocarpum* {1}, *Urtica dioica* {2/1}, indet. plants {18}; **monocotyledons:** on rotten stems, culms or leaves of *Alisma plantago-aquatica* {1}, ?*Cyperaceae* indet. {1}, *Iris pseudacorus* {2}, *Poaceae* indet. {2}, *Scirpus silvaticus* {1}, *Triticum aestivum* {1}, *Typha latifolia* {1}, *Zea mays* {2}; **pteridophytes:** petioles of *Pteridium aquilinum* {1}, **woody plants:** on rather undecayed to very rotten bark {1} and wood {6} of twigs and branches, 5–9 mm {4} or 40 mm {1} thick, of *Alnus* sp. {2}, ?*Euonymus europaeus* {1}, *Populus* sp. {1}, *Sambucus nigra* {1}, indet. angiosperm {4/1}, cupule of *Aesculus hippocastanum* {1}, fruit of *Acer* {1}, main vein of strongly sceletonized leaf of indet. angiosperm {1}. **Associated** with *Calycina discreta* {1}, *C. herbarum* {1}, *Cistella grevillei* {1}, *Cyathicula cyathoidea* {2}, *C. paludosa* {1}, *Hymenoscyphus macroguttatus* {1}, *H. repandus* {2}, *H. scutula* {1}, *Leptosphaeria acuta* {1}, *Trichopeziza sulphurea* {1}, *Pyrenopeziza atrata* {1}, but often not associated with other ascomycetes. **Altitude:** 2–1800 m (temperate to subalpine, atlantic to subcontinental). **Desiccation tolerance:** not tested, probably intolerant concerning the asci and paraphyses.

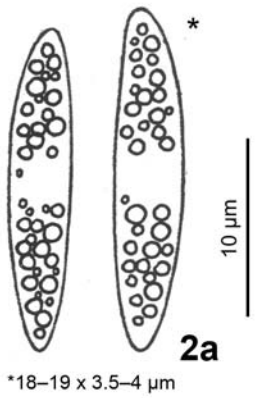
Remarks: *Hymenoscyphus menthae* is well characterized in the living state by a more or less yellow receptacle due to carotenoids, a much longer than wide, whitish stipe, rather large, homopolar, multiguttulate ascospores, and asci arising from simple septa. The epithet *menthae* suggests host specifity, but the long list of hosts on which it was recorded indicates a polyphagous, mostly herbicolous species which is rather common in temperate Europe. The macroscopically indistinguishable and closely related *H. repandus* (W. Phillips) Dennis differs in much smaller spores with a rather low lipid content.

Before I studied the type material of *H. menthae* in 1997, I treated the present species under its later synonym *H. consobrinus* (Baral & Krieglsteiner, 1985: 124), while I misapplied the name *H. menthae* for a fungus which is now named *H. macroguttatus* (*loc. cit.*: 131), based on the spore contents in the protologue. Other authors like Hengstmengel (1996) followed my misinterpretation of the name *H. menthae*. In 1985 I separated these two species mainly by spore guttulation (see also my figure in Baral, 1986: 8). Additional characters were only seen in the colour of the disc, being usually yellow-ochraceous in *H. menthae* while more whitish in *H. macroguttatus*, and in the spores which are slightly shorter and never distinctly curved in *H. macroguttatus*. Without knowing Hengstmengel's (1984) unpublished study, I later detected the sharp difference in the ascus base between the two species. Quite early, however, I became aware that the protologue of *Helotium menthae* W. Phillips as cited in Dennis (1956: 78) deviates from my early concept of *H. menthae* in the bright yellow apothecial colour (see Baral & Krieglsteiner, 1985: 132).

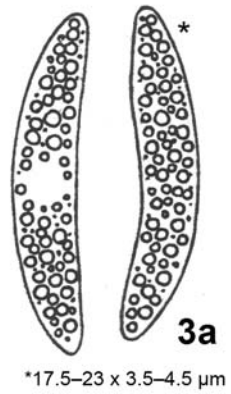
Dennis (1956: 79) mentioned a British collection on *Epilobium* under the name *Helotium consobrinum*, with spores 16–21 × 3–3.5 µm (without drawing), but considered this to be only a yellow form of *H. scutula* var. *solani*. Since he did not take much care on spore contents and ascus croziers, *H. menthae* was misinterpreted by me until I restudied the type myself (see also the brief report in Baral *et al.*, 2006: 157 and below under *H. macroguttatus*). Three syntypes and one paratype deposited in K and M were examined (Figs 11–13), showing multiguttulate spores and the absence of croziers. The material was found to be homogeneous and conspecific with the later *H. consobrinus*. Therefore, the name *H. menthae* must be adopted to replace *H. consobrinus* (see Krieglsteiner, 1993: 65).

Svrček (1962: 100) reported only a single collection under the name *Helotium consobrinum*, from Lower Tatra on stems of ?*Gentiana asclepiadea*, with spores *20–23 × 3.5–4 µm with a "granular content" when observed in water but with two drops when mounted in 10% KOH. Without referring to this name or collection, he later (Svrček, 1985: 150, 153, 172–3, 178) believed that *Hymenoscyphus vitellinus* (Rehm) O. Kuntze is the correct name for a "commonly occurring" herbicolous species, "easily recognizable" already by its external appearance. Svrček recorded this species mainly on dicotyledonous, seldom on monocotyledonous herbs, and I feel that his concept of *H. vitellinus* is largely congruent with *H. menthae* in the present circumscription. Examination of an isotype of *H. vitellinus* in M (Rehm Ascomyc. Exs. 513) showed, however, that Rehm's taxon is a member of the difficult *H. scutula*-complex and needs further study to evaluate its taxonomic identity (see Figs 56–57).

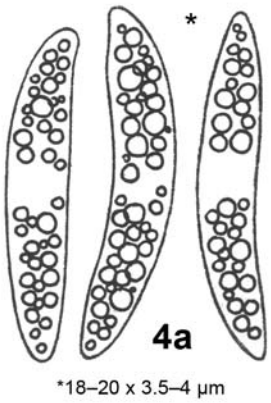
Also Matheis (1976: 19) misinterpretated *Hymenoscyphus vitellinus*, based on two collections on *Solanum dulcamara* from Switzerland (Thurgau, Barchetsee) which R.W.G. Dennis identified as belonging to this taxon. Judging from his unillustrated description especially of the apothecia, Matheis was probably dealing with *H. menthae*. Velenovský (1934: 191) placed *Helotium vitellinum* (as "*H. vitellum*") in synonymy of *Helotium repandum* W. Phillips by giving a spore length of 6–12 µm for Bohemian samples on various herbs. From this he distinguished *H. repandum* var. *rumicis* Velen. with 15–30 µm long spores, which is a synonym of *H. menthae* according to the present study of the type. Also on page 407 Velenovský (*loc. cit.*) appears to have included *H. menthae* in his concept of *H. repandum* by giving a spore length of 10–18 µm. The name *H. consobrinus* was not mentioned, either by Velenovský or by Matheis.



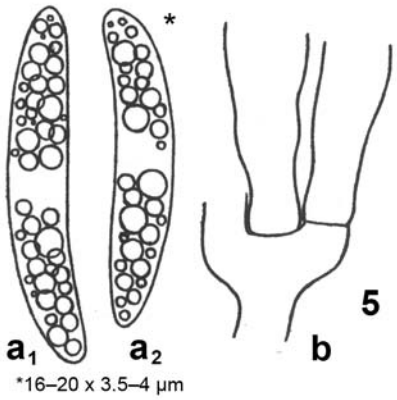
H.B. 455: Stuttgart, Weilimdorf, stem of *Lamium galeobdolon*



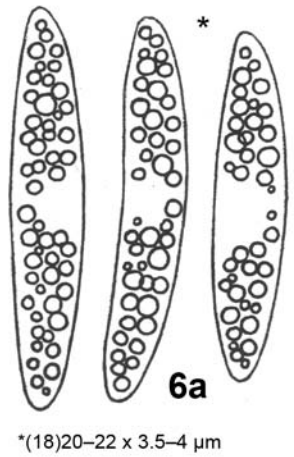
R.T. 1230: Neustadt/ Weinstraße, Hambach, stem of ?*Rumex*



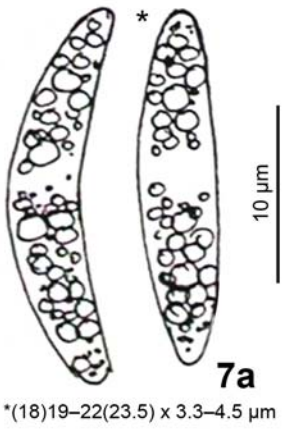
H.B. 345: Stuttgart, Feuerbach, stem of ?*Urtica*



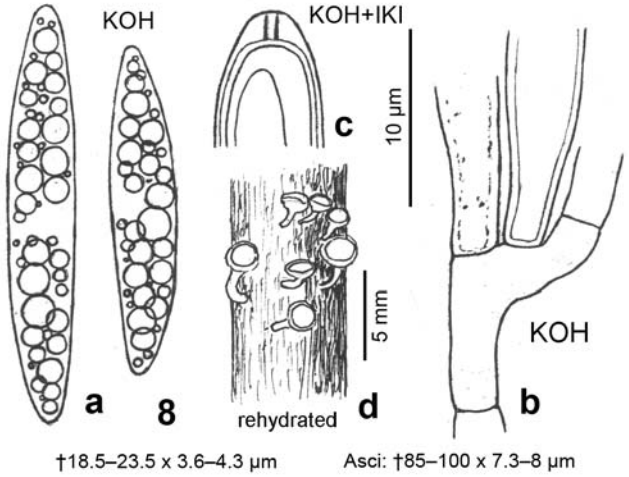
H.B. 5846a: Feldkirch, Ruggell, stems of *Solidago canadensis* (1) and twig of *Sambucus nigra* (2)



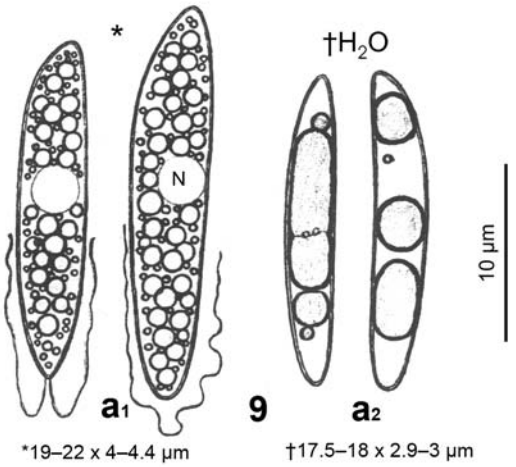
H.B. 457: Stuttgart, Weilimdorf, stem of *Rumex*



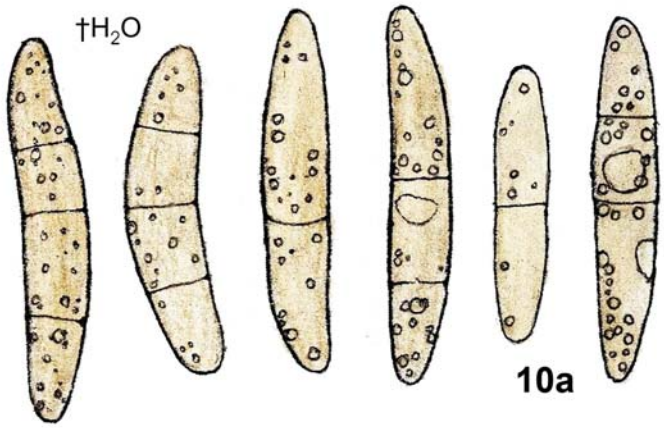
H.B. 8581: Rehna, *Solanum dulcamara*



B.D. 85/205: Gent, Wachtebeke, twig of *Populus*



H.B. 3250a: Tübingen, Dettenhausen, stem of *Anthemis nobilis* (but membrane from H.B. 3250b *Coreopsis verticillata*)



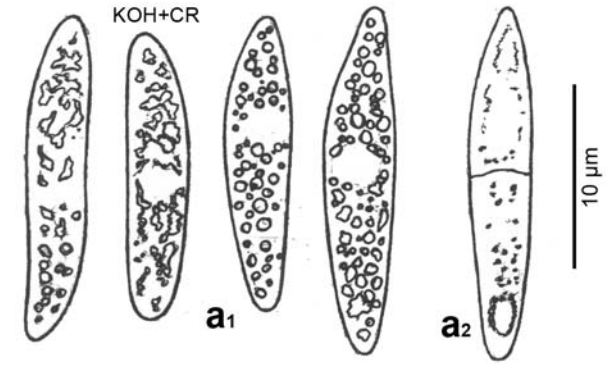
B.D. 87/194.1: Gent, Wachtebeke, stem of *Agrimonia eupatoria*

Fig. 2–10. *Hymenoscyphus menthae*. – a. mature ascospores (7 and 10: overmature; N = nucleus); b. simple-septate ascus bases; c. apex of nearly mature ascus in IKI; d. rehydrated apothecia. – Living state (except for 8, 9a2, 10). In Fig. 9a1 a thin membrane slips off the spores; note that in the dead spores of Fig. 9a2 the lipid pattern was distorted in the fresh apothecium by fusion of the LBs (compare also *H. scutula*, Fig 59), but in those of Fig. 8a it remained undistorted when the apothecium was rehydrated. – Fig. 3a: based on a drawing by R. Thate; Fig. 7: *del*. T. Richter; Fig. 9: taken from Baral (1992: fig. 22).

Based on a reexamination of type material, Svrček (1985) considered four of Velenovský's taxa as conspecific with his concept of *Hymenoscyphus vitellinus*. The present study of these types revealed three of them to be synonyms of *H. menthae*, whereas one (*H. geiphilum*) is undoubtedly not *H. menthae* because of its predominantly scutuloid spores, but probably conspecific with *H. vitellinus* in its original sense (see under *H. scutula*).

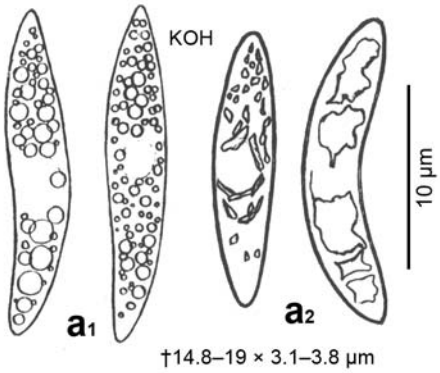
Hengstmengel (1984 and pers. comm.) studied the species (as *H. consobrinus*) from 48 collections from the Netherlands and sometimes Belgium made mainly between 1943–2013, a few also in the 19th century (between 1865–1895). Declercq (pers. comm.) lists *H. menthae* 236 times for Belgium for collections made between 1985–2014. I examined 8 of his herbarium specimens, and confirmed 7 of them (one was *H.* cf. *repandus*: B.D. 94/117, on a leaf gall of *Salix*). Declercq observed multiguttulate spore contents in most of his collections, while he found a "very wide range" of ascus and spore dimensions: the living spores exceptionally attained a size of 30 × 4.5 µm, and the living asci 135 × 12 µm. Ascus dimensions in the available literature, including Boudier's protologue and drawing, all clearly refer to the dead state and are, therefore, considerably smaller than those given for the living state in this paper. In only a few collections (made mostly late in the year, e.g. B.D. 87/194.1) Declercq observed some overmature 1–3-septate spores with "pale brown to brown walls" (Fig. 10a).

Siepe (1988) studied 13 collections from western Münsterland (Nordhein-Westfalen) and included a drawing of living multiguttulate spores and paraphyses for one of them, but he neglected the ascus base. Van Vooren (2009) described and illustrated a collection from a subalpine site in Fribourg (Switzerland) on stems of *Caltha* in the living state, with multiguttulate spores and paraphyses, and asci without croziers. The description given by Lizoň (1992: 15) under the name *H. consobrinus* lacks remarks on spore guttulation and croziers. I feel it is a mixture of *H. menthae* (or *H. macroguttatus*?) (CUP-G 1061, spores fusoid) and true *H. vitellinus* (PRM 614219, spores scutuloid), but the data are too insufficient. Grauwinkel (1987: 61) described a single collection of what was probably *H. menthae* (judging by the macroscopic description). Yet, he studied the specimen in dry state in "L4", and thus illustrated in his drawings and photos



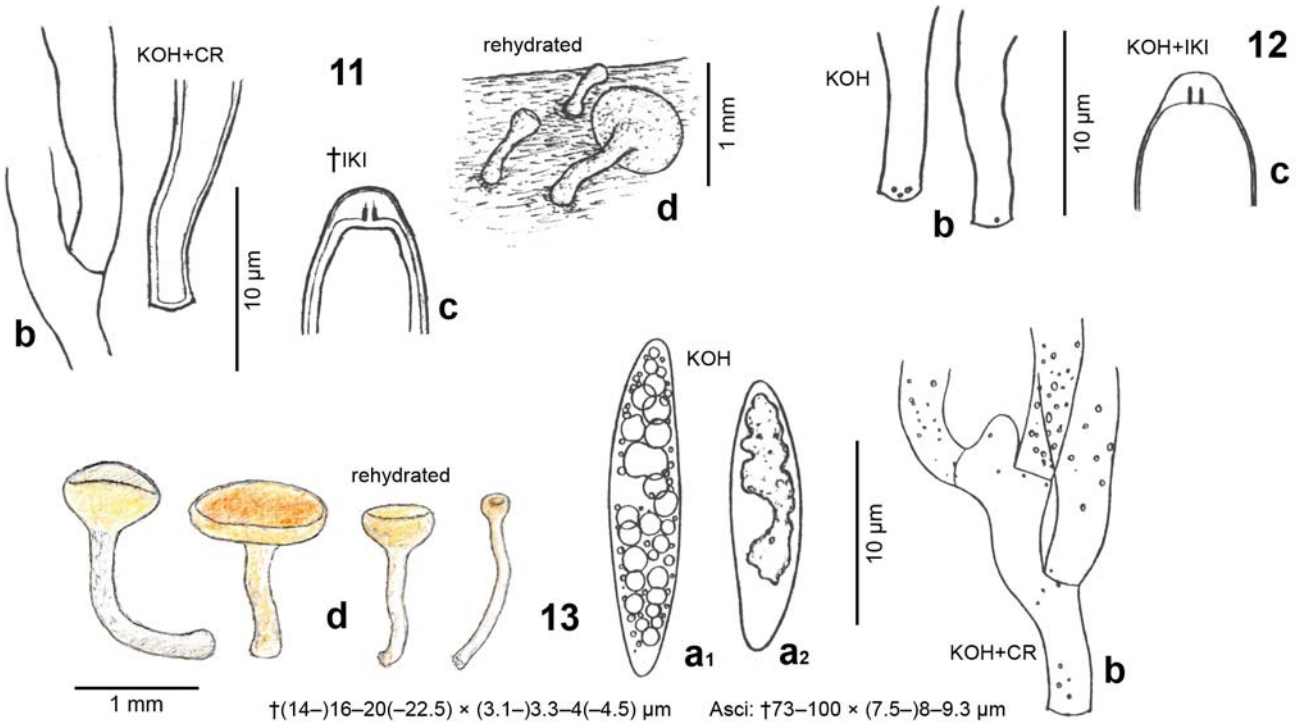
†15–19 × 3.3–3.8 µm Asci: †90–108 × 8.3–10.7 µm

K(M) 31758: Shrewsbury, stems of *Mentha sativa* - Paratype of *Helotium menthae* in Herb. M.C. Cooke



†14.8–19 × 3.1–3.8 µm

M-0206414: Shrewsbury, stems of *Mentha* - Isolectotype of *Helotium menthae* in Herb. W. Phillips, Elv. Brit. No. 188



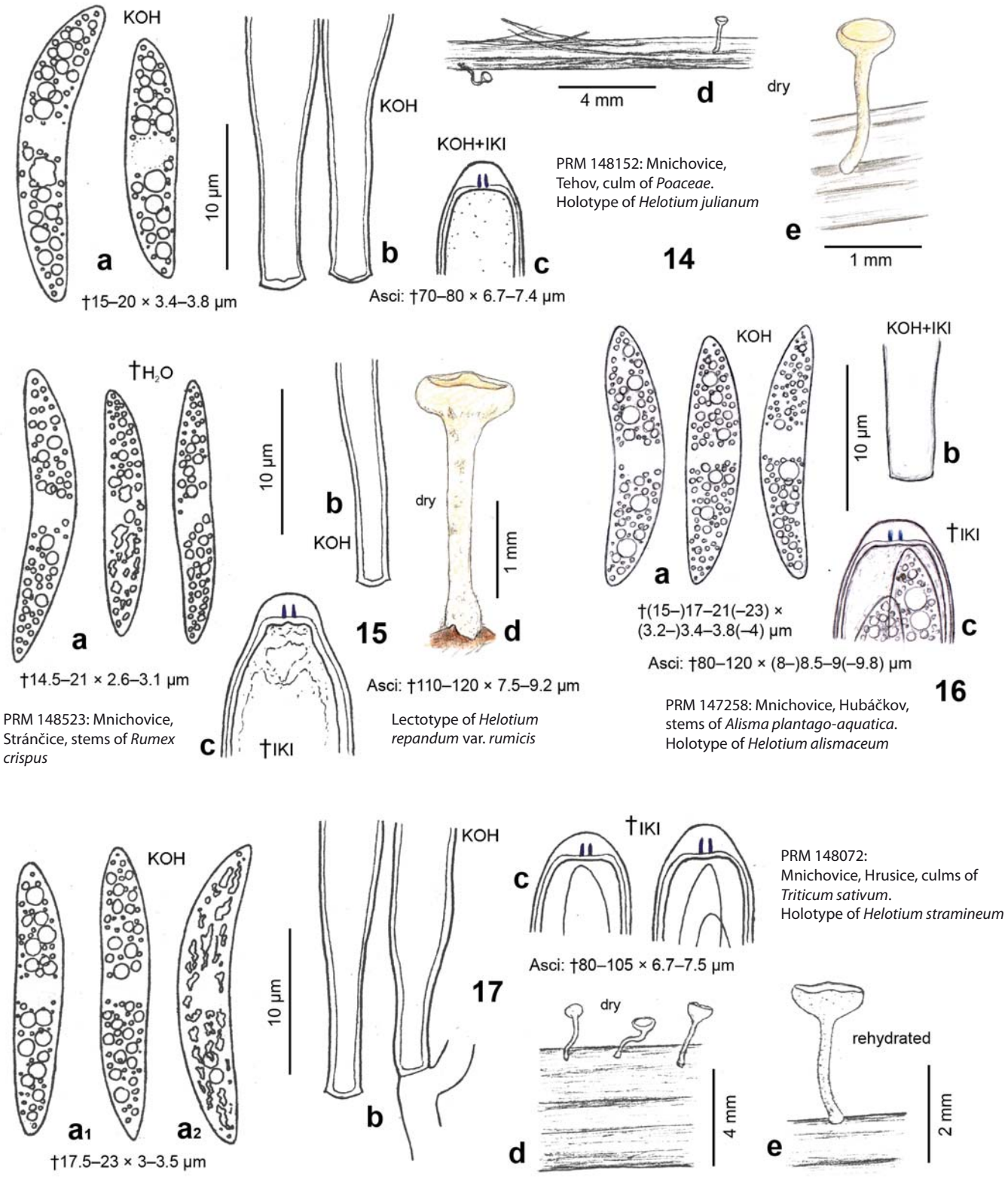
†(14–)16–20(–22.5) × (3.1–)3.3–4(–4.5) µm Asci: †73–100 × (7.5–)8–9.3 µm

K(M) 52786: Shrewsbury, stems of *Mentha* - Lectotype of *Helotium menthae* in Herb. W. Phillips, Elv. Brit. No. 188

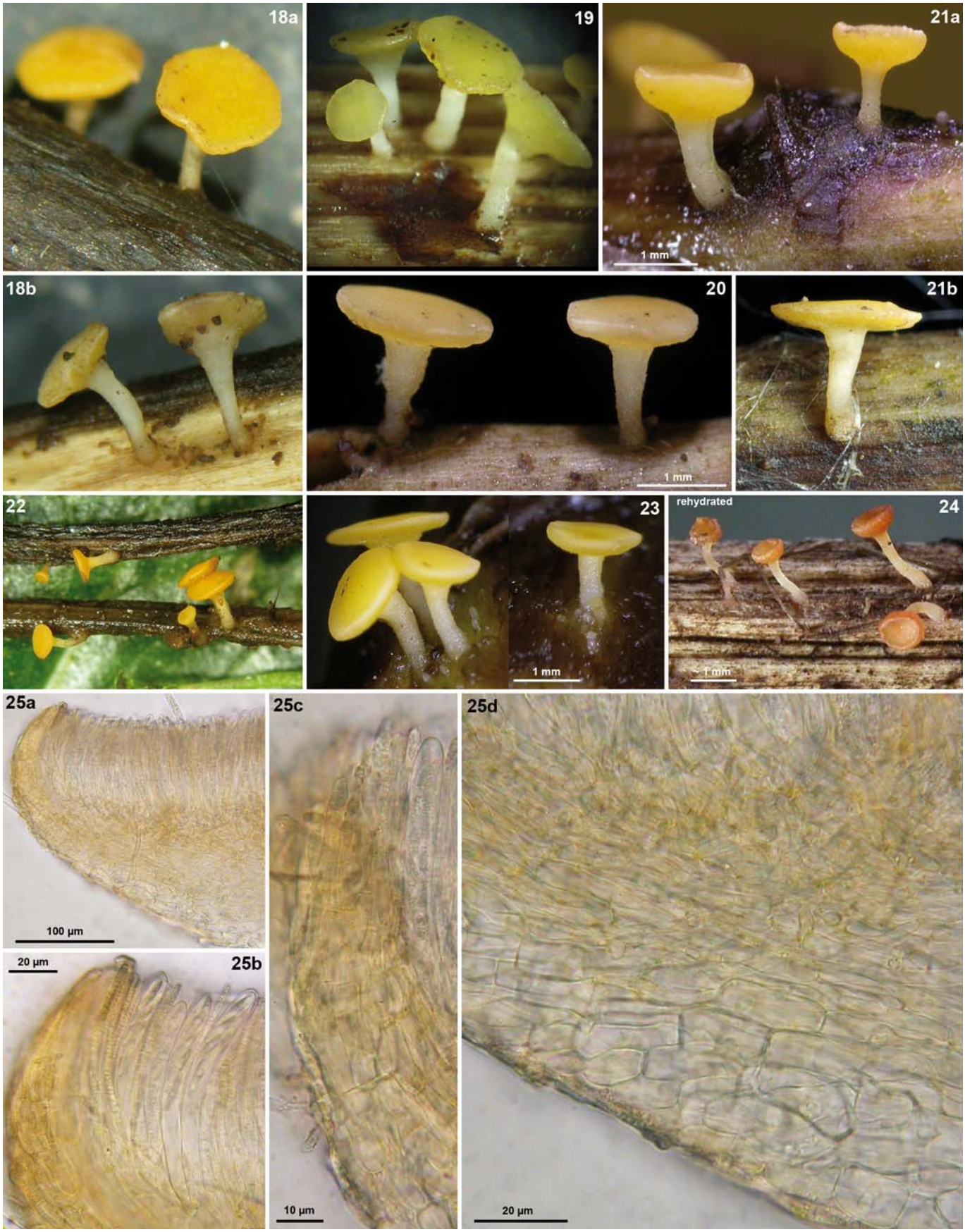
Figs 11–13. *Hymenoscyphus menthae* (type). – a. ascospores (a1: multiguttulate, more or less undistorted lipid pattern, a2: lipid disintegrated or strongly distorted; b. simple-septate ascus bases; c. apices of immature asci in IKI; d. rehydrated apothecia. – All in dead state.

only dead spores with confluent lipid content. Siepe (*loc. cit.*) drew attention to this inferior method of studying herborized samples, resulting in the loss of species-specific characters.

A report by Zhao & Hosoya (2014) under the name *H. menthae* refers to a collection on fruits of *Hydrangea*, with slightly scutuloid spores, judging by their photo (fig. 4 I) and description ("rounded at the proximal end, pointed towards the distal end"), whereas their drawing (fig. 5 E) shows homopolar spores. The asci are said to be "arising from croziers but obscure", and the original oil drop pattern is unknown due to the study of dead herbarium material. The authors refer to the concept of *H. menthae* in Baral & Krieglsteiner (1985), i.e., in the sense of *H. macroguttatus*. A still unreleased sequence of the illustrated collection (TNS-F-40052, AB926063) is said to be 100% identical to another one in GenBank (AY348588, HMAS 75934, as *H.* cf. *menthae*), a sample described by Zhang & Zhuang (2002: 36) on unidentified wood from Sichuan (as *H.* cf. *consobrinus*), with spores "very slightly narrower at one end". This sequence, however, is very unrelated to both *H. macroguttatus* and *H. menthae*. Koukol (pers. comm.) found a fungus on *Fraxinus* petioles in Czechia with almost exactly the same sequence as HMAS 75934.



Figs 14–17. Types of Velenovský's taxa reidentified as *Hymenoscyphus menthae*. – a. ascospores; b. simple-septate ascus bases; c. apices of immature or mature asci in IKI; d–e. dry and rehydrated apothecia. – All in dead state.



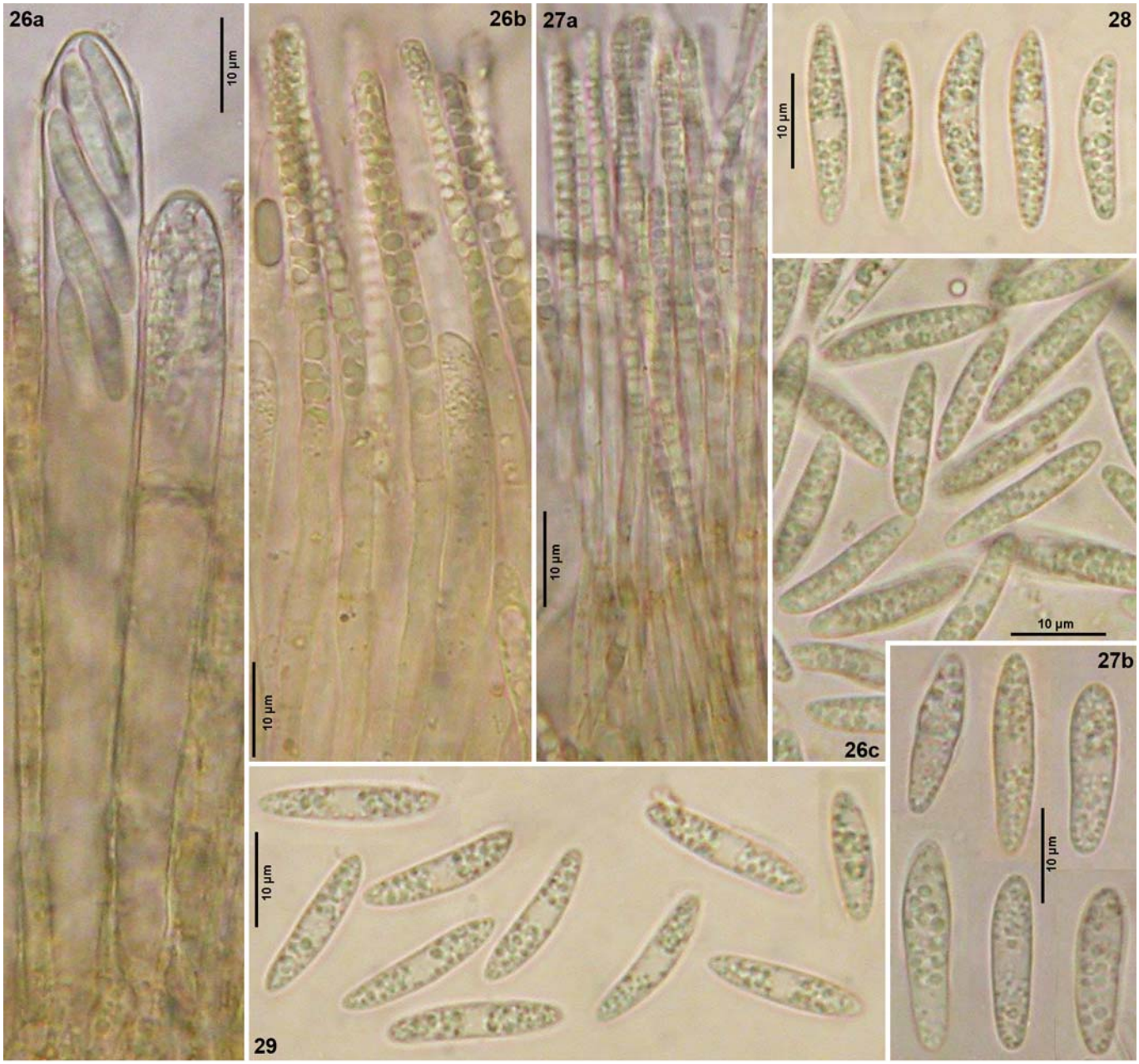
Figs 18–25. Hymenoscyphus menthae. 18–24. apothecia (fresh state, but rehydrated in 24). 25a–d. median section of apothecium, b–c: margin, d: flanks. – All micrographs in living state. – 18. 24.VII.2011 (Luzern, *Impatiens noli-tangere*, photo U. Graf), 19. 29.VII.2010 (Chemnitz, *Fallopia japonica*, photo B. Mühler), 20. H.B. 8581 (Rehna, *Solanum dulcamara*), 21. H.B. 9541 (Yorkshire, *Epilobium hirsutum*), 22. H.B. 8493 (Obwalden, *Caltha palustris*, photo U. Graf), 23. H.B. 8854a (Schwerin, *Epilobium hirsutum*), 24. PRM 147258 (Mnichovice, *Alisma plantago-aquatica*, lectotype of *Helotium alismaceum*).

The brief original description of ***Helotium menthae*** by Phillips (in Phillips & Plowright, 1881: 69; Shropshire, on stems of *Mentha*) does not permit recognition of the species. It includes an egg-yellow disc, a white slender stipe, and fusiform, often curved spores (14–20 × 3–5 µm) being pointed at one or sometimes both ends, containing two to four "nuclei" (oil drops). Probably because no illustration was supplied, the name was rarely taken up by authors. Also no mention was made by Phillips about its relationship to other species. Later, Phillips (1887: 137) reduced his taxon to a variety of *H. scutula*, a view which was followed by other authors, and altered the description to "disc bright yellow", spores with "2 to 3 guttulae".

Authentic material of *H. menthae* was reexamined by Oudemans (1890: 315) and Dennis (1956: 78, fig. 71E). When Oudemans described his *Phialea appendiculata* Oud., an accepted later synonym of *H. scutula*, on *Mentha* in the Botanical Garden of Amsterdam, he examined also authentic *H. menthae* sent to him by W. Phillips for comparison. Oudemans concluded that *P. appendiculata* represents a clearly different species, based on its strongly heteropolar, much larger spores (20–26 × 4–5 µm) with distinct setulae at the ends, also in the quantity of oil drops (2–6 medium-sized guttules in a row). Detailed data on *H. menthae* were not given by him.

Dennis (*loc. cit.*) was apparently unaware of Oudemans' study when he reexamined W. Phillips' type "Elv. Brit. No. 188" in Herb. M.C. Cooke, for which he figured homopolar, non-septate spores with both ends pointed. Dennis placed it in synonymy of *Helotium scutula* var. *solani* (P. Karst.) P. Karst., based on an authentic specimen in Herb. Karsten which, however, deviates by consistently slightly scutuloid spores (Dennis, 1956: fig. 71B). In both specimens, Dennis did not see any setulae on the spores, and his drawings do not show the spore contents. Based on Dennis' restudy, *Hymenoscyphus scutula* var. *solani* (P. Karst.) Ahmad is here assumed to be a synonym of *H. vitellinus* (see below).

In the present reexamination of the type of *H. menthae* (Phillips Elv. Brit. 188, two specimens studied from K, one from M), the spores were found to be very often multiguttulate when still inside the asci (Figs 12–13 [a1]). A size of †(14–)16–20(–22.5) × (3.1–)3.3–4(–4.5) µm was evaluated in KOH or KOH+CR. The asci arise from simple septa and measure †73–100 × (7.5–)8–9.3 µm, and react medium to stron-



Figs 26–29. *Hymenoscyphus menthae*. 26a. mature and immature ascus; 26b, 27.a. paraphyses with refractive vacuoles (VBs) in upper part and minute yellow-orange LBs (carotenoid) in lower part; 26c, 27b, 28, 29. mature, freshly ejected ascospores (in Fig. 29 with delicate sheath). – All in living state. – 26. H.B. 8581 (Rehna), 27. H.B. 8493 (Obwalden), 28. H.B. 8854a (Schwerin), 29. H.B. 8866a (Chemnitz).

gly blue (bb) in IKI. The disc of the rehydrated apothecia was 0.6–1.1 mm diam, the stipe 0.5–1.5(–1.8) × 0.12–0.2 mm. Phillips & Plowright (1881) and Phillips (1887) described the spores as 14–20 × 3–5 µm, acute at one end, sometimes at both, often curved, with 2-4 guttules. The disc is said to have been egg-yellow, plane to convex, the slender stipe and underside of cups white. The three specimens studied by me bear the printed label "188. *Helotium menthae* Phill., Shropshire, Shrewsbury, on dead stems of *Mentha*, *leg*. W. Phillips", and thus concur with the data given by Phillips in the protologue. They are, however, devoid of original handwriting.

A further specimen (K(M) 31758) bears Phillips' original handwriting ("*Helotium Menthae* mihi. On stems of *Mentha sativa*. Shrewsbury") and a sketch of an ascus and some spores ("0.015–02 × 003–005") with granular contents (!). It was sent by Phillips to M.C. Cooke (Dennis, 1956: 78) and was considered by Dennis to be "evidently the type collection". Ascus and spore characters concurred with the above (Fig. 11). The original handwriting would indicate that this is the holotype. However, the collection data given in the protologue read: "Elv. Brit., No. 188 (...) On dead stems of *Mentha*. Shrewsbury". The above spore size falls in the scope given in the protologue. However, since the substrate is identified at the species level and particularly because of the granular spore contents as opposed to large guttules in the protologue, K(M) 31758 is probably a different collection, as was also suggested by Hengstmengel (1996: 203). Dennis was obviously unaware of the fact that Phillips originally published *H. menthae* at the species level, since he cited as basionym "*Hymenoscypha scutula* var. *menthae* Phill., Brit. Discom., p. 137, 1887", and I was likewise unaware in Baral & Krieglsteiner (1985) of the true basionym *Helotium menthae* W. Phillips.

Although my studies indicate that Phillips' material is homogeneous, a lectotype must be chosen. It is most likely that further duplicates of "No. 188" exist, distributed by Phillips in other herbaria, and it seems to be impossible to be sure on which duplicate Phillips based his diagnosis. Phillips issued his exsiccatae in the year when his publication appeared (Hengstmengel, 1996: 201), therefore he possibly made the description before dividing the material. The nomenclatural rules demand that one of the syntypes cited in the protologue must be chosen as lectotype. I designate here the specimen "Phillips, Elv. Brit. No. 188, deposited in K(M) 52786" as the lectotype of Helotium menthae. This consists of ca. 30 apothecia in good condition, two of which I have examined (Fig. 13).

Although Phillips probably described the apothecia in the fresh state, I am forced to suppose that his statement of 2–4-guttulate spores derives from dead material. This would concur with the common practice of gathering microscopic data from herbarium material when preparing the manuscript. A little doubt remains, however, since *H. menthae* may rarely occur as a mixture with *H. macroguttatus* (see below).

In contrast to *H. menthae*, Boudier's (1909: pl. 488) detailed illustration of the holotype of ***Helotium consobrinum*** was based on a fresh specimen and shows living multiguttulate paraphyses and spores, the latter with a homopolar, ellipsoid-fusoid shape (Fig. 30). Boudier (1907: 114) considered his new taxon to differ from *H. virgultorum* and *H. scutula* by multiguttulate spores being acute at both ends, and by a bulbous stipe base. As further characteristics he emphasized the yellow disc and the white, downy stipe. Boudier did not study the ascus base, nevertheless the correct interpretation of *H. consobrinum* by Hengstmengel (1984), Baral & Krieglsteiner (1985) and Siepe (1988) is beyond doubt, and does not necessitate reexamination of the type. A revision of authentic material of *H. consobrinum* seems not to have been done in the past, and type material was not requested in the present study. Grelet (1949: 53) merely copied Boudier's description.

Boudier (1911: 284) stated to have repeatedly seen the species in autumn, always on *Rumex acetosa* ("Oseille"). His measurements of living spores as given in the text (*15–26 × 3–5 µm) concur very well with my present description of *H. menthae* (*15–26 × 3.5–4.5 µm). Also when evaluating the spore size from his plate, the gained measurements [*(12.5–)18.5–25 × 3–4.3 µm] well correspond to mine. This suggests that Boudier's calibration was quite correct, contrary to the current assumption that he gave 10% too high values. In fact, discrepancies in measurements can be explained but the study of herbarium material or the use of lethal reagents (Siepe, 1988; Baral, 1992: 347).

The spores of ***Helotium julianum*** Velen. (from culms of a small grass) are described by Velenovský (1940: 185) as containing minute granules, while they are said to be "eguttulate" in Svrček's (1985: 153) revision (the guttules in the dead spores were invisible because Svrček mounted in water or media like MLZ). The apothecia are said to have originally been white. The synonymy with *H. menthae* was suggested by Svrček (as *H. vitellinus*) and is confirmed here from the reexamined holotype (Fig. 14): nearly all spores are multiguttulate (in KOH), homopolar, and measure 15–20 × 3.4–3.8 µm (Svrček: 17–20.5 × 3–3.5 µm, Velenovský: 20–25 × 5–6 µm). The asci arise from simple septa and are relatively small (70–80 × 6.7–7.4 µm, Svrček: 70–100 × 7–10 µm, Velenovský: 70–80 × 6–8 µm); the apical ring reacts only faintly blue in IKI (Svrček "amyloid"). The large spore width in the protologue is in conflict with the given ascus size which does not permit biseriate spore arrangement, while the spore length excludes a uniseriate arrangement.

Helotium repandum* var. *rumicis Velen. is, according to Svrček's (1985: 172) revision, clearly a synonym of *H. menthae*: Svrček described and figured the spores as "filled with minutely granular content". Also Velenovský (1934: 191) reported them as densely filled with guttules, and the hymenium as egg-yellow ("*vitello*"). Velenovský assigned to this variety records on various herbs and grasses. Actually, a total of 30 specimens are deposited by him under this name at PRM (Svrček, 1985: 172). The present reexamination of the lectotype (Fig. 15) concurs with Svrček's species concept: nearly all spores are multiguttulate (visible already in water), homopolar, and measure in water 14.5–21 × 2.6–3.1 µm (Svrček: 14–21.5 × 3–4 µm, Velenovský: 15–30 µm). The asci arise from simple septa and measure 110–120 × 7.5–9.2 µm (Svrček: 80–95 × 7–8 µm, Velenovský: 80–125 µm). The apical ring is strongly blue in IKI, while Svrček stated "very slightly amyloid". Svrček reported "numerous irregular lumps or crystals in the excipulum (in NH_4OH)". This I consider extracellular lipid which forms round drops upon squeezing. These drops did not stain in CRB, and did not disappear in KOH.

Helotium stramineum Velen., on culms of *Triticum*, was described by Velenovský (1940: 185) without indicating the spore content. The yellow apothecial colour and the large asci and spores suggest *H. menthae*. Svrček (1985: 178) found "eguttulate" spores (probably in water or MLZ). Reexamination of the holotype (Fig. 17) confirms Svrček's opinion nearly all spores are multiguttulate (in KOH), homopolar, and measure 17.5–23 × 3–3.5 µm (Svrček: 16–17.5 × 3–3.5 µm, Velenovský: 18–25 × 2–3 µm). The asci arise from simple septa, and measure 80–105 × 6.7–7.5 µm (Svrček: 85–90 × 8–9.5 µm, Velenovský: 100–130 × 8–10 µm); the apical ring is strongly blue in IKI (Svrček: "amyloid but often also inamyloid").

Helotium alismaceum Velen. was considered by Svrček (1985) as "close probably" to *H. menthae* (as *H. vitellinus*), but to represent a "very distinct species" which differs in the fresh state in a grey-lilac disc and lilac receptacle, also in an angular, almost dentate margin. According to Svrček, the lilaceous colour is due to a "vacuolar pigment" in the slender hyphae of the marginal excipulum (pale violaceous), also in the excipular cells at the base of the receptacle (violet-brownish). Abundant crystals up to 12 µm across were seen by him in the excipulum (unclear whether outside the cells, not drawn on his sketch). Svrček saw both pigment and crystals in the "lectotype" and a presumed topotype collected shortly afterwards on the same substrate (IX.1926, Mnichovice, PRM 148281). Since Velenovský did not mention this second collection in the protologue, the first collection (30.VIII.1926, PRM 147258, Svrček erroneously as 148258) should be taken as the holotype of *H. alismaceum*.

In the present reexamination of the holotype (Fig. 16, 24), no violaceous pigment could be discerned at all, either macroscopically

Fig. 30. ***Hymenoscyphus menthae*** (holotype of *Helotium consobrinum*). – Paris, Montmorency, stems of *Rumex acetosa*. – From BOUDIER (1909: pl. 488).

or inside the cells. The disc was yellowish-cream when rehydrated (Fig. 24), or dirty reddish-brown in the large overmature apothecia. Apparently the lilaceous pigment fades with the age of the material. Whether this pigment represents a species-specific character remains unclear. Also no crystals could be discerned. In KOH the spores are consistently multiguttulate and measure (15–)17–21(–23) × (3.2–)3.4–3.8(–4) µm (Svrček: 18–20.5 × 3.5–4.5 µm, Velenovský: 15–20 × 3 µm). The asci arise from simple septa and measure 80–120 × (8–)8.5–9(–9.8) µm (Svrček: 85–100 × 10–12 µm, Velenovský: 100–120 × 10–12 µm), and the apical ring is strongly amyloid when KOH-pretreated. The overmature spores were 1(–3)-septate and up to 26.5 × 5.5 µm when 3-septate. 3-septate spores were otherwise only seen by Declercq (pers. comm.) in a collection on *Agrimonia* (Fig. 10) and by Hengstmengel (pers. comm.) in one on *Rubus* (H.B. 400b).

Both the holotype and the authentic specimen represent a mixture with the type of *Helotium septembrinum* Velen., a taxon which was thought to be a synonym of *Cyathicula cyathoidea* (Bull. ex Mérat) Thuem. by Svrček (1985: 176, as *Conchatium cyathoideum*), but in the present reexamination it is considered to be a synonym of *Calycina discreta* (P. Karst.) O. Kuntze. There is, however, a very sparse third species in association with the more senescent apothecia of *H. alismaceum* in the holotype, with short and stout apothecial stipes, septate hairs and larger spores (10–14 × 2.5 µm), which Svrček did not mention and which might be a *Calycina* too.

Two specimens in Velenovský's herbarium under the name ***Helotium microsporum*** Velen. were reidentified by Svrček (1985: 160) as *H. vitellinus* (in his sense), while the lectotype of *Helotium microsporum* (on *Lysimachia vulgaris*) was found by him to represent *Lachnum salicariae* (Rehm) Velen.

Intrahymenial parasitism: A hyphomycete that superficially resembles the genus *Acremonium* Link was observed in some senescent apothecia of two collections of *H. menthae*, but so far not in any other discomycete (Fig. 66). The species has characteristic ellipsoid, large-guttulate, hyaline conidia *5–7 × 2.5–3.6 µm formed on narrow, unbranched, hyaline phialides (but sometimes with a single lateral branch). These occur in abundance among the living paraphyses which they slightly exceed, while asci were absent in these apothecia.

The conidia do not cohere in chains and apparently do not form a slimy mass, therefore, they probably do not belong to *Acremonium*. Grauwinkel (1987: 61, figs 22c, 23a) reported conidia produced on "hairs" of the apothecial stipe of *H. menthae*. In my opinion, this is also a hyphomycete which, like the above, grows parasitic on *H. menthae*, but differs in longer fusoid conidia which are formed in chains and contain only two small polar drops. With these characteristics it might represent a species of *Acremonium*.

Phylogeny: Three European strains of *Hymenoscyphus menthae* (from Mecklenburg-Vorpommern, Baden-Württemberg and Liechtenstein) were sequenced from dry apothecia for the ITS rDNA region by Queloz (pers. comm.). The three sequences were completely identical in the entire ITS region, and one of them is present in GenBank (KM114537). A sequence of *H. repandus* (H.B. 9057, ITS+LSU, KT876975) differs by 5.5% in the ITS from *H. menthae*, whereas other species of *Hymenoscyphus* show much higher distances to these two species. It seems probable that also *H. peruni* (Velen.) Svrček will belong in relationship with the above two species, based on their similar morphology which includes homopolar spores and presence of yellow carotenoids.

The closest match in the ITS of *Hymenoscyphus menthae* and *H. repandus* in GenBank (BLAST, 92% similarity) is *Amylocarpus encephaloides* Curr. (= *Plectolitus acanthosporum* Kohlm.), a cleistothecial species of unknown affinities within the *Helotiales*, with ± globose, amyloid ascospores, each with about 25 setulae 5–10 µm long (Kohlmeyer, 1960). With 85–87% similarity, species of *Roesleria*, *Cyathicula*, *Phaeohelotium* and *Cudoniella* appear, but no *Hymenoscyphus* with scutuloid spores. Also when testing a BLAST with the LSU region of *H. repandus* (D1-D2), *A. encephaloides* is with 97% the closest match, and other species appear with 94%, but no sexual state of a *Helotiaceae* is shown. This raises the question whether in the future *H. menthae* and its allies deserve a genus of their own.

Ecology: *Hymenoscyphus menthae* is a plurivorous species that fruits on a large variety of host plants, mainly herbaceous stems, including monocots. The collections on woody plants (including leaves and fruits) examined in the present study concur very well with those on herbaceous stems. Also Hengstmengel (1984 and pers. comm.) and Declercq (pers. comm.) included woody substrates, together 13 collections (twigs and branches, rarely stumps of *Alnus*, *Lonicera*, *Populus*, *Rhododendron*, *Sambucus* and *Salix*). Extraordinary substrates reported by them are female catkins of *Betula*, cupules of *Fagus*, seeds of *Acer*, petioles of *Populus* and *Pteridium*, and jute.

Further herbaceous hosts (genera not mentioned above) recorded by J. Hengstmengel include *Centaurea* sp., and by B. Declercq *Crepis paludosa*, *Geum urbanum*, *Glechoma hederacea*, *Heracleum sphondylium*, *Humulus lupulus*, *Juncus effusus*, *Melandrium rubrum*, *Scutellaria galericulata*, *Stachys palustris*, *Teucrium scorodonia*, and *Valeriana officinalis*. The most frequent hosts of *H. menthae* in Declercq's list are *Epilobium hirsutum*, *Rubus fruticosus*, and *Urtica dioica*.

Krieglsteiner (2004) listed for the Rhön region (between Thüringen, Hessen and Bayern) as further hosts (genera not mentioned above): *Genista tinctoria*, *Geranium silvaticum*, *Stellaria nemorum*, and *Symphytum officinale*. He recorded various plant associations, for instance *Angelico-Cirsietum oleracei*, *Caricetum rostratae*, or *Valeriano-officinalis-Filipenduletum ulmariae*) and characterized the habitat as acidic to base-rich, nutrient-poor or -rich, fresh to wet, sunny or shaded. Also from Mainfranken (region around Würzburg and Schweinfurt) he repeatedly observed *H. menthae* (Krieglsteiner, 1999).

H. menthae starts to fruit very early in summer, usually in June or even May. This concurs with the phenology of *H. repandus* and *H. peruni*, but is in contrast to most of those species which are closely related to *H. scutula* and *H. fructigenus*. This early fruiting of *H. menthae* was also stated by other authors: Siepe (1988) gave 1. June to August, rarely until 1. Oct., based on 13 collections from NW-Germany. Svrček (1985: 173) wrote "already in May". Hengstmengel (1984) noted (May–)July–Sept.(–Nov.) for 16 collections from the Netherlands. A further 23 collections from his country which he studied at a later date, are mainly from (May–)June–Aug. but also Sept.–Oct. Declercq's 236 samples derive with rather equal frequency from May–Oct., but rarely also from Apr. and Nov. This suggests that the fungus shows a longer fruiting period in (sub)atlantic regions due to a milder climate (see Tab. 1). Engel (1987), however, gave 9.IX.–12.XI. for 8 collections on *Sambucus ebulus*, and Boudier's holotype was even collected in December (Boudier, 1907).

During my visit to R.P. Korf's laboratory in Ithaca (New York) in 1985, I was able to collect and examine *H. menthae* near his estate Exe Island in Canada in the fresh state. The species seems therefore to be widespread in the northern hemisphere.

Specimens included (all on dead herbaceous stems or culms if not otherwise indicated):

Canada: Ottawa, 85 km S of Ottawa, 4 km NW of Portland, Big Rideau Lake, Exe Island, 125 m, indet. dicot. herb, 3.VIII.1985, H.O. Baral (ø). — **Great Britain: Yorkshire**, 11.5 km E of Doncaster, 2.4 km SE of Lindholme, Hatfield Moor, 2 m, *Epilobium hirsutum*, 17.V.2011, J.H. Petersen & T. Laessøe (J.H.P.-11.139, H.B. 9541 ø). – **West Midlands**, Shropshire, Shrewsbury, ~70 m, *Mentha*, undated, collector unknown [Phillips, Elv. Brit. No. 188, K(M) 52786, lectotype of *Helotium menthae*; K(M) 52787, M-0206414, isolectotypes, H.B. 4496 ø]. – ibid., "*Mentha sativa*" (= *M.* × *verticillata*), collector unknown [M.C. Cooke, Herb. Mycol. 1885, K(M) 31758, paratype, H.B. 5881 ø]. – 4.5 km NNE of Telford, S of Muxton, Muxton Marsh, 88 m, *Cirsium*, 8.IX.2013, P. Thompson (P.T. 8/9/13 No. 15, d.v.). – **Herefordshire**, 26 km NNW of Hereford, 1.5 km WNW of Yarpole, Croft Castle Estate, 160 m, indet. herbaceous stem, 9.VIII.1996, A. Leonard, vid. B. Spooner (K(M) 180206, n.v.). – **East England, Cambridgeshire**, 11 km W of Peterborough, Nene valley, 15 m, *Lythrum salicaria*, 1.IX.2013, M. Yeo (M.Y.). – **South East England, Hampshire**, 5.5 km N of Lymington, ~2 km SE of Brockenhurst, New Forest, Royden Reserve, 20 m, indet. herbaceous stem, 9.VIII.1996, A.C. Leonard, vid. B. Spooner (K(M)

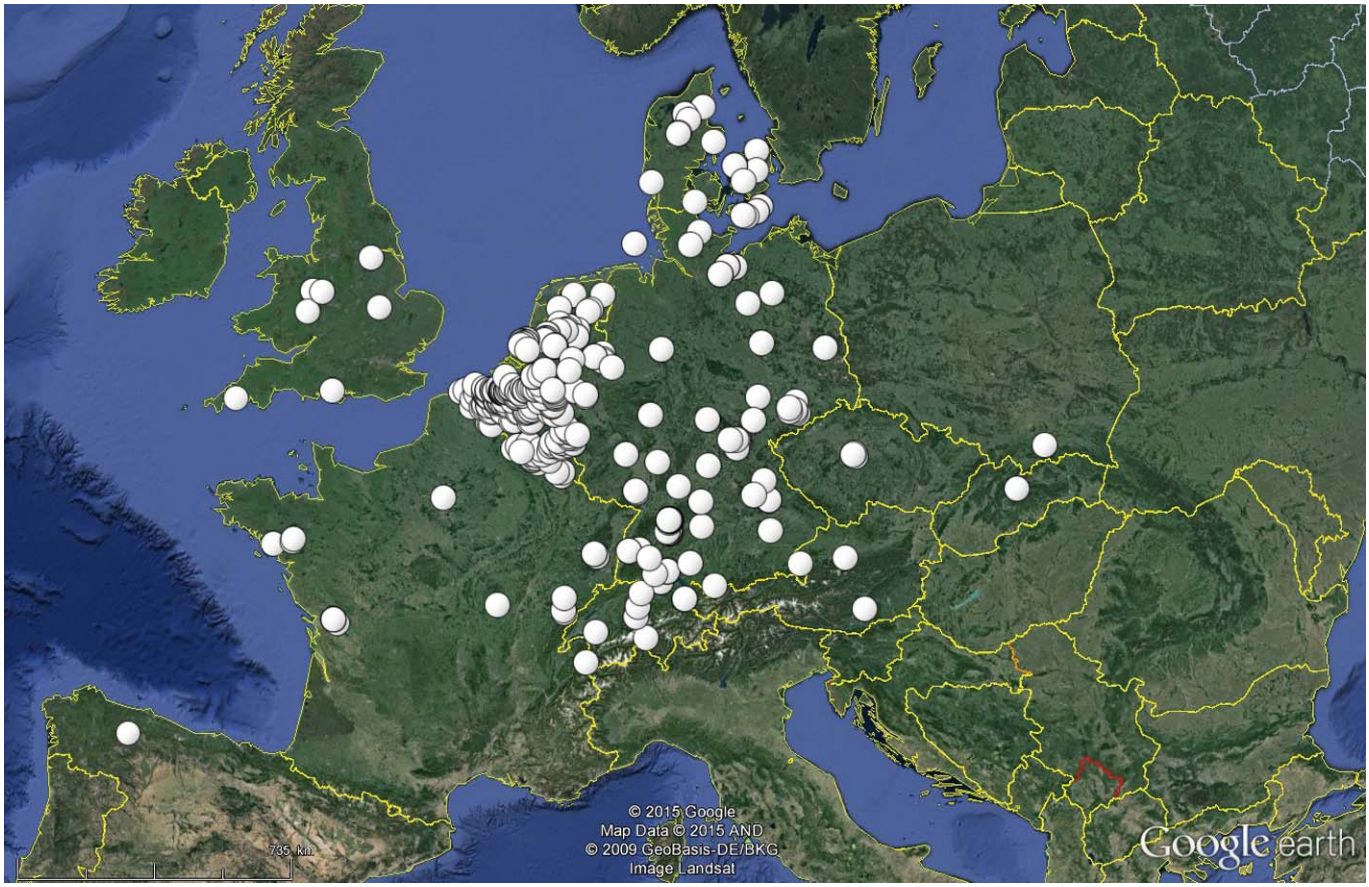


Fig. 31. Known distribution of *Hymenoscyphus menthae* [including data from J. Hengstmengel, B. Declercq and T. Læssøe (pers. comm.) which are not in the list of included specimens]. Further records within Germany are found, e.g., in the database of the German Mycological Society (DGfM).

39418, n.v.). – **South West England, Cornwall**, 8 km ESE of St. Austell, 3 km WSW of Fowey, Menabilly, 40 m, twig of indet. woody plant, 16.V.1982, E. Batten (K(M) 163384, E.B. 779, n.v.). – **Netherlands: Utrecht**, 5 km SE of Amersfoort, S of Leusden, 5 m, *Lysimachia vulgaris*, 7.XI.1979, T. Boekhout, vid. J. Hengstmengel (L, d.v.). – **Gelderland**, 11 km ENE of Nijmegen, NW of Kekerdom, 10 m, ?*Mentha*, 29.VI.2002, S. Helleman (S.H. 239, d.v.). – **Noord-Brabant**, 1 km W of Boxmeer, Brestbos, 18 m, stems of *Saponaria officinalis*, 18.IX.2015, S. Helleman (S.H. 838). – **Belgium: West-Vlaanderen**, 14.5 km ENE of Kortrijk, 3 km SE of Waregem, OudMoregembos, 45 m, twig of *Alnus*, on wood, 15.VI.1991, B. Declercq (B.D. 91/063). – **Oost-Vlaanderen**, 24 km NE of Gent, 3.2 km NW of Sinaai, Heirnisse, *Zea mays*, 4.VI.1994, B. Declercq (B.D. 94/082). – 16 km NNE of Gent, 1.3 km NW of Wachtebeke, railway through OCMW-forest, 12 m, *Agrimonia eupatoria*, 21.X.1987, B. Declercq (GENT, B.D. 87/194.1, H.B. 5878 ø). – 2.5 km SSE of Wachtebeke, Puyenbroeck, 8 m, twig of *Populus*, on wood, 16.VIII.1985, B. Declercq (B.D. 85/205, H.B. 5871 ø). – **Limburg**, 4.5 km SW of Genk, 2.5 km E of Bokrijk, De Maten, 44 m, leaf of *Typha latifolia*, 26.VI.1992, B. Declercq (B.D. 92/072). – 5 km SW of Genk, 4 km NNE of Diepenbeek, Augustijnenvijver, 45 m, petioles of *Pteridium aquilinum*, 5.VIII.1991, B. Declercq (B.D. 91/090). – **Wallonie**, Namur, 19 km NE of Charle-Ville, 0.2 km SE of Vresse, Pont des Deux Eaux, 190 m, branch of *Alnus*, on wood, 21.VII.1994, B. Declercq (B.D. 94/098). – **France: Bretagne**, Morbihan, 5.3 km S of La Gacilly, La Provostaie, 4 m, *Epilobium*, 3.VI.2008, J.-P. Priou (J.P.P. 28118, d.v.). – 0.3 km E la Gacilly, 11 m, dicot. herb, 3.VII.2015, J.-P. Priou (J.P.P. 15147, d.v.). – 7.3 km SSE of Vannes, SSE of Séné, 1 m, *Poaceae*, 6.VI.2009, J.-P. Priou (J.P.P. 29105, d.v.). – **Poitou-Charentes**, Deux-Sèvres, 12.5 km WSW of Niort, 1 km ENE of Le Vanneau-Irleau, Marais Poitevin, *Lycopus europaeus* and *Eupatorium cannabinum*, 3 m, 31.V. and 24.VI.2007, M. Hairaud (M.H. 40607, d.v.). – 10.5 km SSW of Niort, 1.8 km NW of Granzay-Gript, river La Courance, 25 m, *Angelica sylvestris*, 8.VI.2007, M. Hairaud (M.H. 100607, d.v.). – **Île-de-France**, Val-d'Oise, ~15 km N of Paris, Montmorency, 'dans les champs', ~100 m, undated, *Rumex acetosa*, collector unknown (type of *Helotium consobrinum*, d.v.). – **Lorraine**, Vosges, 4.5 km NE of Gérardmer, Col et l'Etang de Martimpré, MTB 7807/3, 795 m, ?*Cyperaceae*, 18.VI.1989, H.-O. Baral & J. Deny (ø). – ibid., *Mentha*, 18.VI.1989 (ø). – 8.5 km ESE of Gérardmer, Lac de Retournemer, MTB 7907/2, 780 m, root of ?*Potentilla palustris*, 23.VI.1990, E. Weber (ø). – **Franche-Comté**, Doubs, 5 km SE of Besançon, E of La Vèze, marais de Saône, 385 m, *Cirsium*, 13.IX.2013, G. Moyne (ø, d.v.). – 30.5 km S of Besançon, 3,8 km WNW of Levier, 702 m, *Senecio fuchsii*, 11.VI.2010, G. Moyne (ø, d.v.). – 4.3 km SSW of Levier, Forêt de Maublin, 795 m, indet. herb, 5.IX.2012, G. Moyne (ø, n.v.). – **Bourgogne**, Saône-et-Loire, 12 km WNW of Autun, NNE of La Grande-Verrière, 400 m, *Apiaceae*, 23.X.2015, J.-P. Priou (J.P.P. 15188). – **Rhône-Alpes**, Haute-Savoie, 6 km NE of Passy, Chatelet d'Ayères, 1390 m, indet. herb, 1.VII.2004, J.-L. Cheype (d.v.). – **Spain: Asturias**, 11 km NW of Villablino, W of Puerto de Leitariegos, 1540 m, *Caltha palustris*, 15.VII.2008, J. Linde, vid. E. Rubio (E.R.D. 3616, d.v.).– **Germany: Schleswig-Holstein**, Helgoland, Oberland, ornithological station, MTB 1813, 50 m, indet. dicot. herb, 31.VIII.1985, T.R. Lohmeyer (T.L. 85/96). – 15 km ESE of Eckenförde, NW of Felm, An der Wurth, 20 m, indet. dicot, 6.IX.2014, M. Kamke (M.K. 315/14, n.v.). – 6.7 km W of Nortorf, 1.3 km WNW of Burgstedt, inflorescence of *Cirsium*, 50 m, 17.VIII.2014, H. Lehmann & M. Kamke (M.K. 287/14, d.v.). – 4.5 km SSE of Mölln, 4 km NW of Gudow, Drüsen-See, 24 m, *Mentha aquatica* and *Lycopus europaeus*, 16.VI.2012, T. Richter & M. Lüderitz, vid. M. Kamke & T. Richter (M.K. 45/12, n.v.). – **Nordrhein-Westfalen**, 9.5 km NE of Borken, WSW of Velen, Landsberg-Allee, MTB 4107, 60 m, *Urtica dioica*, 6.VII.1983, K. Siepe (ø). – 3.5 km NE of Stadtlohn, Almsicker Bahnhof, MTB 3907/4, 55 m, cupule of *Aesculus hippocastanum*, 28.VI.1991, K. Siepe (K.S. 91/19). – 9.7 km NE of Borken, Velen, Geeste, 58 m, indet. *Apiaceae*, 4.VII.1984, K. Siepe (K.S. 84/51). – 6 km E of Haltern, E of Overath, Hullerner Stausee, 52 m, indet. dicot herb, 1.X.1995, F. Kasparek & K. Siepe (ø, d.v.). – 21 km WNW of Mönchengladbach, 3 km NW of Brüggen, Depot, MTB 4702/2, 63 m, indet. dicot, 2.VII.2013, H. Bender (ø, d.v.). – 2.5 km SE of Mönchengladbach, Bresgespark, 55 m, *Urtica dioica*, 21.IX.2008, H. Bender (ø, d.v.). – 2.5 km E of Mönchengladbach, Volksgarten, MTB 4804/2, 50 m, indet. angiosperm twig, 26.VIII.2013, H. Bender (ø, d.v.). – Mecklenburg-Vorpommern, 8 km SW of Rehna, 2.7 km NE of Dechow, Staatsforst Rehna, MTB 2231/4, 60 m, *Impatiens noli-tangere*, 25.VI.2007, T. Richter (d.v.). – ibid., *Lycopus europaeus*, 18.VII.2007, T. Richter (ø). – ibid., *Solanum dulcamara* (H.B. 8581 ø). – 15 km NE of Schwerin, 7 km ENE of Gadebusch, Vietlübber See, 52 m, *Epilobium hirsutum*, 18.V.2008, T. Richter (H.B. 8854a, sq.: ined.). – 5.5 km SSE of Mölln, 3.5 km NW of Gudow, Krebssee, 35 m, leaves of *Iris pseudacorus*, 30.V.2009, T. Richter (n.v.). – 10 km W of Wittenberge, N of Wanzer, Aland-Niederung, Hohe Garbe, 17 m, *Lysimachia vulgaris*, 13.VI.2015, T. Richter (n.v.). – **Sachsen**,

15 km NW of Chemnitz, 3 km NW of Burgstädt, Brausetal, MTB 5042/4, 270 m, indet. dicot. herb, 19.VIII.1995, M. Eckel (M.E. 95/2606). – 10 km WNW of Chemnitz, 2.2 km ENE of Limbach-Oberfrohna, NE of Schafteich, 360 m, *Zea mays*, 30.VIII.2013, B. Mühler (ø). – 24 km NNE of Chemnitz, 1.2 km ENE of Beerwalde, 260 m, fruit of *Acer*, 17.VI.2012, B. Mühler (ø, d.v.). – 3 km ENE of Chemnitz, Zeisigwald, MTB 5143/4, 370 m, *Fallopia japonica*, 29.VII.2010, B. Mühler (ø, d.v.). – 9 km ESE of Chemnitz, 2.5 km W of Erdmannsdorf, Edelmannsbachtal, 375 m, *Cirsium*, 12.VI.2008, B. Mühler (H.B. 8866a ø). – 6 km NNE of Chemnitz, W of Glösa, Kinderwaldstätte, 330 m, *Scirpus silvaticus*, 26.VII.2014, B. Mühler (ø, d.v.). – **Thüringen**, 4 km WSW of Sonneberg, 1 km NW of Wildenheid, 355 m, ?*Apiaceae*, 1.VII.2012, I. Wagner (d.v.)– 3 km SSE of Sonneberg, 1 km SE of Oberlind, Mittlere Flutmulde, 368 m, *Impatiens glandulifera*, 12.VII.2013, I. Wagner (d.v.). - 3.5 km S of Sonneberg, 3.3 km E of Neustadt, Unterlind, Steinach, 350 m, *Impatiens glandulifera*, 22.VII.2014, I. Wagner (d.v.). – 7.5 km SE of Neustadt, 1.5 km SW of Sichelreuth, Herrenteiche, 330 m, *Impatiens glandulifera*, 28.VIII.2013, I. Wagner (d.v.). – **Rheinland-Pfalz**, 14 km NW of Bingen, Bacharach, park, MTB 5912/2, 75 m, ?*Rubus idaeus*, ~10.VII.1990, G. Grangladen (ø). – 3.5 km SSW of Neustadt, W of Hambacher Schloß, MTB 6614/4, 340 m, ?*Rumex*, 19.VII.1976, R. Thate (R.T. 1230, KR). – ~5 km W of Neustadt, 2 km S of Lambrecht, Heidenbrunner Tal, MTB 6614/1, 250 m, indet. herb, 22.VI.1976, R. Thate (R.T. 1211). – **Hessen**, 8 km NE of Darmstadt, 2 km SSW of Messel, Sülzwiese, MTB 6018/3, 155 m, indet. herbaceous plant, 2.VIII.1977, H.O. Baral & P. Zinth (ø). – **Baden-Württemberg, Stuttgart**, 5.2 km WNW of Stuttgart, 2.2 km S of Weilimdorf, Möglinger Stellerain, MTB 7220/2, 380 m, *Rubus fruticosus*, 22.IX.1975, H.O. Baral (ø). – ibid., *Rumex*, 13.IX.1975, H.O. Baral (H.B. 457 ø). – ibid., *Rumex*, 11.VII.1976, H.O. Baral (with ?*Acremonium*, ø). – ibid., *Rumex*, 18.VII.1976, H.O. Baral. – ibid., *Cirsium*, 22.IX.1975, H.O. Baral. – ibid., 380 m, *Lamium galeobdolon*, 13.IX.1975, H.O. Baral (H.B. 455 ø). – 1.8 km S of Weilimdorf, Hasenbrünnele, MTB 7220/2, 360 m, *Lamium galeobdolon*, 13.VI.1976, H.O. Baral (ø). – 1.5 km SSW of Weilimdorf, Frauenholz, MTB 7120/4, 365 m, *Rubus idaeus*, 14.IX.1975, H.O. Baral (H.B. 1698). – ibid., ?*Angelica sylvestris*, 27.VIII.1985, O. Baral (ø). – 1.2 km NE of Solitude, Sandkopf, Daimlerplatz, MTB 7220/2, 426 m, indet. dicot. herb, 11.VI.1975, H.O. Baral (H.B. 284 ø). – ibid., 22.VII.1977, H.O. Baral (ø). – ibid., 15.VI.1975, H.O. Baral (H.B. 1911b). – ibid., *Lysimachia vulgaris*, 29.VII.1976, H.O. Baral (ø). – 0.8 km S of Bergheim, Vogelsang, MTB 7220/2, 400 m, on leaf of indet. deciduous tree, 21.VI.1976, H.O. Baral (ø). – 3 km SSE of Solitude, Glems, MTB 7220/2, 430 m, ?*Solanum dulcamara*, 11.VI.1976, H.O. Baral (ø). – Rotwildpark, MTB 7220/2, *Impatiens*, 21.VI.1976, H.O. Baral. – 2 km SW of Feuerbach, Heimberg, MTB 7220/2, 330 m, ?*Urtica dioica*, 11.VII.1975, H.O. Baral (H.B. 345 ø). – 1 km E of Büsnau, Pfaffenwald, MTB 7220/4, 415 m, *Chamaenerion angustifolium*, 5.VIII.1976, H.O. Baral (ø). – 1 km SE of Gerlingen, Gänsewiesenweg, MTB 7220/1, 385 m, root of indet. dicot. herb, 5.VIII.1976, H.O. Baral (ø). – **Schönbuch**, 10.5 km NNE of Tübingen, N of Dettenhausen, Gärtnerei Zimmermann, MTB 7320/4, 415 m, *Thalictrum dipterocarpum*, 24.IX.1988, G. Haupter (ø). – ibid., *Anthemis nobilis*, 24.VIII.1987, G. Haupter (H.B. 3250a ø). – ibid., *Coreopsis verticillata*, 12.X.1987, G. Haupter (H.B. 3250b ø). – 5.5 km NNW of Tübingen, 2.2 km NNW of Bebenhausen, Jungfernhäule, MTB 7420/1, 390 m, *Solanum dulcamara*, 15.VII.1988, H.O. Baral (ø). – 1 km SSW of Bebenhausen, Geißhalde, MTB 7420/1, 465 m, indet. dicot. herb, 28.VI.1977, H.O. Baral (ø). – 5 km NE of Tübingen, S of Pfrondorf, Obere Mähder, MTB 7420/4, 390 m, *Rubus idaeus*, 4.VIII.1988, H.O. Baral (ø). – ibid., 375 m, *Lysimachia vulgaris*, 30.VII.1987 (ø). – ENE of Pfrondorf, Tiefenbach, MTB 7420/2, 400 m, twig of ?*Euonymus europaeus*, 19.VII.1986, H.O. Baral (ø). – 2 km NE of Pfrondorf, Zeitungseiche, MTB 7420/2, 470 m, *Impatiens nolitangere*, 18.VIII.1988, H.O. Baral (ø). – 2.8 km NNE of Pfrondorf, Büchelersklinge, MTB 7420/2, 450 m, *Solanum dulcamara*, 27.VII.1997, H.O. Baral (H.B. 5873a, with ?*Acremonium*, sq.: ined.). – ibid., *Solanum dulcamara*, 20.IX.1998 (ø). – **Schwarzwald**, 0.6 km SW of Hornberg, Storenbach, 450 m, *Impatiens glandulifera*, 31.VIII.2014, H.O. Baral (H.B. 9923b ø). – 2 km SW of Schwenningen, ENE of Zollhaus, Kugelmoos, MTB 7917/3, 713 m, *Filipendula ulmaria*, 26.VII.1988, H.O. Baral (ø). – 8 km NE of Emmendingen, ~1.7 km SE of Freiamt, MTB 7813/1, 390 m, *Rubus idaeus*, 30.VIII.1975, H.O. Baral, vid. J. Hengstmengel (H.B. 400b, d.v.). – ibid., ?*Rumex* (H.B. 346 ø). – 8 km NE of Radolfzell, 1 km SE of Bodman, S of castle, Grieß, MTB 8220/1, 430 m, *Fallopia japonica*, 19.VIII.1976, H.O. Baral (ø). – ibid., 20.VII.1975, H.O. Baral (H.B. 378 ø). – ibid., 23.VII.1975, H.O. Baral (H.B. 377 ø). – **Oberschwaben**, 5.3 km E of Aulendorf, 4.5 km NW of Bad Waldsee, Brunnenholzried, MTB 8024/1, 575 m, indet. dicot. herb, 3.VIII.1977, H.O. Baral (ø). – **Bayern, Oberfranken**, 7 km NE of Lichtenfeils, 2 km SSW of Weidhausen, Eisenberg, 310 m; 1.5 km S of Weidhausen, Mäuresrangen & Rangen, 330 m, MTB 5832; 10 km NNW of Coburg, 1.7 km SW of Tremersdorf, Finkenflug, 480 m, MTB 5631; *Sambucus ebulus*, 9.IX.–12.XI.1986, H. Engel (H.E., d.v.). – **Unterfranken**, 23 km ENE of Würzburg, ESE of Volkach, Halbmeilesee, 230 m, indet. herb, 20.VI.1995, L. Krieglsteiner (n.v.). – **Oberpfalz**, 11.5 km NNE of Amberg, 1.3 km SW of Hirschau, Kreuzweiher, MTB 6437/4, 420 m, indet. dicot. herb, 4.IX.1987, E. Weber (REG). – 5.5 km NW of Velberg, Deusmauer Moor, 470 m, indet. herb, 8.VII.1994, L. Krieglsteiner (L.K., n.v.). – 6.5 km NW of Regenstauf, 1.3 km WSW of Ziegelhütte, Irrweiher, MTB 6838/1, 360 m, *Peucedanum palustre*, 27.VII.1990, E. Weber & H.O. Baral (ø). – ibid., ?*Galeopsis bifida* (ø), 27.VII.1990, H.O. Baral & E. Weber. – **Niederbayern**, 5.5 km WNW of Landshut, NNW of Eugenbach, Bucher Graben, MTB 7438, 425 m, on debris of indet. woody plant, 1.IX.1991, G. Rambold (M). – **Schwaben**, 2 km E of Bad Oberdorf, 1.3 km SSE of Oberjoch, 1450 m, *Caltha palustris* and *Ranunculus aconitifolius*, 27.VI.2008, S. & P. Rönsch (P.R., d.v.). – **Switzerland: Thurgau**, 4.5 km NW of Frauenfeld, ~S of Horben, Ittingerwald, MTB 8419/1, 485 m, ?*Lamiaceae*, 13.VI.1985, P. Blank (P.B. 34). – ibid., indet. dicot. herb, 24.VI.1986, P. Blank (P.B. 227) – 4 km NW of Schaffhausen, 2.3 km WSW of Thayngen, Moos, MTB 8218/3, 430 m, *Iris pseudacorus*, 28.VII.1988, P. Blank (ø). – **Aargau**, 4 km WNW of Bremgarten, 1.5 km NE of Wohlen, 480 m, indet. angiosperm wood, 21.V.2011, U. Graf (ø). – **Luzern**, 9 km NW of Luzern, 1 km S of Neuenkirch, Buechberg, 600 m, *Impatiens noli-tangere*, 24.VII.2011, U. Graf (ø, d.v.). – **Obwalden**, 7 km W of Sarnen, 4 km WNW of Salden, Glaubenberg, Ritzenmatt NE of Hohnegg, 1420 m, *Caltha palustris*, 12.V.2007, U. Graf (H.B. 8493 ø). – **Tessin**, 13 km WSW of Airolo, 2.3 km SW of All'Acqua, E of Alpi di Cruina, *Caltha palustris*, 1800 m, 2.VI.1988, P. Blank (P.B. 732). – **Fribourg**, 16 km NNE of Montreux, 5 km WSW of Gruyères, N of Mt. Moléson, Les Joux Devant, 1270 m, *Caltha palustris*, 13.VI.2009, N. Van Vooren (N.V. 2009.06.17, d.v.). – **Liechtenstein:** 4 km WNW of Feldkirch, 1.8 km NE of Ruggell, Ruggeller Riet, MTB 8721, 430 m, *Solidago* ?*canadensis*, 8.VII.1997, R. Wiederin, J.P. Prongué & H.O. Baral (H.B. 5846a, J.P.P., sq.: KM114537). – ibid., twig of *Sambucus nigra*, on wood (H.B. 5846b). – **Austria: Steyr**, 17 km SW of Steyr, WSW of Obergrünburg, Tiefenbach, MTB 8051/3, 400 m, *Rumex*, 26.VII.1993, K. Helm (ø). – **Czechia: Bohemia**, 28 km SE of Praha, 3.3 km SE of Mnichovice, Hrusice, new cemetry, 380 m, *Triticum aestivum* (as *T. sativum*), VI.1939, J. Velenovský (PRM 48072, holotype of *Helotium stramineum*, H.B. 5820 ø). – 4 km NNW of Mnichovice, Tehov, 450 m, indet. *Poaceae*, 11.VII.1938, J. Velenovský (PRM 148152, holotype of *Helotium julianum*, H.B. 5821 ø). – 2-3 km NW of Mnichovice, Stráncice, 420 m, *Rumex crispus*, X.1927, J. Velenovský (PRM 148523, lectotype of *Helotium repandum* var. *rumicis*, H.B. 5822 ø). – 3 km SSE of Mnichovice, W of Hrusice, Hubáčkov, 325 m, *Alisma plantago-aquatica*, 30.VIII.1926, J. Velenovský (PRM 147258, lectotype of *Helotium alismaceum*, H.B. 8050a ø). – **Poland: Lesser Poland**, 9.5 km NNW of Nowosądecki, SE of Tęgoborze, Dunajec water reservoir, *Polygonum*, 27.VII.1991, K. Henke (M). – **Slovakia: Baskobystrický kraj**, Lower Tatra, 15 km NNW of Brezno, on the south slopes of Chopok above Srdiečko, ?1600 m, 7.IX.1960, J. Kubička (n. 199, Svrček, 1962: 100).

Hymenoscyphus macroguttatus Baral, Declercq & Hengstm., *in* Baral *et al*., *Sydowia*, 58 (2): 157 (2006) – Figs 32–51.

≡ *Hymenoscyphus pteridicola* K.S. Thind & M.P. Sharma, *Nova Hedw.*, 32: 125, figs 5–7 (1980), *nom. illegit.* [non *Hymenoscyphus pteridicola* (P. Crouan & H. Crouan) Kuntze, = *Cyathicula pteridicola* (P. Crouan & H. Crouan) Dennis].

Typification: India, Jammu, Batote, Sanasar, petioles of *Pteris vitatta*, 6.IX.1973, M.P. Sharma (PAN 3988, holotype).

Etymology: *macroguttatus* referring to the large lipid bodies in the mature living ascospores; *pteridicola* growing on ferns.

Misapplication: *H. menthae s.* Baral & Krieglsteiner (1985), Hengstmengel (1996), Zhang & Zhuang (2002) = *H. macroguttatus*; *H. scutula var. solani s.* Korf & Zhuang (1985) = *H. macroguttatus*.

Apothecia erumpent from minute cavities beneath the epidermis {5}, also superficial if epidermis absent, scattered to ± gregarious in rather small groups, solitary, rarely two emerging from one spot; disc fresh 0.5–2(–2.5) mm diam. {18}, milky-white to pale cream {11}, sometimes pale yellow {7}, round, slightly concave to flat with somewhat raised margin {12}, becoming medium convex with age {4}, margin and exterior smooth or finely pubescent, whitish; stipe 0.2–0.4 {1}, 0.4–1.5 {15}, 1.5–3 mm {6}, or 2–7(–10) mm {5} long, (0.1–)0.15–0.3(–0.35) mm {11}, below receptacle sometimes 0.4–0.5 mm wide {3}, concolorous, smooth or finely pubescent-velvety, towards base partly pale to bright (reddish-)brown {9}, usually narrowed, rarely slightly bulbous; exterior of senescent apothecia turning cream-ochraceous to redbrown {9}, hymenium becoming yellowish-cream or sometimes orange with age. **Asci** *90–115(–120) × 9–10.8 {8} or 10.3–11.8 µm {2}, †(70–)75–100(–107) × (7.7–)8–10(–11) µm {13}, 8-spored, spores (*) obliquely biseriate, (†) biseriate or ± uniseriate

below, *pars sporifera* *41–52 µm long {6}, †55–75 µm {2}; apex of dead asci slightly to strongly conical(-truncate), apical dome †2.3–2.6 → 1–2.2 µm thick, apical ring strongly {11} or faintly {1} blue (BB) in IKI, occupying the lower 1/2–2/3 {7} or 2/3–9/10 {13} of dome, *Hymenoscyphus*-type (sometimes also *Calycina*-like, Fig. 49b); base with ± short stalk arising from croziers {28} (very rarely with an "arch" surrounding a small perforation, Fig. 41). **Ascospores** free *(14.5–)16–20(–21)((–25)) × (3.5–)3.8–5(–5.5) µm {18}, †(15–)16.5–21(–22.3) × (3.2–)3.5–4.3(–5) µm {13}, always non-septate within the living mature asci, cylindric-fusoid-naviculate (cigar-shaped), rarely with slight median constriction, homopolar with both ends shortly tapered {27} (obtuse to subacute), sometimes very slightly scutuloid {4}, straight to very slightly curved or inequilateral, no sheath observed, without setulae {22} but sometimes with ca. 0.3–0.5(–1) µm long minute appendages {6} (difficult to see); living spores consistently with two large refractive LBs (1.8–)2.5–3.3(–4) µm diam. close to the central nucleus and 1(–2) smaller ones (1–2.5 µm diam.) towards each end {25}, these are surrounded by numerous minute LBs (high lipid content), wall surface CRB– {2}; aged spores becoming 1-septate {2}, somewhat increasing in width, remaining hyaline and smooth. Paraphyses apically straight, cylindrical {11} or slightly inflated (fusoid-submoniliform) {4}, rounded, terminal cell *(23–)28–50(–58) {2} × 2.5–4 {2} or (3–)4–5.6 {2} µm, †15–58 {3} × 2–3 {4} or 3–4(–4.3) {3} µm, lower cells *9–25(–30) × (2.2–)3–3.5(–5) µm {3}, †(1.7–)2.5–3 µm wide; VBs multiguttulate, rather strongly refractive, subhyaline, medium large, biseriately arranged {12}, remaining globose or eventually becoming elongate-angular, extending (15–)22–40(–60) µm from tip {6}, disappearing optically in dead cells, plasma then golden- or reddish-ochraceous in terminal cell (†H_2O or KOH); yellow LBs not seen at septa, dichotomously branched and anastomosing near base. **Medullary excipulum** hyaline, of rather loose *textura intricata*, cells *30–65 × 2–4(–5.5) µm {1}, †1.3–5 µm wide {1}, delimited from ectal excipulum by a parallel, ca. 50–70 µm thick layer of *t. porrecta*. **Subhymenium** not much differentiated, walls strongly violet in CRB. **Ectal excipulum** hyaline, of (†) slightly to medium gelatinized *t. prismatica* from base to margin, oriented at a ~0–35° angle to the surface, at lower flanks ca. 35–50 µm thick, cells ± rectangular, *14–25(–33) × (4–)5–9(–10) µm {1}, †(8–)13–28(–40) × 5–12(–14) µm {4}, common walls †1–2 µm thick; cortical hyphae ± one-layered, †3–4.5 µm wide {1}, occurring mainly on stipe and near margin, undulating in surface view, partly filled with refractive VBs (multiguttulate), these cells when dead with light amber- to reddish-brown plasma (in KOH), cortical cells sometimes with abundant flexuous hair-like outgrowths (†7–10 × 2.5–3 µm).

Habitat: predominantly in damp places (in open moist meadows, ditches, in bank communities of rivulets or small lakes, e.g. *Glycerietum maximae*) but also in shady woods or in gardens remote from water bodies, the substrate lying on very wet to rather dry ground, rarely in up to 1.5 m above ground; on previous year's, rather rotten herbaceous stems of **herbaceous dicotyledons:** *Fallopia dumetorum* {1}, *F. japonica* {8/2}, *F. sachalinensis* {3}, *Hypericum* sp. {2}, *H. maculatum* {2}, *H. perforatum* {2}, *Lycopus europaeus* {2/1}, *Lysimachia vulgaris* {3/1}, *Persicaria dubia* (= *Polygonum mite*) {1}, *P.* ?*hydropiper* {1}, *Rubus fruticosus* {1}, *R. idaeus* {1}, *Rumex hydrolapathum* {1}, *Scrophularia nodosa* {1}, *Solidago canadensis* {1/1}, *Teucrium scorodonia* {1}, indet. plant {1}; **pteridophytes:** petioles of *Pteris vitatta* {1}; **woody plants:** petioles of *Acer pseudoplatanus* {1}, rather rotten bark (periderm) of 2–5 mm thick corticated twig of *Alnus glutinosa* {1}, twigs and leaf tendrils of *Vitis vinifera* {1}, fruits (seeds) of *Prunus serotina* {1}. **Associated** with *Calycellina chlorinella* {2}, *Calycina discreta* {3/1}, *Diaporthe arctii* {1}, *Hyaloscypha albohyalina* {1}, *Hymenoscyphus menthae* {1}, *H. scutula s.l.* {7}, *H.* ?*virgultorum* {1}, *Lachnum* sp. (on *Fallopia*) {1}, *Lophiostomataceae* {1}, *Mollisia* ?*revincta* {2}. **Altitude:** 0–700 m a.s.l. in Central Europe, up to 1285 m in S-France. **Desiccation tolerance:** some paraphyses and mature asci survived 1–2 days in the dry state, though being dead in another sample after a 3/4 day, many ascospores still viable after 2 weeks.

Remarks: *Hymenoscyphus macroguttatus* is easily recognized by its predominantly homopolar ascospores which contain large guttules in the living state, and by the asci arising from croziers. Dimensions of asci and spores are almost the same as in *H. menthae* (see Tab. 3). A further feature was found in the cells of the ectal excipulum which are often distinctly shorter and more gelatinized compared to *H. menthae*.

Notable variation was observed in the length of the apothecial stipe which is considerably longer and also narrower in some collections, also in spore size, particularly in width. Samples on woody substrates showed partly slightly wider spores. One of them, which grew on a xeric *Crataegus* twig up to 1 m above ground, was not included in the description because of extraordinarily short and wide spores (Fig. 42). This sample deviates from *H. subferrugineus* (Nyl.) Dennis by the large LBs in its spores. Another not included specimen, on *Castanea* leaves from Tenerife, deviates by rather short, partly slightly scutuloid spores [*14.5–15.5(–17) × (3.3–)3.6–3.9(–4.2) µm].

Distinct yellow colours were rarely observed in *H. macroguttatus*, but this feature is of minor value since also *H. menthae* may sometimes deviate by being almost white. Based on spore morphology and ascus croziers, *H. macroguttatus* might be confused with *Phaeohelotium epiphyllum* (Pers.) Hengstm. or *P. monticola* (Berk.) Dennis, which differ in a much thicker, always rather short stipe and an ectal excipulum of *textura angularis*, at least at the lower flanks.

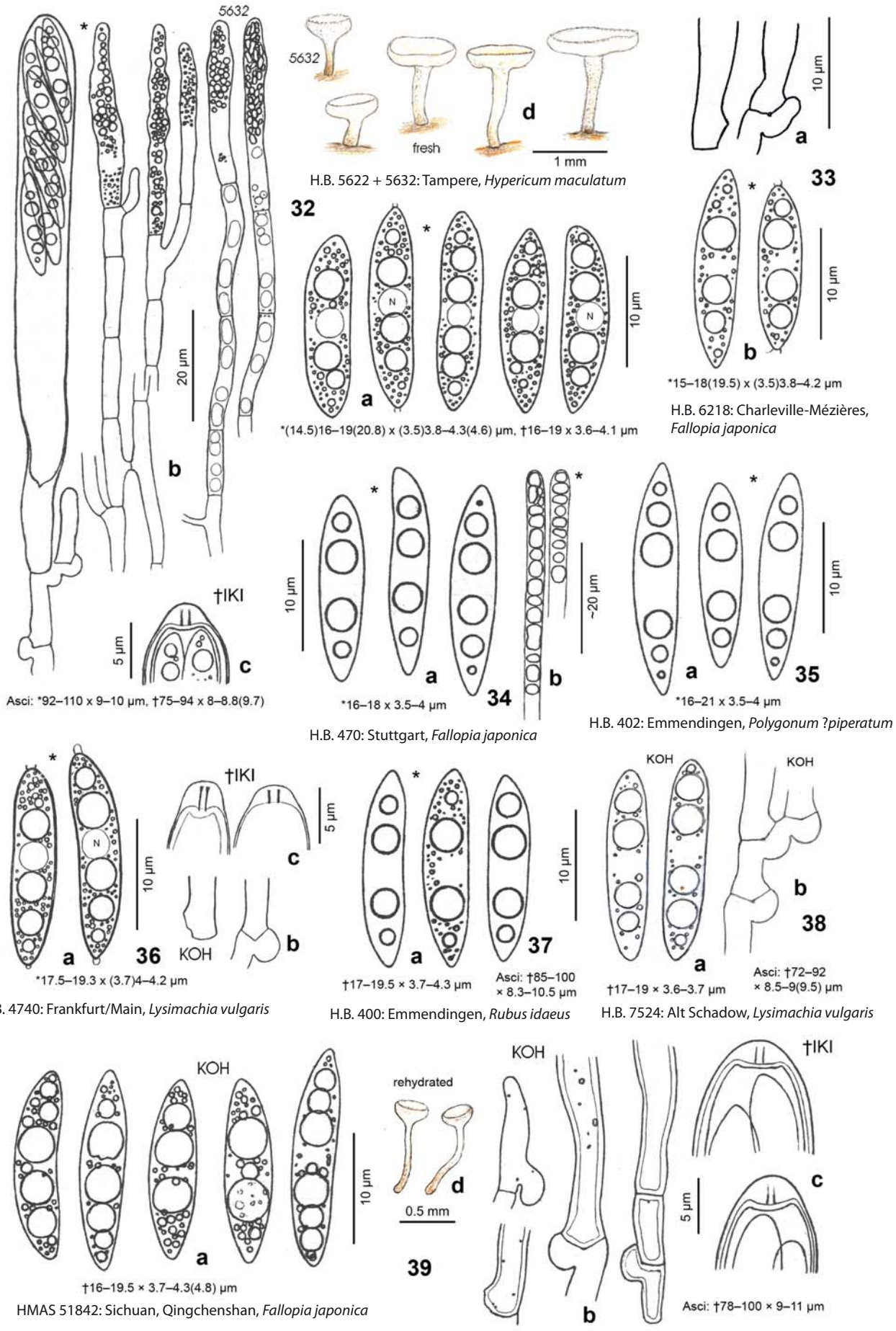
The name *H. menthae* was earlier misapplied by me (Baral & Krieglsteiner, 1985: 131) and subsequently by Hengstmengel (1996: 201) for the present taxon based on Dennis' (1956: 78, fig. 71 E) brief redescription and illustration of the type material and his remark that a specimen on *Teucrium* (fig. 71 E) represents "exactly the same form". While Dennis figured the type without spore guttules, the *Teucrium* sample shows two very large though mostly ellipsoid oil drops in the spores, reminiscent of *H. macroguttatus*, and also the cited protologue includes 2–3-guttulate spores. In the absence of information on the ascus base, the identity of the two collections remained obscure, however, and only when the type of *H. menthae* was reexamined by me (see above), this misinterpretation became obvious.

Hengstmengel (1996) distinguished *H. macroguttatus* (as *H. menthae*) from *H. menthae* (as *H. consobrinus*) and *H. scutula* mainly by the presence of croziers (from the latter also by spore shape). Spore guttulation was neglected by him because his work was mainly based on herbarium material. In the present study which was conducted between 1997–2015, Hengstmengel's observation on croziers was fully and independently confirmed based on material different from Hengstmengel's. However, Hengstmengel followed my earlier interpretation of *H. menthae* without examining type material of the two species.

Under the name *H. menthae*, Hengstmengel (1996) described *H. macroguttatus* from herbarium material of three collections from Netherlands, on stems of *Rubus* and *Fallopia japonica* (as *Polygonum cuspidatum*). The asci he reported to arise from croziers, and the dead spores as 14–21 × 3–4(–5) µm, sometimes slightly scutuloid though predominantly ellipsoid-fusoid. The depicted dead spores show 3–6 medium-sized, ± globose, partly regularly arranged gut-

Tab. 2 – Phenology of the here included collections of *Hymenoscyphus macroguttatus*.

Apr		May		Jun		Jul		Aug		Sep		Oct		Nov		Dec	
0	0	0	0	0	0	0	1	2	10	8	13	6	3	1	1	0	0



Figs 32–39. *Hymenoscyphus macroguttatus*. – a. mature ascospores, containing refractive guttules (LBs, the minute guttules are omitted in Figs 34–35 and partly 37; N = nucleus); b. ascus and paraphyses, the latter containing refractive vacuolar guttules (VBs), mature ascus bases with croziers; c. ascus apices of immature and nearly mature asci in IKI, with euamyloid apical ring; d. apothecia. – Living state, except for Figs 32c, 36b, c, 39a–d.

Tab. 3. Comparison of teleomorph features between *Hymenoscyphus menthae* and *H. macroguttatus* (important characters in bold)

	H. menthae	*H. macroguttatus*
Hymenium (fresh)	**pale to bright yellow-ochraceous**, rarely milky-white	**milky-white to pale cream**, sometimes light yellow
Base of stipe (fresh)	white, often ± bulbous	white or light greyish–brown, not bulbous
Height of amyloid ring	1/2–2/3 (–5/6) of dome	(1/2–) 2/3–9/10 of dome
Asci	*90–120 (–130) × 8.5–10.5 (–12) µm	*90–115 (–120) × 9–11 (–11.8) µm
Asci arising from	**simple septa**	**croziers**
Ascospore length (free)	*((13–)) (15–) 17–22 (–26) µm	*(14.5–) 16–20 (–21) ((–25)) µm
Width (free)	*((2.8–)) 3.5–4.2 (–4.5) µm	*(3.5–) 3.8–5 (–5.5) µm
Length/width ratio (free)	*(4.5–) 4.8–5.8 (–6.1)	*(3.7–) 3.9–5 (–5.5)
Slightly scutuloid spores	absent	rarely present
Curvature	straight to medium curved	straight to slightly curved
Short polar appendages	absent	sometimes present
Membranous sheath	sometimes present	absent
Content of living mature spores	**multiguttulate**	**oligoguttulate**
Large LBs	**0.7–1.3 (–1.5) µm diam., numerous**	**(1.8–) 2.5–3 (–4) µm diam., 2–6 per spore**
Overmature spores	1 (–3)-septate	1-septate
Sublanceolate paraphyses	absent	present or absent
Yellow LBs (carotenoids)	**present near septa**	**absent**
Phenology	(IV–) V–X (–XII)	(VII–) VIII–X (–XI)

tules which appear to correspond to the original aspect of the living spores.

While Hengstmengel (1996 and pers. comm.) lists 4 collections for the Netherlands made between 1952–1997, Declercq (pers. comm.) lists 26 collections for Belgium made between 1987–2008. I examined 6 of Declercq's herbarium specimens and confirmed their identity as *H. macroguttatus*. In a collection on *Hypericum* (B.D. 94/114) Declercq observed comparatively large asci (*90–125 × 9.5–12 µm) and spores (exceptionally up to *24 µm long).

A collection on *Alnus* bark (H.B. 4757b) was studied by me in the fresh state but drawn later in the dead state (Fig. 41). It fully agrees with those on herbaceous stems, but has a spore width at the upper range of *H. macroguttatus*. Another sample (on *Vitis*, Figs 46, 48) examined by Bemmann (pers. comm.) also fits well, though showing spores at the upper range (*16.8–20 × 4.2–5.5 µm).

A collection on *Fallopia* from Sichuan (HMAS 51842 = CUP-CH 2413) under the name *H. scutula* var. *solani* (Korf & Zhuang, 1985: 500) and later *H. menthae* (Zhang & Zhuang, 2002: 37) is here considered conspecific with *H. macroguttatus* (Fig. 39). It differs merely in relatively tiny apothecia (rehydrated 0.4–0.6 mm diam., stipe 0.5–0.8 × 0.07–0.12 mm) and a rather faint instead of strong iodine reaction of the apical ring. This collection was identified as *H. scutula* by Lizoň (1992: 45). Another sample (HMAS 51841, CUP-CH 2388) mentioned by Korf & Zhuang (1985) and Zhang & Zhuang (2002), collected one day earlier on an unidentified stem in the same area, was not studied by me. A recent report under the name *H. macroguttatus* by Zheng & Zhuang (2013) from Hubei on herbaceous stems and leaf veins (HMAS 264159) has similarly tiny apothecia (white when fresh, 0.2–0.6 mm diam., stipe 0.5–1 × 0.1–0.15 mm). The homopolar or only sometimes slightly scutuloid spores [†13.5–17.8 × 4–5 (–5.5) µm, as "scutuloid"] were erroneously described as "with or without cilia" but are consistently without setulae (Zhuang, pers. comm.). The large LBs in the dead spores appear in their micrograph as empty regions because of the applied highly viscous medium (CB). The spores seem to fit the here included Chinese specimens though being slightly shorter and wider. Mainly because of the deviating ITS sequence (see below) this record is here not included in the scope of *H. macroguttatus*.

Reexamination of the isotype of *H. pteridicola* in TAAM (Fig. 40) revealed rather close concordance with the European specimens here assigned to *H. macroguttatus*, although the asci and spores when mounted in KOH are wider (†18.5–21 × 4.5–5.3 µm) than those gained from European samples in the same medium. On the other hand, the protologue data [80–115(–121) × 8–10.5 µm, 16–22.5 × 3–4.5 µm] fit quite well those from Europe when compared in the dead state. Because of these size differences, Hengstmengel (pers. comm.) expressed some doubts about the conspecificity of the Indian collection with those from Europe. He also saw some differences in the more obtuse spore ends and slightly larger oil drops as illustrated on my drawing, and in minute hairs at the margin as reported in the protologue (but hair-like outgrowths were abundant also in a specimen on *Lysimachia*, H.B. 5876). Thind & Sharma (1980) misleadingly described the spores as "aguttulate", although in one of the drawn spores 4 rather large guttules are indicated. There is also a discrepancy in the collection data. On the label of TAAM 198505 the date is 6.IX.1973, while the protologue says 6.IX.1972.

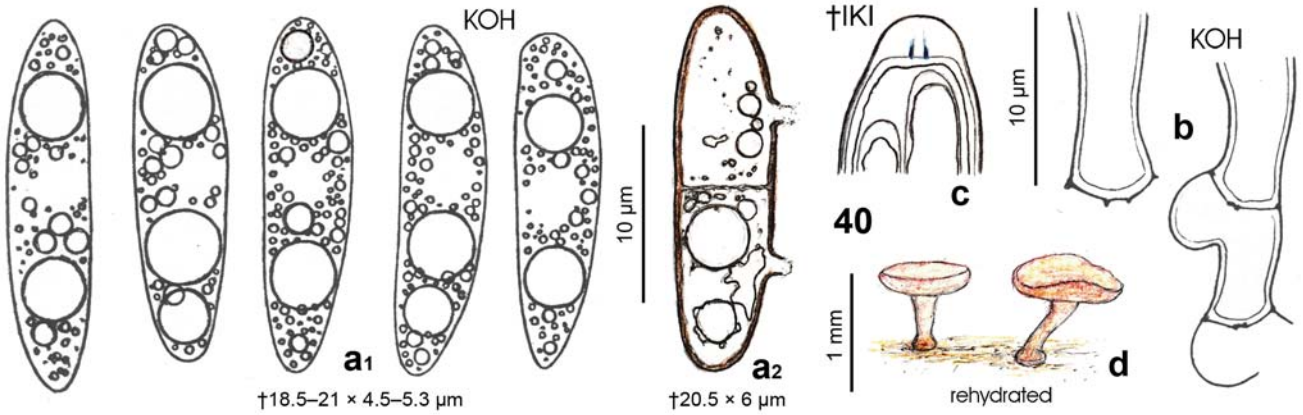
Besides the holotype, two further records from India possibly belong to *H. macroguttatus*. One was on stems of an *Asteraceae* and was tentatively identified as *Helotium scutula* by Thind & Singh (1961: 296, fig. 2 A–C). The spores are figured as homopolar and described as "aguttate", the apothecia as externally creamy brown, very finely tomentose by mostly flexuous hairs, and the asci as not bluing in iodine. The authors did not stress the shape of the spores but mainly their shorter length and absence of setulae as deviating from typical *H. scutula*. The other record on unidentified herbaceous stems was named *Helotium sublateritium* Berk. & Broome by Thind & Singh (1971) and, apart from the smooth apothecia, appears to me not distinct from the former collection, although the figured left spore looks slightly scutuloid (the type of *H. sublateritium* has coinsistently scutuloid, multiguttulate spores and will be discussed in a separate paper).

Phylogeny: In five European strains of *H. macroguttatus* (from Finland, Luxembourg, Hessen, and Baden-Württemberg) the ITS rDNA was sequenced by Queloz (pers. comm.) from the dry apothecia. In the entire ITS region these five sequences are identical. One of them is present in GenBank (DQ431179). *H. macroguttatus* from Hubei (KC416306) and four sequences of *H. scutuloides* Hengstm. from China (AY348589, AY348590, AY348591) differ by 1.5% (7 nucleotides) from *H. macroguttatus* and by 2.3% from each other. This seems to indicate that three different species are involved. The latter three sequences were uploaded in GenBank as *H. scutula*, but were reidentified by Zheng & Zhuang (2013) as *H. scutuloides*, based on asci with croziers and ascospores partly with setulae (the latter not visible on their micrograph of dead spores). Also within these three se-

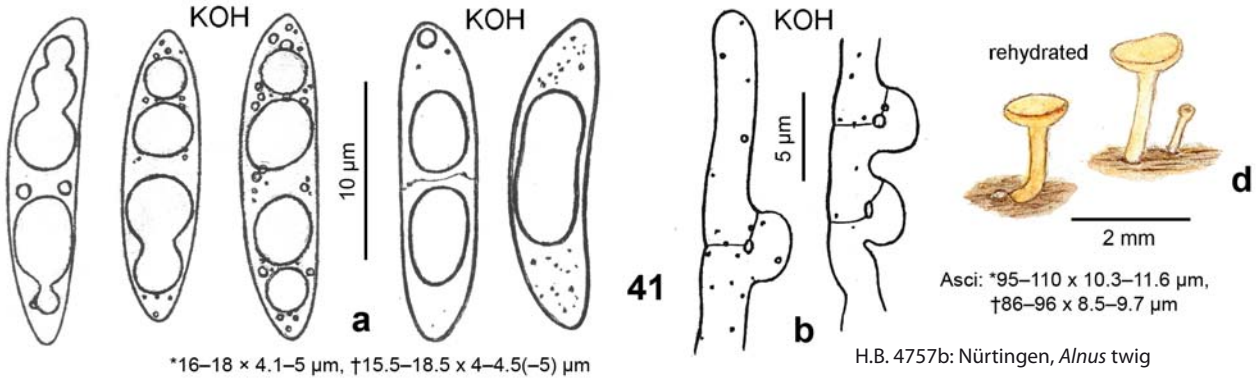
quences of *H. scutuloides* no variance in the ITS region is observed. Two further strains under the name *H. scutula*, which are identical in the ITS, deviate from the former by only 1 nucleotide and are, therefore, to be considered as conspecific: AY789432 (Wang *et al*., 2005, strain MBH29259, without collection data) and an unpublished sequence (Queloz & Berndt, pers. comm.; Switzerland, Zürich, rivulet at Wappenswil, indet. herbaceous stem, 3.X.1997, J. Schneller no. 87-284, Z Myc 337).

In the phylogenetic analysis of Zheng & Zhuang (2013), European and Chinese *H. macroguttatus* form with *H. scutuloides* a highly supported clade which clusters with medium support within the large genus *Hymenoscyphus*. Also in an unpublished analysis of the LSU region, in which only a few sequences are available, *H. scutuloides* (AY789431) clusters among *Hymenoscyphus* species with scutuloid spores. The distance of this clade to the *H. menthae-H. repandus* group is 17.5–18% in the ITS and 8.5% in the LSU (D1-D2).

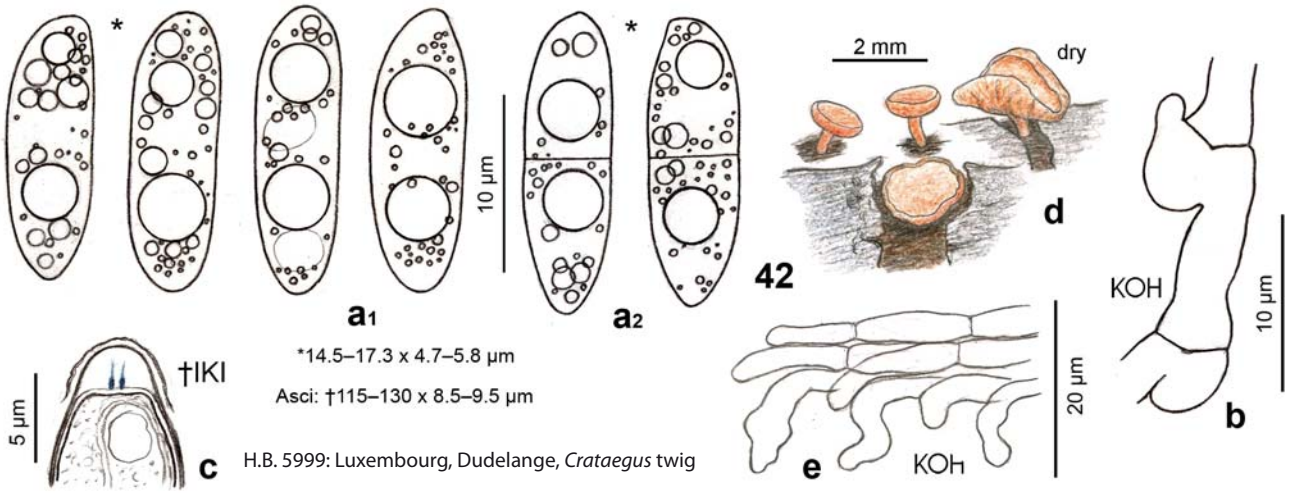
Ecology: Unlike *Hymenoscyphus menthae*, *H. macroguttatus* was found fruiting only in late summer and autumn (Tab. 2). Except for this deviating though strongly overlapping phenology, ecological differences between *H. menthae* and *H. macroguttatus* could hardly be discovered. Both species inhabit a wide variety of hosts, mainly herbaceous stems (including monocots), rarely also woody substrates. Nevertheless, certain host preferences can be derived from the present data, for instance, *Hypericum* (mainly *H. perfora-*



TAAM 198505: Jammu, Batote, *Pteris vitatta* petioles, isotype of *H. pteridicola*



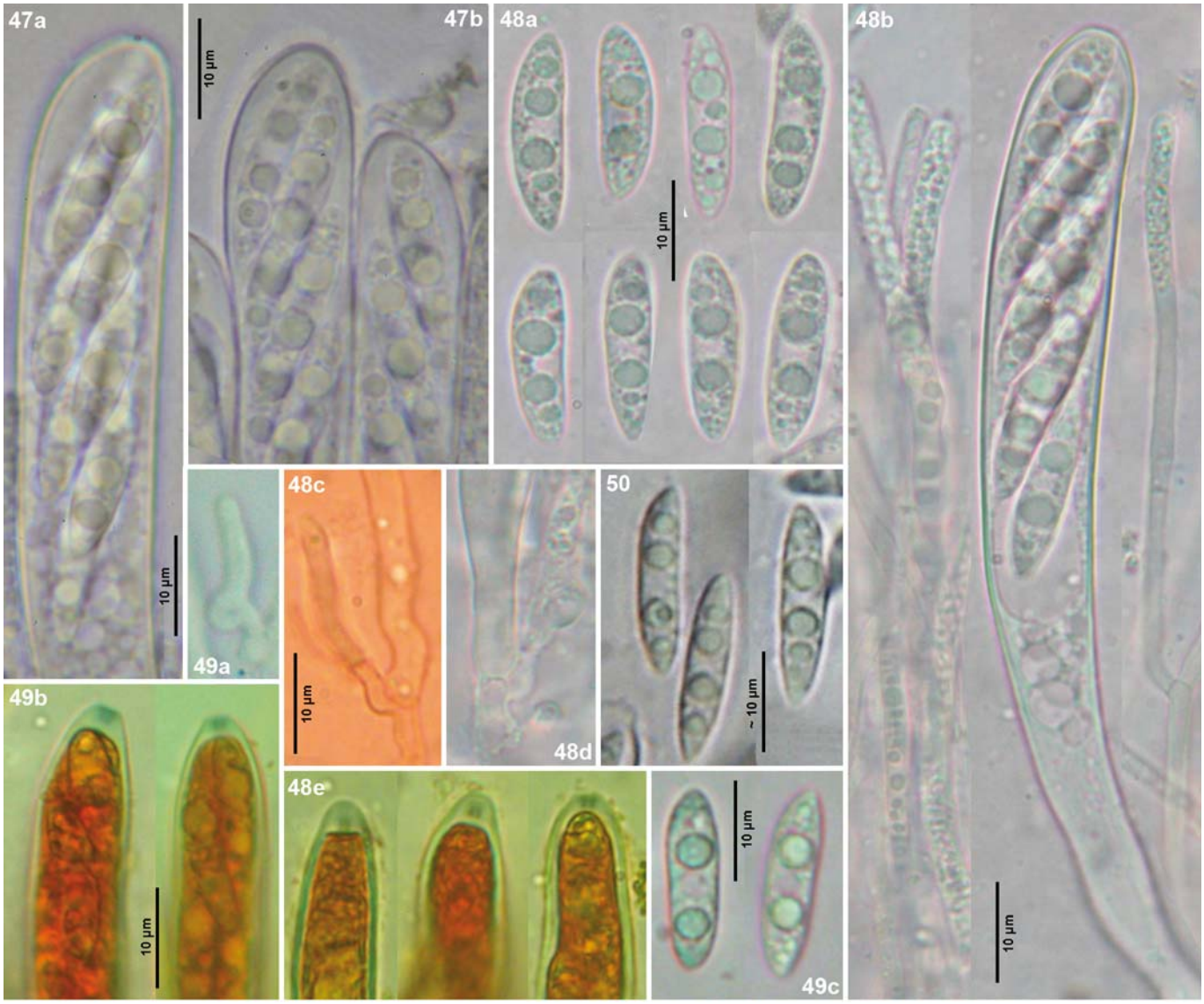
H.B. 4757b: Nürtingen, *Alnus* twig



H.B. 5999: Luxembourg, Dudelange, *Crataegus* twig

Figs 40–41. *Hymenoscyphus macroguttatus*. **Fig. 42.** *H.* cf. *macroguttatus*. – a. ascospores (a1 mature, a2 overmature), containing refractive guttules (LBs), in Fig. 41a with distorted lipid pattern; b. ascus bases with croziers; c. apices of nearly mature asci in IKI; d. apothecia. – Dead state, except for Fig. 42a.

Figs 43–46. *Hymenoscyphus macroguttatus*. – Apothecia in fresh state, except for 43h (senescent) and 43g, i (rehydrated). 44c. collection site. – 43. H.B. 9963 (Mönchengladbach, *Fallopia japonica*, photo H. Bender, except for 43g, i), 44. H.B. 7563a (Luxembourg, Hamm, *Fallopia sachalinensis*, photo G. Marson), 45. H.B. 7577 (Tübingen, Pfrondorf, *Fallopia sachalinensis*), 46. 18.IX.2010 (Heidelberg, Kleingemünd, *Vitis vinifera*, photo M. Bemmann, scale unknown).



Figs 47–50. *Hymenoscyphus macroguttatus*. – 47a–b, 48b. Mature asci shortly before full turgescence, paraphyses with refractive vacuoles (VBs) in upper and lower part; 48e, 49b. Apex of immature and mature asci, with euamyloid apical ring; 48c–d, 49a. Ascus base with croziers; 48a, 49c, 50. Mature, freshly ejected ascospores. – Living state, except for 48c (in CRSDS), 48e & 49b (in IKI). – 47. H.B. 7563a (Luxembourg, Hamm, *Fallopia sachalinensis*, photo G. Marson), 48. 18.IX.2010 (Heidelberg, Kleingemünd, *Vitis vinifera*, photo M. Bemmann), 49. 16.X.2009 (Heidelberg, Ziegelhausen, *Fallopia dumetorum*, photo M. Bemmann), 50. H.B. 9963 (Mönchengladbach, *Fallopia japonica*, photo H. Bender).

tum) was 13 times the host of *H. macroguttatus* (8× in Declercq's list) but so far never of *H. menthae*. Extraordinary substrates of *H. macroguttatus* are seeds of *Prunus serotina* and twigs of *Alnus* and *Vitis*. Declercq's records are almost always on herbaceous stems, often on *Lysimachia vulgaris*. Additional hosts in his list are stems of *Galeopsis tetrahit* and the two so far sole records on monocots, leaves of *Typha latifolia*.

The plant communities in which *H. menthae* and *H. macroguttatus* were found, appear to be more or less the same and are also very diverse. Obviously, both species prefer to colonize rotten herbaceous stems which lie on the ground under a condition of rather long-lasting humidity, often in close vicinity to standing or running water, but sometimes also far away from damp places. Krieglsteiner (2005: 604) classified the vegetation at his only record in the Rhön region (H.B. 7034) as *Fraxino-Aceretum pseudoplatani*.

The herbaceous stems on which the two species fruit appear to have died off in the previous year rather than two years ago. This would mean that colonization by ascospores during the period of fructification takes place on recently dead or perhaps still-living plant parts. The long fructification period of *H. menthae* suggests that several generations of apothecia occur in one year, perhaps on the same stem.

Specimens included (all on dead herbaceous stems or culms if not otherwise indicated):

Finland: Pikanmaa, 17 km SW of Tampere, 11 km NW of Lempäälä, Säijä, 82 m, *Hypericum maculatum*, 2.X.1996, U. Söderholm (H.B. 5622, U.S. 2529 ø). – 24 km SW of Tampere, 1 km S of Laukko, Himonhaka, 85 m, *Hypericum maculatum*, 13.X.1996, U. Söderholm (H.B. 5632, sq.: ined.). – **Great Britain: West Midlands**, 12 km ENE of Wolverhampton, 1 km N of Pelsall, 147 m, *Rumex hydrolapathum*, 6.IX.2015, P. Thompson (H.B. 9969). – **East England: Suffolk**, 3.7 km ESE of Halesworth, N of Wenhaston, path from Low Road to Chapel, Bicker's Heath, 13 m, *Fallopia sachalinensis*, 22.X.2005, E. Batten & S. Francis (E.B. 4638, d.v.). – ibid., 6.XI.2005 (E.B. 4644, d.v.). – **Netherlands: Zuid-Holland**, 5 km NNE of Leiden, NE of Warmond, Huys te Warmont, 5 m, *Fallopia japonica*, 24.IX.1952, R.A. Maas Geesteranus (9046, L, as *Polygonum cuspidatum*, J. Hengstmengel 1996 as *H. menthae*, d.v.). – **Zeeland**, 9.5 km NNW of Middelburg, 1.5 km NE of Oostkapelle, Oranjezon (Waterleidingduinen), 8 m, seeds (stones) of *Prunus serotina*, 10.X.1997, E. Batten & S.M. Francis, vid. J. Hengstmengel (E.B. 3680, d.v.). – **Belgium: West-Vlaanderen**, 7 km ENE of Ostende, 2 km NE of Bredene, Blutsyde, 2 m, *Lycopus europaeus*, 25.VIII.1994, B. Declercq (B.D. 94/111). – **Oost-Vlaanderen**, 24 km NE of Gent,

3.2 km NW of Sinaai, Heirnisse, 5 m, *Hypericum perforatum*, 26.VIII.1994, B. Declercq (B.D. 94/114). – 17 km NE of Gent, 1.5 km NE of Wachtebeke, Axelsvaardeken, 6 m, *Solidago canadensis*, 6.X.1995, B. Declercq (B.D. 95/102). – 11 km SW of Gent, 4 km NE of Deinze, Ooidonk castle, 15 m, *Lysimachia vulgaris*, 19.IX.1987, B. Declercq (GENT, B.D. 87/157). – 6 km E of Deinze, 2.5 km NE of Nazareth, Hospice forest, 23 m, *Teucrium scorodonia*, 16.XI.1991, B. Declercq (B.D. 91/161). – **Limburg**, 5 km SW of Genk, 4 km NNE of Diepenbeek, Augustijnenvijver, 45 m, *Persicaria dubia*, 17.IX.1991, B. Declercq (B.D. 91/103). – **Luxembourg: Gutland**, 2.5 km E of Luxembourg, SW of Hamm, river Alzette, 251 m, *Fallopia sachalinensis*, 17.VIII.2004, G. Marson (H.B. 7563a, sq.: ined.). – 5.5 km S of Luxembourg, 1.2 km SW of Hesperange, between Wéineguecht and Schausenheck, 272 m, *Fallopia japonica*, 13.VIII.2004, G. Marson (ø). – **France: Rhône-Alpes**, Ardèche, 7 km E of St.-Cirgues-en-Montagne, 5 km WNW of Burzet, le Cros du Loup, 1285 m, *Hypericum*, 16.IX.1990, C.M. Swart-Velthuyzen & C. Besch (H.B. 4228, C.S.). – 5.8 km ESE of St. Cirgues-en-Montagne, 3 km S of Usclades-de-Rieutord, Lac Ferrand, 1255 m, *Hypericum*, 22.IX.1990, C. SwartVelthuyzen (ø). – Isère, 13 km N of La-Tour-du-Pin, 1 km NW of Morestel, 233 m, *Fallopia ?japonica*, 29.IX.1999, H.O. Baral (H.B. 6498). – **Champagne-Ardennes**, Ardennes, 24 km NNE of Charleville-Mézières, 6 km ESE of Fumay, S of Hargnies, marais du Ry de Sol, 435 m, 25.VIII.1998, *Fallopia japonica*, 25.VIII.1998, R. Dubois, vid. M. Langlois (H.B. 6218). – **Germany: Schleswig-Holstein**, 14 km E of Rendsburg, S of Bredenbek, Felder Holz, MTB 1625/343, 24 m, *Lycopus europaeus*, 2.IX.2012, H. Lehmann (d.v.). – **Brandenburg**, ~8 km SE of Bad Freienwalde, ~N of Wriezen, MTB 3250/41, 5 m, substrate?, 2.X.2011, V. Kummer, vid. T. Richter (n.v.). – 55 km SE of Berlin, 2 km N of Alt Schadow, Neuendorfer See, Kessel Tschinka, MTB 3849/4, 50 m, *Lysimachia vulgaris*, 25.VIII.1994, V. Kummer (V.K., H.B. 7524 ø). – **Sachsen**, 36 km N of Chemnitz, 4 km E of Leisnig, Klosterbuch, 160 m, *Fallopia japonica*, 15.IX.2013, S. Pohlers, vid. B. Mühler (unpres., d.v.). – 23 km ENE of Chemnitz, 4 km ENE of Oederan, Kirchbach, 430 m, *Fallopia japonica*, 27.VIII.2012, B. Mühler (unpres., d.v.). – 6 km NNE of Chemnitz, 1 km E of Glösa, Indianerteich, 325 m, ?*Solidago canadensis*, 28.VIII.2014, B. Mühler (unpres., d.v.). – 25 km S of Chemnitz, 3 km SW of Geyer, Hermannsdorfer Wiesen, 680 m, ?*Lycopus europaeus*, 30.VII.2014, B. Mühler (unpres., d.v.). – 2.3 km SSW of Geyer, Waldschänke, 670 m, *Rubus fruticosus*, 9.IX.2011, B. Mühler (unpres., d.v.). – **Nordrhein-Westfalen**, 5.8 km NE of Mönchengladbach, 1 km E of Neuwerk, S of Abtshof, MTB 4704/4, 40 m, *Fallopia japonica*, 28.VIII.2014, H. Bender (H.B. 9963). – **Baden-Württemberg**, 7 km E of Heidelberg, 1.5 km SE of Ziegelhausen, Kleingemünderstraße, *Fallopia dumetorum*, 16.X.2009, M. Bemmann (ø, d.v.); – 9 km E of Heidelberg, 1 km N of Neckargemünd, ESE of Kleingemünd, 130 m, twig of *Vitis vinifera*, on bark and leaf tendrils, 18.IX.2010, M. Bemmann (ø, d.v.). – 3.8 km NW of Stuttgart, 1.8 km SW of Feuerbach, Heimberg, MTB 7120/4, 370 m, ?*Lysimachia vulgaris*, 15.X.1975, H.O. Baral. – 5.5 km W of Stuttgart, 1.2 km E of Solitude, Nippenburgerle, MTB 7220/2, 440 m, *Fallopia japonica*, 15.IX.1975, H.O. Baral (H.H. 10268). – ibid., *Scrophularia nodosa*, 22.IX.1975, H.O. Baral (ø). – 6 km WSW of Stuttgart, 1.2 km NE of Büsnau, Schattenseen, MTB 7220/2, 420 m, *Lycopus europaeus*, 18.IX.1975, H.O. Baral. – 1.5 km E of Tübingen, 1 km W of Lustnau, Österberg, 410 m, *Fallopia ?japonica*, 18.X.1997, H.O. Baral (H.B. 5936). – 5.3 km NE of Tübingen, ESE of Pfrondorf, Auchtert, MTB 7420/4, 395 m, *Fallopia sachalinensis*, 26.IX.2004, E. Weber (H.B. 7577, sq.: ined.). – 4 km ESE of Nürtingen, Kräuterbühl, MTB 7322/3, 340 m, twig of *Alnus glutinosa*, on bark, 26.IX.1992, H.O. Baral (H.B. 4757b). – Emmendingen, Kloster Tennenbach, MTB 7813/3, 280 m, *Persicaria ?hydropiper*, 31.VIII.1975, H.O. Baral. – 8 km NE of Emmendingen, ~1.7 km SE of Freiamt, MTB 7813/1, 390 m, *Rubus idaeus*, 30.VIII.1975, H.O. Baral (H.B. 400a). – **Hessen**, 6 km SW of Frankfurt. Goldstein, Am Wiesenhof,

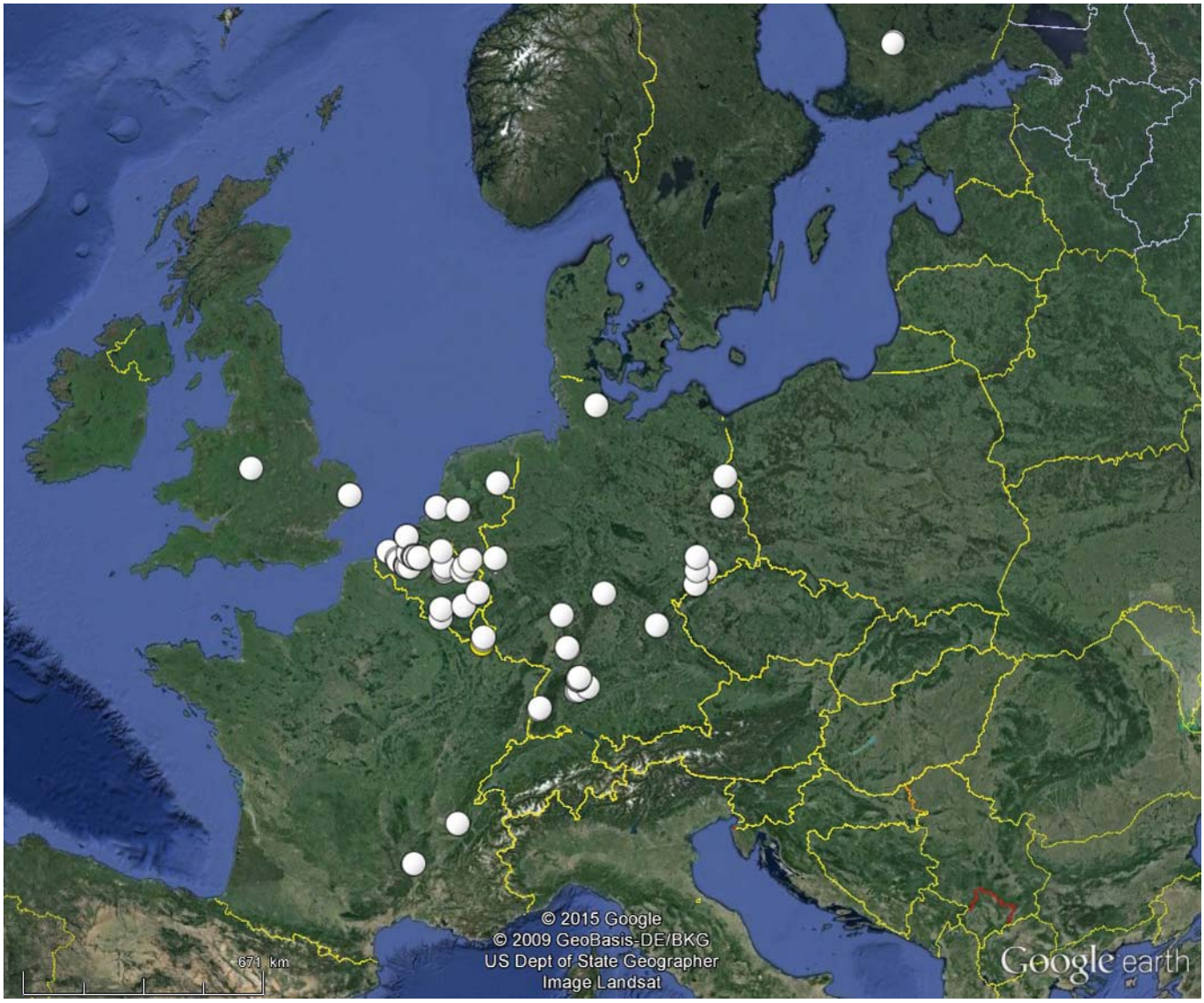


Fig. 51. Known distribution of *Hymenoscyphus macroguttatus* (including data from Hengstmengel and Declercq, pers. comm., which are not in the list of included specimens).

MTB 5917, 100 m, *Lysimachia vulgaris*, 9.IX.1992, W. Pohl (H.B. 4740, sq.: ined.). – **Rhön**, 7 km NNE of Gersfeld, 2.6 km WNW of Ehrenberg-Wüstensachsen, Schafstein, MTB 5425/4, 750 m, petiole of *Acer pseudoplatanus*, 15.IX.2001, L. Krieglsteiner (H.B. 7034, Krieglsteiner 2004 erron. as 2002, sq.: DQ431179). – **Bayern, Oberfranken**, 8 km NE of Pegnitz, 3.5 km SW of Creußen, Craimoos, MTB 6135, 460 m, *Hypericum perforatum*, 4.VIII.1992, W. Beyer (Beyer, 1998: 184, unillustrated). – **India: Jammu & Kashmir**, 60 km NE of Jammu, 5.5 km W of Batote, Sanasar, petioles of *Pteris vitatta*, 6.IX.1973 (or 1972?), M.P. Sharma (isotype of *H. pteridicola*, TAAM 198505, H.B. 5975 ø; holotype in PAN 3988, n.v.). – **China: Sichuan**, 55 km NW of Chengdu, Guan Xian, Qingchenshan, wood above Jianfugong, ~800 m, 19.IX.1981, *Fallopia japonica*, R.Y. Zheng & R.P. Korf (HMAS 51842 [also in CUP-CH 2413 n.v.], as *H. scutula* var. *solani* or later *H. menthae*, host as *Polygonum cuspidatum*, H.B. 5828 ø).

Not included: Luxembourg: Gutland, 10 km ESE of Esch-sur-Alzette, 2.3 km SE of Dudelange, Därebësch, 270 m, twig of *Crataegus*, on wood, 9.XII.1997, G. Marson (H.B. 5999). – **Macaronesia: Tenerife**, 11 km ENE of Puerto de la Cruz, 1.7 km SE of La Matanza, N of Tabares, La Morra, 736 m, Fayal-Brezal, on leaves of *Castanea vesca*, 10.II.2008, E. Beltrán *et al.*, vid. L. Quijada (TFC Mic. 20653, d.v.). – **China, Hubei**, W of Wufeng, Houhe, 800 m, indet. herbaceous stems (and leaf veines), 13.IX.2004, W.Y. Zhuang & C.Y. Liu 5610 (HMAS 264159, d.v., sq.: ITS: KC416306, see Zheng & Zhuang, 2013; as yet unavailable: LSU: KJ472244, TUB: KJ472275).

Hymenoscyphus obscuratus K.S. Thind & H. Singh, *Trans. Brit. mycol. Soc.*, 59: 526, fig. 3 (1972).

Etymology: probably because of the brown apothecial colour.

This species was reported by Thind & Singh (1972) only from the type collection (on herbaceous stems, Parbati [Parvati] valley, Kulu [Kullu] hills, Pulga, NW-Himalaya, Himachal Pradesh, India, 29.IX.1965, H. Singh (PAN 3115, as "PUI"), holotype; isotypes in BPI, CUP, K). The protologue comes close to *H. macroguttatus*: the ascospores have a size of †16–20 × 3.2–4.2 µm and are figured with a homopolar shape (described as "fusoid"). Although they are described as aguttulate and aseptate, the schematic drawing, which shows dead spores inside dead asci, seems to illustrate pseudosepta, i.e. plasma bridges, which indicate the presence of two large central and two smaller polar LBs. However, the dark brown exterior of receptacle and stipe, the latter "almost black at the point of attachment" due to dark brown amorphous matter, and the long asci (†100–130 × 7–9.5 µm) deviate from *H. macroguttatus*. The entire fungus is said to be light to dark brown, but it remains unclear how the colour was in the fresh state. This species was not examined in the present study and awaits reexamination, especially for the ascus base, but also concerning the spore number and setulae, in order to exclude *H. sharmae*. *Lambertella mussooriensis* K.S. Thind & H. Singh was described in the same paper. It shows very similar spores and might be a *Hymenoscyphus* too, being extraordinary in apothecia up to 12.5 mm diam. and truncate ascus apices (described as "obtuse").

Hymenoscyphus sharmae Baral, *spec. nov.* – MB 814405 – Figs 52–55

Diagnosis: Resembling *Hymenoscyphus macroguttatus* and *H. trichosporus* in ascospore size and shape, the former also in spore contents, the latter and also *H. scutuloides*, *H. seminis-alni* and *H. trichosporus* in the presence of conspicuous setulae at the spore ends, differing from all in 4-spored asci.

Typification: India, Uttar Pradesh, Nainital, Kilbury, stems of *Pimpinella acuminata*, 11.VIII.1973, M.P. Sharma (TAAM 194665, holotype).

Etymology: referring to the collector, M.P. Sharma.

Misapplication: Thind & Sharma (1980: 128, figs 3–4), as *H. scutula* var. *solani*.

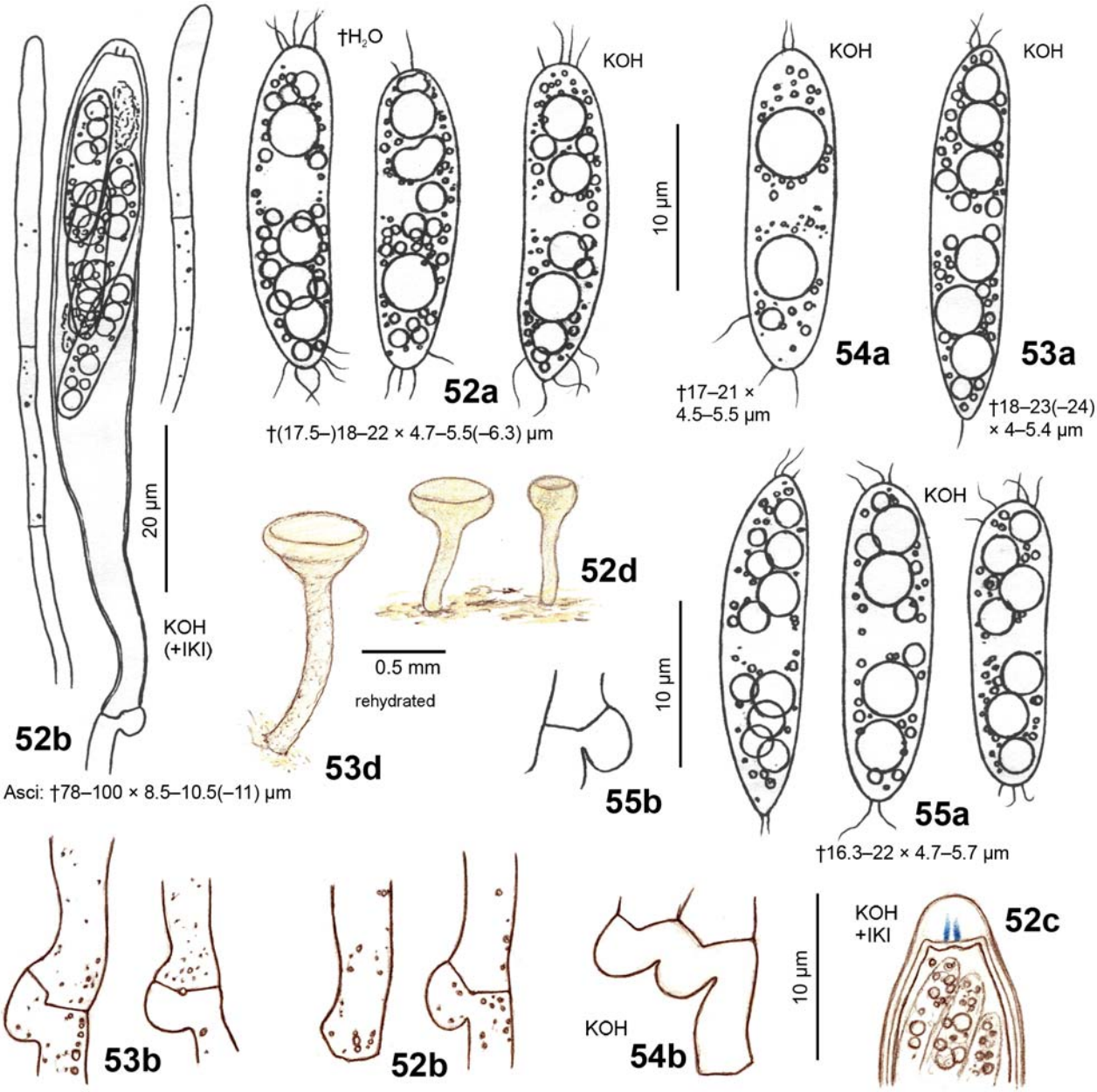
Apothecia rehydrated 0.3–0.7(–1) mm diam. {4}, scattered to gregarious, solitary, pale yellowish-ochraceous (Sharma: cream to light yellow when fresh), stipe 0.4–1.2(–1.7) mm high, 0.1–0.15 mm wide {4}, somewhat glassy-translucent. **Asci** †75–107 × (8.5–)9–11 (–12.5) µm {4}, 4-spored {6}, rarely a few asci 3-, 5- or 6-spored {2}, immature asci 8-spored (~4 spores early aborting); apex of dead asci medium to strongly conical, with pronounced apical dome 2.8 → 2 µm thick, with an amyloid ring reacting strongly blue (BB) in IKI, occupying only the lower half of the dome {3}, *Hymenoscyphus*-type; base with ± long stalk arising from croziers {7}. **Ascospores** †(16.3–)17–22(–24) × (4–)4.5–5.6(–6.3) µm {7}, non-septate, cylindric-ellipsoid to -fusoid, straight to slightly inequilateral, not or scarcely constricted at the centre, homopolar or very slightly scutuloid (heteropolarity rarely recognizable in free spores), ends rounded to obtuse, sometimes subacute (especially at the base), each end with (1–)2–4(–6) very delicate, 1.5–3 µm long setulae {7}; with 1 {4} or 2–4 {3} large LBs ~1.8–3.2(–4) µm diam. and many much smaller ones in each half (high lipid content). **Paraphyses** cylindrical, straight, not or slightly widened above, apex rounded, ± equaling the asci, terminal cell †21–48 × 1.7–4 µm {3}, lower cells †18–30 × 1.5–2 µm {1}, with anastomoses near base; remnants of VBs in terminal cells sometimes perceptible by a pale golden-ochraceous, refractive content (in H_2O). **Ectal excipulum** hyaline, of medium thick-walled (gelatinized) {5}, horizontal *textura prismatica* in receptacle, cells at flanks †10–26 × 4–7.5 µm {2}, of *t. porrecta* in stipe; externally covered by a loose network of narrow hyphae with a yellowish-ochraceous content (remnants of VBs). **Medullary excipulum** not studied.

The new species could only be studied in the dead state, based on several herbarium specimens collected in 1973 in India and preserved at TAAM. It seems to be closely related to *H. macroguttatus*. It has a very similar ascospore size, shape, and guttulation, and deviates only slightly in a tendency to a slightly higher number of large LBs, and in slightly wider asci and distinctly wider ascospores. As in *H. macroguttatus* the asci arise from croziers. The new species differs mainly in two striking characters. (1) More than ca. 95% of the studied asci were 4-spored, and the remaining ones 3-, 5- or 6-spored. Immature asci are 8-spored, and it is not easy to detect the aborted spores in the dead state within the mature asci. Only 3–6 spores attain full size and are well visible, whereas 2–5 spores abort more or less half-sized and are collapsed, at least inside of dead asci. (2) Most of the free spores in a preparation possess very delicate, rather long setulae, 1–6 at each end. The setulae are usually invisible when the spores are still inside the asci, but can well be seen in free spores mounted in water, KOH, or KOH+CR. Despite their length and number they are not as apparent as in *H. scutula*. It is thus not surprising that they were overlooked by Thind & Sharma (*loc. cit.*).

Four-spored asci represent a rather unexpected character of *Hymenoscyphus* in its restricted sense. Perhaps therefore, not enough attention is paid to ascospore numbers in studies of this genus. Thind & Sharma (1980) reported and illustrated 8-spored asci for the present material, apparently without carefully checking this feature. However, not all of the collections cited by these authors appear to exist at TAAM, and to clarify their conspecificity requires reexamination.

Only one potential *Hymenoscyphus* species with 4-spored asci came to my notice: *Helotium tetra-ascosporum* Rea (Scotland, on *Phalaris*). However, setulae were not reported there, and the spores are stated to be longer and narrower (21–27 × 3.5–4.5 µm) than in *H. sharmae*. There is also a *Helotium tetrasporum* (Feltgen) Boud., which is a synonym of *Phialea winteri* Rehm following Dennis (1964: 69), but was combined as *Bisporella tetraspora* (Feltgen) S.E. Carp. by Carpenter (1981).

Some further discrepancies can be found between the present description of *H. sharmae* and that by Thind & Sharma (1980). The asci and ascospores are reported much smaller, 64–85 × 3.6–7.5 µm and 13–16.5(–18.2) × 3.7–4.5 µm, respectively, although the narrow ascus width hardly concurs with the given spore width, particularly since the authors describe the spores as biseriate. The remark "guttules disappearing at maturity" is possibly a misinterpretation that arose when the authors studied a water mount and saw not only li-



India, Uttar Pradesh, on stems of *Polygonum amplexicaule*, 52: TAAM 194665 (Kilbury, holotype), 53: TAAM 194666 (Mussoorie), 54: TAAM 194670 (Tiffon Top), 55: TAAM 194667 (Land's End)

Figs 52–55. ***Hymenoscyphus sharmae*** (holotype and paratypes). – a. Mature ascospores; b. Mature ascus and paraphyses, ascus bases with croziers; c. Apex of not fully mature ascus with euamyloid apical ring; d. Apothecia. – All in dead state.

ving spores in their preparation but also dead, seemingly eguttulate ones. I have seen only a few free spores, and these always contained a high amount of lipid, with the LBs often fused, however (spores with fused LBs are intentionally omitted in my drawings). Overmature spores showing reduced lipid contents could not be found.

All collections of *H. sharmae* examined by me were identified by Thind & Sharma (1980) as *H. scutula* var. *solani*. I have studied all seven specimens deposited in TAAM, but none of the duplicates which are said to be deposited at PAN, and none of the four further collections cited by Thind & Sharma. There is a discrepancy concerning the host genus. On the TAAM labels the host is indicated as "*Pimpinella* sp." or "*Pimpinella acuminata*" (*Apiaceae*), although Thind & Sharma say "*Polygonum* sp." or "*Polygonum amplexicaule*" (*Polygonaceae*) for all eleven specimens listed. Based on the anatomy of the 1–4 mm thick stems in the holotype, this question could so far not be solved.

H. scutuloides Hengstm. and *H. seminis-alni* Baral, Grauw. & M. Eckel concur with *H. sharmae* in the presence of several setulae at each spore end, and in the presence of croziers. The two species differ in distinctly heteropolar (scutuloid), narrower spores, and 8-spored asci. I have studied *H. scutuloides* from a fresh collection from Liechtenstein, on stems of *Filipendula ulmaria* (H.B. 5845). *H. trichosporus* Dougoud differs in 8-spored asci and a lignicolous habitat.

Specimens examined (all on dead herbaceous stems, all issued as *Helotium scutula* var. *solani*):

India: Uttar Pradesh (Uttarakhand), NW-Himalaya, ~3 km NW of Nainital, Kilbury [Road], ~2200 m, *Pimpinella acuminata*, 11.VIII.1973, M.P. Sharma (TAAM 194665, holotype, H.B. 5976 ø; isotype in PAN 11078, n.v.). – 1.7 km N of Nainital, Snow View [Point], ~2250 m, indet. *Apiaceae*, 7.VIII.1973, M.P. Sharma (TAAM 194668, PAN 11057). – ibid., *Pimpinella* sp., 7.VIII.1973, M.P. Sharma (11058, TAAM 194669). – 1.3 km WNW of Nainital, Tiffon (Tiffin) Top, 2270 m, *P. acuminata*, 6.VIII.1973, M.P. Sharma (TAAM 194671, PAN 11050). – ibid., *Pimpinella* sp., 7.VIII.1973, M.P. Sharma (TAAM 194670, PAN 11051, H.B. 5979 ø). – 2.5 km W of Nainital, NE of Khurpatal, Land's End, 2100 m, *P. acuminata*, 9.VIII.1973, M.P. Sharma (TAAM 194667, PAN 11066, H.B. 5977 ø). – Mussoorie, The Park, ~2000 m, *Pimpinella* sp., 27.VIII.1973, M.P. Sharma (TAAM 194666, PAN 11124, H.B. 5978 ø).

Taxa with more or less heteropolar, scutuloid ascospores (*H. scutula* agg., *H. vitigenus*)

Hymenoscyphus scutula (Pers.) W. Phillips [as '*scutulus*'], *Man. Brit. Discomyc.*: 136 (1887).

≡ *Helotium scutula* (Pers.) P. Karst., *Bidr. Känn. Finl. Nat. Folk*, 19: 110 (1871).

≡ *Peziza scutula* Pers., *Mycol. Eur.*, 1: 284 (1822).

(?) = *Hymenoscyphus vitellinus* (Rehm) Kuntze, *Revis. gen. pl.*, 3 (2): 486 (1898).

≡ *Helotium vitellinum* Rehm, *Ber. naturhist. Augsburg*, 26: 124 (1881).

≡ *Helotium scutula* f. *vitellinum* (Rehm) Rehm, *in* Winter, *Rabenh. Krypt.-Fl.*, Edn 2, 1.3(lief. 40): 794 (1893) [1896].

≡ *Phialea vitellina* (Rehm) Sacc., *Syll. fung.*, 8: 262 (1889).

(?) = *Helotium geiphilum* Velen., *Monogr. Discom. Bohem.*: 193 (1934).

(?) = *Hymenoscyphus scutula* var. *solani* (P. Karst.) S. Ahmad, *Ascomycetes of Pakistan*, 1: 207 (1978).

≡ *Helotium scutula* var. *solani* P. Karst., *Not. Sällsk. Fauna Fl. Fenn. Förh.*, 11: 234 (1870) [1871].

For further synonyms see in Species Fungorum.

Typification: *scutula*: location unknown, undated (type not located). – *vitellinus*: Germany, Bayern, Schwaben, Ausgburg, stems of *Filipendula ulmaria*, X.1878, M. Britzelmayr (Rehm Ascomyc. Exs. 513, S-F104311, lectotype, designated here, MBT 203036). – *geiphilum*: Slovakia, Prešov, Tatranská Lomnica, Vysoké Tatry, rhizoms of *Geum rivale*, VII.1924, A. Pilát (PRM 147239, lectotype).

– *scutula* var. *solani*: South Finland, location unknown, stems of *Solanum tuberosum*, 27.X., P. Karsten (type not located).

Etymology: *scutula*: after the apothecial disc resembling a small shield; *vitellinus*: named after the apothecial colour, like egg yolk; *geiphilum*, *solani*: after the host plant, *Geum* and *Solanum*.

Misapplication: *H. vitellinus s.* Svrček (1985), Matheis (1976) = *H. menthae*, except for the type of *H. geiphilum*.

Hymenoscyphus scutula is a very common and wide-spread species on herbaceous stems, known especially from Europe and North America (White, 1942), characterized by strongly heteropolar ("scutuloid") ascospores with one, rarely two conspicuous setulae at each end, which have a length of (0.5–)2–3(–5) µm, and asci arising from simple septa. Spores of a typical collection are as illustrated on Fig. 59. The name has presently a long list of synonyms in Species Fungorum, although not all of them can safely be included in the scope of this rather variable species. Type material appears never to have been located or reexamined. White (1942) studied various collections of *H. scutula* in which either some or almost all spores possessed setulae, but included also a sample entirely without setulae (type of *Helotium gracile* Cooke & Peck), for which he figured the absence of croziers. White (1944) treated the type of *H. fucatus* (W. Phillips) Baral & Hengstm. merely as a variety of *H. scutula*, although it deviates, according to his redescription and accurate illustration, in distinctly larger spores and particularly the presence of croziers.

How widely the concept of *H. scutula* should be adopted is difficult to say. For instance, lignicolous samples currently referred by me to *H. virgultorum* are not easy to separate. Perhaps only those populations with rather small LBs in the spores belong to the latter species. The caulicolous taxa *H. vitellinum* and *H. geiphilum* as redescribed here from their types (Figs 56–58) cannot safely be separated from *H. scutula* by morphology, therefore, I tentatively accept them as synyonms of *H. scutula*. Also a specimen on bark of *Vitis* might belong in the scope of *H. scutula* (Fig. 61).

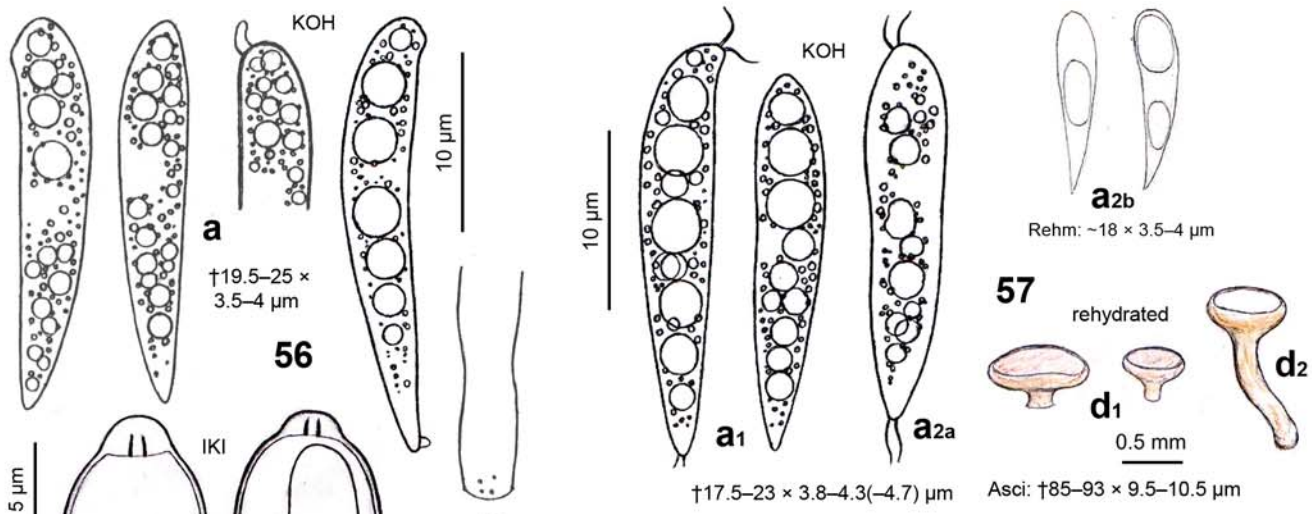
According to Saccardo (1889: 262), Rehm established ***Helotium vitellinum*** based on a specimen on rotten stems of *Filipendula* ("*Spiraea*") *ulmaria* from Augsburg, with yellow, 2 mm tall apothecia with discs eventually becoming orange-red, 1.5 mm diam., asci 75–80 × 9 µm, and heteropolar spores 18 × 4 µm containing 1–2 large "nuclei". Later Rehm (1893: 794) included collections from Berlin on *Filipendula* and *Lysimachia vulgaris*, and reduced it to a form of *H. scutula*. He distinguished it from typical *H. scutula* by smaller spores (18–20 × 3–3.5 vs. 18–25 × 4–5 µm), also by smaller apothecia (0.3–1.5 vs. 0.3–3 mm diam.) with shorter (rarely up to 1 vs. 0.5–5 mm) and much more delicate stipes.

Carpenter (1981: 270) examined the "holotype specimen" from S ("Augsburg, auf *Spiraea ulmaria*, Oct 1878, Britzelmayr s.n. [ex Herb. Rehm]") and agreed with the opinion of White (1942) and Dennis (1956) that *H. vitellinus* is a synonym of *H. scutula*. Without personal study, Lizoň (1992: 43, 46) accepted this synonymy. The present type study confirms this opinion. However, since this species complex is in bad need of molecular work, conclusions about synonymies are to be considered as premature at the moment.

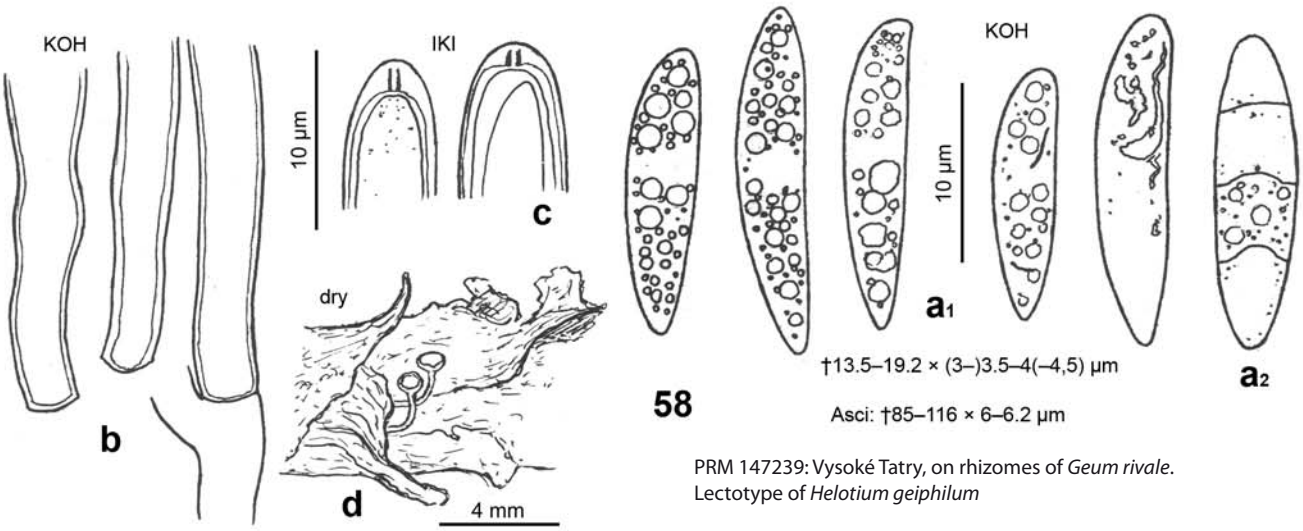
H. vitellinus was examined by me from holo- and isotype material in M (X.1991) and S (VIII.1999) (Figs 56–57). Although Carpenter (1981) did not mention the existence of different convolutes at S, the online database of the herbarium in Stockholm lists two specimens, S-F10431 ("lectotype") and S-F10432 ("isolectotype"). Since Rehm's private herbarium is located in S, the specimens there frequently contain his original handwriting and sketches, which is also the case on the label of S-F10432, which bears a sketch of two spores (Fig. 57 a2b) and a diagnosis, including asci ~75–80 × 9 µm and spores ~18 × 3.5–4 µm. It seems, therefore, that convolute S-F10432 was the one that Rehm had used when preparing the protologue. However, this convolute contains only very few apothecia, and only a single ascospore was found by me in the examined apothecium (Fig. 57 a2a), but no asci. In contrast, S-F10431 contains abundant apothecia rich in asci and spores (two of them are documented on Fig. 57 a1). Carpenter (1981) obviously meant with "holotype" the convolute S-F10432, and in naming it so he followed a current practice. Yet, this specimen seems to be rather useless for microscopic examination. I here follow the printed denomination on the two convolutes and designate specimen S-F10431 as **lectotype** of *Helotium vitellinum*.

Differences among the examined convolutes in M and S were noted in stipe length (1–1.3 mm in S-F10432, 0.2–0.6 mm in M, 0.1–0.5 mm in S-F10431), while stipe width was always in the range of 0.1–0.2 mm (rehydrated). The microscopic characters were found to conform, except that in S more spores with distinct setulae were observed. All spores were found to be strongly heteropolar (scutuloid), which is in accordance with Rehm's illustration on the label of S-F 10432 which shows strongly clavate spores with obtuse apex and acute base. They are frequently multiguttulate though often with some rather large globose LBs, and generally longer than stated by Rehm. What Rehm illustrated on the label (Fig. 57 a2b) and described as "with 1–2 large oil drops" in the protologue, refers to spores in which the oil drops fused to large elongate aggregations. Comparatively short setulae (0.5–2.5 µm) were seen in a few spores only, 1(–2) at each end. The asci arise from simple septa and have strongly reactive apical rings (blue without KOH-pretreatment, type BB). Thus, *H. vitellinus* does not significantly differ from typical *H. scutula*, including the presence of setulae. An error occurred in the statement of Lizoň & Kučera (2014) about the setulae which are in fact only predominantly absent in this collection, not entirely.

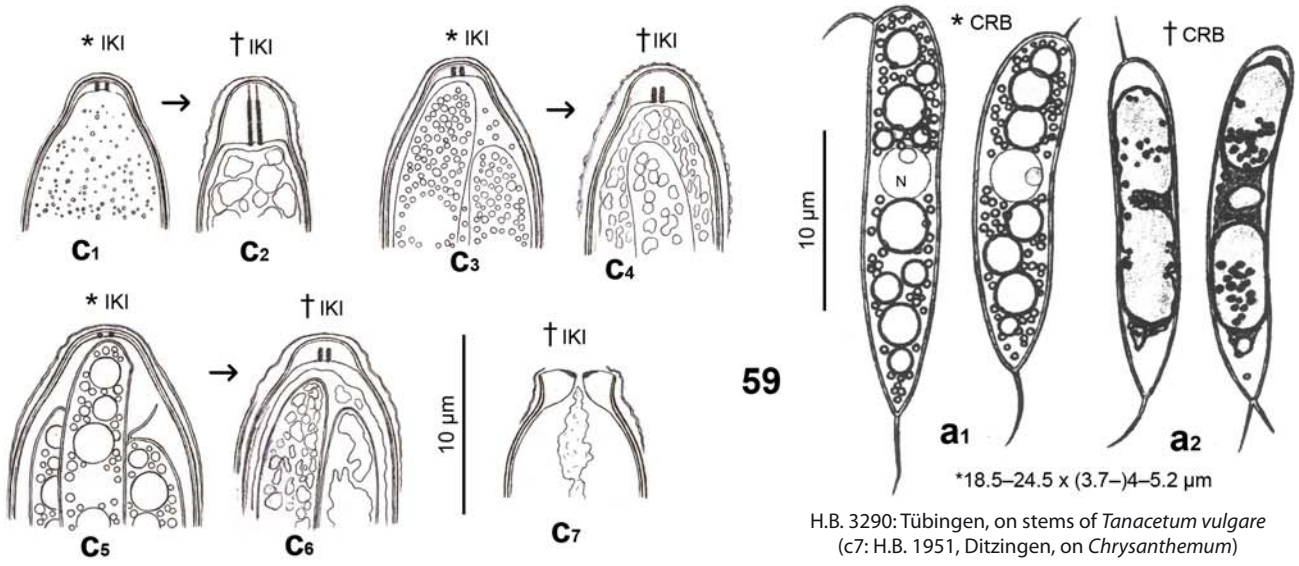
When Svrček (1985: 150, Tab. VII, fig. 1) revised the lectotype of ***Helotium geiphilum*** Velen. (Vysoké Tatry, VII.1924, on rhizomes of *Geum rivale*, PRM 147239), he found the spores to be fusiform, rounded at both ends or very slightly attenuated towards the base, eguttulate, 15–19 × 3.5–4 µm, sometimes 1-septate and distinctly greyish in MLZ. The contents of the paraphyses stained reddish-brownish in MLZ. Velenovský (1934: 193), however, described them as guttulate, but gave only a very brief description without illustration. With some hesitation, Svrček suggested *H. geiphilum* to be conspecific with "*Hymenoscyphus vitellinus*" (*s.* Svrček, = *H. menthae*), but he was unsure as the apothecia were described by Velenovský as entirely flesh-coloured.



Rehm 513: Augsburg, stems of *Filipendula ulmaria*. Holo- (57-2) and isotypes of *Hymenoscyphus vitellinus* (56: M-0206430, 57-1: S-F10431, 57-2: S-F10432)



PRM 147239: Vysoké Tatry, on rhizomes of *Geum rivale*. Lectotype of *Helotium geiphilum*



H.B. 3290: Tübingen, on stems of *Tanacetum vulgare* (c7: H.B. 1951, Ditzingen, on *Chrysanthemum*)

Figs 56–58. Types of *Helotium vitellinum* and *H. geiphilum*, here reideintified as *Hymenoscyphus* (?)*scutula*; **Fig. 59.** *H. scutula* (typical collection). a. mature ascospores (but overmature in Fig. 58a2; N = nucleus), b. ascus base with simple septa, c. immature and mature ascus apices (emptied in c7), d. apothecia. – Dead state, except for 59a1, c1, c3, c5). Fig. 59a is taken from Baral (1992: fig. 21), Fig. 59c from Baral (1987: fig. 10). – Note that the dead spores in Fig. 59a2 died in the fresh apothecium, therefore, the lipid bodies have undergone complete coalescence (compare also H. menthae on Fig 9). Fig. 57a2b: drawing by Rehm on label in S-F10432. Coalescence masks the striking difference between the two taxa.

Reexamination of the lectotype (Fig. 58) revealed the spores to be predominantly slightly scutuloid so that, for most of the free spores, it is possible to recognize their upper and lower ends. They are finally 1(–3)-septate, and setulae were not observed on any of them. Several spores were found to be multiguttulate (in KOH). The asci arise from simple septa and the apical ring reacts strongly blue in IKI. Despite the smaller and less scutuloid spores and the much narrower asci (Svrček: 95–110 × 6–7 µm), I consider this taxon as conspecific with the type of *H. vitellinus* (non *s.* Svrček).

The taxon ***Hymenoscyphus scutula* var. *solani*** was repeatedly applied to collections, even in the modern literature, and appears never to have been raised to species level. For instance, Ahmad (1978: 207) identified a collection from Pakistan with relatively short, heteropolar spores as *H. scutula* var. *solani*. I can only speculate that this might be conspecific with *H. vitellinus*. Yu *et al.* (2000) applied the name (as cf.) to a Chinese collection on a monocot stem, with rather long, strongly scutuloid spores and inamyloid asci. The Indian material reported by Thind & Sharma (1980) as *H. scutula* var. *solani* is described in the present paper as a new species, *H. sharmae*. Korf & Zhuang (1985) used the name for a Chinese collection here referred to *H. macroguttatus* (see above).

Regrettably, the identity of *H. scutula* var. *solani* could not better be clarified in the present study. It was impossible to locate authentic material at H (Niemelä & Huhtinen, pers. comm.), although Dennis (1956: 78, fig. 71 B) examined an authentic specimen from Herb. Karsten, yet without indicating any collection data. Dennis' illustration shows five slightly but distinctly scutuloid, 1-septate, probably overmature spores. Based on their consistently heteropolar shape it seems quite improbable that *H. scutula* var. *solani* is a synonym of *H. menthae* or *H. macroguttatus*. Rather, the taxon might be conspecific with *H. vitellinus* (= *H. scutula*).

Phylogeny: In GenBank the name *H. scutula* appears to be frequently misapplied. The only seemingly trustable ITS sequence concerns a sample from tropical Cuba collected by G. Verkley (CBS 480.97, KC481695), which is genetically close to an unpublished sequence from a Swiss collection identified as *H. scutula* (ZT 4292, Queloz, pers. comm.), though probably not conspecific as it deviates by 10 nucleotides.

Specimens of *H. scutula s.l.* examined and illustrated here: Germany: Hessen, ~6 km NW of Mainz, around Budenheim, ~100 m, branch of *Vitis vinifera*, on bark, undated (autumn), L. Fuckel (Fuckel Fungi Rhen. Exs. 2685, M, H.B. 6010a ø [mixture in syntype of *H. hyalopes*, H.B. 6010b]). – **Baden-Württemberg**, 10 km NW of Stuttgart, Ditzingen, Mittlere Str., 300 m, stems of *Chrysanthemum*, 18.X.1975, H.O. & O. Baral (H.B. 1951). – 5.5 km NE of Tübingen, Pfrondorf, Blaihofstr., 430 m, stem of *Tanacetum vulgare*, 24.X.1987, H.O. Baral (H.B. 3290). – **Bayern, Schwaben**, Ausgburg, ~500 m, *Filipendula ulmaria*, X.1878, M. Britzelmayr (Rehm Ascomyc. Exs. 513, S-F10431 lectotype of *H. vitellinus*, isolectotypes in S-F10432 and M-0206430, H.B. 4497 ø). – **Switzerland: Schaffhausen**, 6.3 km NE of Schaffhausen, 1.2 km NW of Thayngen, Geiger (vineyard), 460 m, on leaves (petioles) and fruit stems of *Vitis vinifera*, 15.XI.1987, P. Blank (P.B. 689, H.B. 6015b ø [mixture with *H.* ?*vitigenus*, H.B. 6015a]). – **Slovakia:** Prešov, ?14 km NNW of Poprad, ?5 km W of Tatranská Lomnica, Vysoké Tatry, ~1800 m, on rhizoms of *Geum rivale*, VII.1924, A. Pilát (PRM 147239, lectotype of *H. geiphilum*, H.B. 5819 ø).

Hymenoscyphus vitigenus (De Not.) Dennis, *Persoonia*, 3 (1): 74 (1964) – Fig. 64.

≡ *Helotium vitigenum* De Not., *Comm. Soc. crittog. Ital.*, 1 (5): 377 (1864) [1863].

≡ *Calycina vitigena* (De Not.) Kuntze, *Revis. gen. plant.*, 3 (2): 449 (1898).

Helotium hyalopes Fuckel, *Jb. nassau. Ver. Naturk.*, 27–28: 63 (1873) [1873–74] – Figs 60, 62.

≡ *Calycina hyalopes* (Fuckel) Kuntze [as '*Hyalopus*'], *Revis. gen. pl.*, 3 (2): 448 (1898).

Typification: *vitigenus*: Italy, Lombardia, Lago Maggiore, Valle Intrasca, branch of *Vitis vinifera*, autumn 1863 (not located according to Lizoň & Kučera, 2014); – *hyalopes*: Germany, Hessen, Budenheim, branch of *Vitis vinifera*, autumn (L. Fuckel, Fungi Rhen. Exs. 2685, M, syntype, four apothecia with shorter and wider spores).

Etymology: *vitigenus*: named after the host plant (*Vitis*); *hyalopes*: after the translucent stipe.

Helotium vitigenum and *H. hyalopes* are currently believed to represent a single species. Their original descriptions recall a possible relationship to *H. macroguttatus* because of their fusoid (homopolar), 2- or 4-guttulate ascospores, or to *H. menthae*, given that the oil drops in the spores have fused during drying. However, when revising a syntype of *H. hyalopes* at M, it turned out to be a mixture of two different species growing in close proximity on the same branch, both possessing distinctly scutuloid spores and asci without croziers. Since the identity of the type of *H. vitigenus* was not clarified in the present study, its synonymy with *H. hyalopes* seems questionable. A published thorough redescription of De Notaris' type material does not appear to exist.

The brief, unillustrated original description of ***Helotium vitigenum*** by De Notaris (1864) concerns a fungus collected on a xeric ("secco") branch of *Vitis vinifera* at Lago Maggiore (Italy) in autumn 1863. Its features include a pale straw-coloured disc, a stipe of moderate length, and 4-guttulate, ellipsoid-fusoid spores 20 µm long. Saccardo (1875: 137; 1883: tab. 1343; 1889: 229) referred to this species two samples from mountainous vineyards in Venetia (Padova and Treviso), on fallen twigs of *Vitis vinifera*, with homopolar, fusoid, guttulate spores 18–20 × 6 µm, and 8-spored asci 110 × 12 µm (Fig. 64).

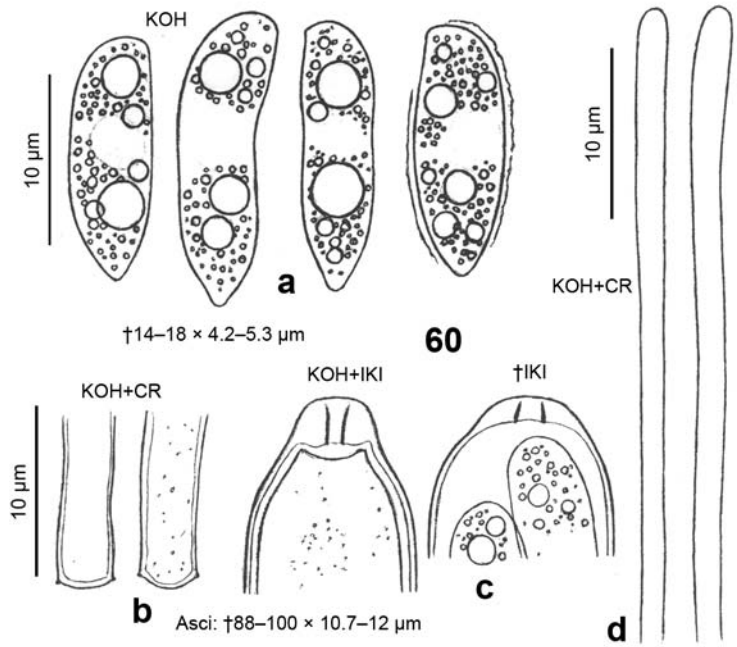
Pirotta (1877) reexamined and illustrated one of Saccardo's specimens (Mycoth. Veneta n. 959), and emended the description of *Helotium vitigenum* by giving much wider asci (90–110 × 16–18 µm), and oblong-fusiform, 2-4-guttulate spores 16–20 × 4–6 µm, while his drawing shows distinctly trapezoid spores. Thümen (1878: 87) merely copied the description of Pirotta. The fungus is said to be a parasite of vine, according to Pirotta (see Rehm, 1893).

The brief and unillustrated protologue of ***Helotium hyalopes*** in Fuckel (1873), issued as Fungi Rhen. Exs. 2685, concerns a fungus collected near Budenheim (NW of Mainz), on xeric ("arid") bark of *Vitis vinifera* in autumn, with oblong-fusiform, biguttulate, subinequilateral spores 16 × 6 µm, "often aggregated in upper part of ascus", and asci 126 × 18 µm (obviously in living state). Rehm (1893: 789) restudied his portion of the exsiccatum and observed rather large (0.5–2 mm diam.) apothecia with long stalks (up to 2.5 × 0.2 mm), fusiform spores 15–20 × 5–6 µm with two large oil drops (possibly by fusion), and 4–8-spored asci 80–120 × 10–12 µm.

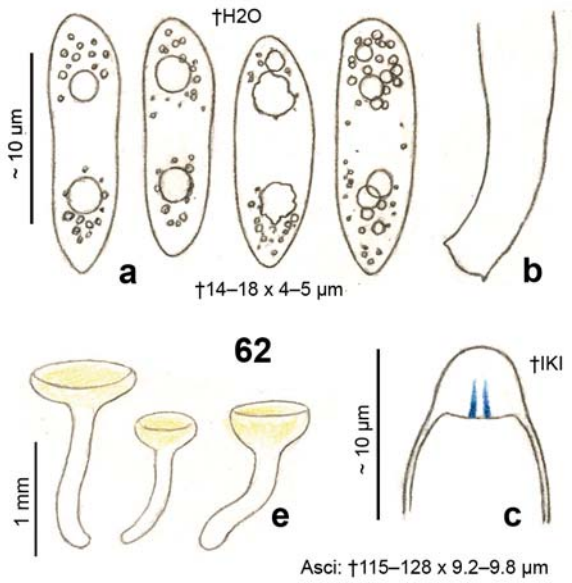
Thümen (1878: 88, pl. 3, fig. 18) gave under *H. hyalopes*, besides Fuckel's diagnosis, also his own observations on Fungi Rhen. Exs. 2685, but did not add personal measurements. He emphasized that the spores were always aggregated in the upper part of the ascus, and the paraphyses only half as long as the asci. The figured ascus is indeed turgescent, with the spores 2–3-seriate and accumulated in the upper half, and the free spores apparently partly scutuloid. That asci were still alive in his preparation appears to tell for some desiccation-tolerance of *H. hyalopes*, unless Thümen received the material from Fuckel in the fresh state.

In the present study, two convolutes of *Helotium hyalopes* of Fungi Rhen. Exs. 2685 in M were examined. As a result, two obviously different species of *Hymenoscyphus* occur in this sample. In the more frequent one, the asci have a strongly euamyloid apical ring, and the spores contain 1–4 large and many small LBs in each half, and some of them possess two very short setulae at the base (Fig. 61). This appears to be conspecific with the type of *H. vitellinus* (?= *H. scutula*). Judging by macroscopy, nearly all of the ca. 50 apothecia seem to represent this species. They are cream when dry, changing to red-brown with age, rehydrated 0.3–0.8 mm diam., stipe 0.2–0.4 mm long.

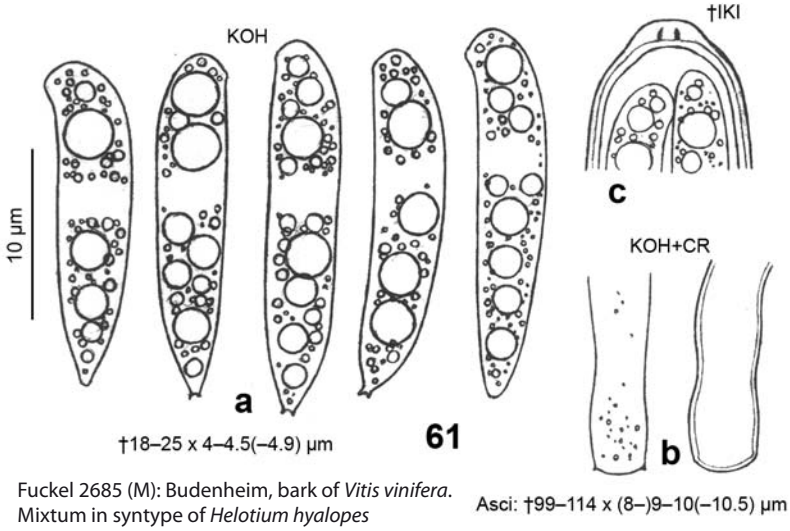
Fuckel (1873) stated that the spores much shorter and wider and the asci longer and especially wider. Indeed, in the smaller of the two convolutes four slightly smaller apothecia in a close though ±



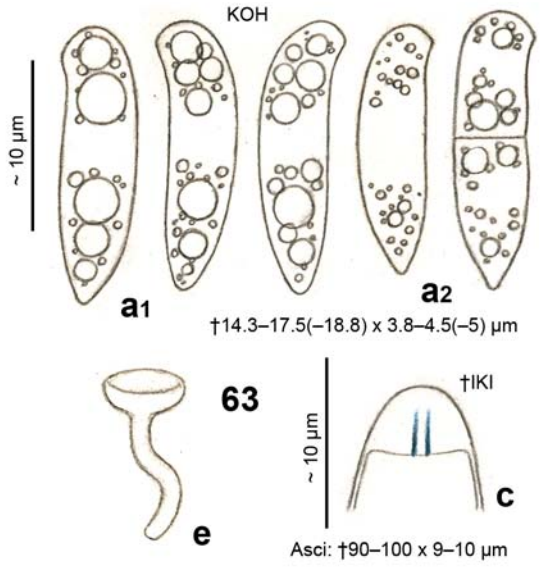
Fuckel 2685 (M): Budenheim, bark of *Vitis vinifera*. Syntype of *H. hyalopes*



P.B. 689 (H.B. 6015a): Schaffhausen, leaf of *Vitis vinifera*



Fuckel 2685 (M): Budenheim, bark of *Vitis vinifera*. Mixtum in syntype of *Helotium hyalopes*



P.B. 689 (H.B. 6015b): Schaffhausen, leaf of *Vitis vinifera*

Figs 60–63. *Hymenoscyphus* spp. on *Vitis vinifera* (bark and leaves). – 60. *Hymenoscyphus* ?*caudatus* (syntype of *Helotium hyalopes*); 61. *H.* ?*scutula*; 62. *H.* ?*caudatus* (Blank, 1989 as *H. vitigenus*); 63. *H.* ?*caudatus*. – a. Mature ascospores (64a2 immature and overmature), b. Simple-septate ascus bases, c. Apices of immature or mature asci, d. Paraphyses, e. Apothecia (rehydrated). – All in dead state.

separate population differ in having a more yellowish disc (rehydrated, 0.3–0.5 mm diam.) and a hyaline, glassy stipe 0.3–0.5 mm long. One of these apothecia was tested (Fig. 60); it differs in shorter and wider asci, and shorter and wider spores. The spores contain 1–2 large and many small LBs in each half, and no setulae were seen at their ends. As in the other species, the asci arise from simple septa and have a strongly euamyloid apical ring. Obviously, this is the taxon which Fuckel had under the microscope, judging from ascus and spore size and from the translucency of the stipe. Only these four apothecia should be considered as the type of *H. hyalopes*.

Because Pirotta (1877) did not see marked differences between the descriptions of *Helotium vitigenum* and *H. hyalopes*, he considered them to be synonymous. The given differences in spore guttulation (4-guttulate in *H. vitigenum*, 2-guttulate in *H. hyalopes*) he considered to be incorrect because he observed variation in the number of drops in Mycoth. Veneta n. 959. Also Rehm (1893) believed that the two taxa are synonymous, based on the descriptions of De Notaris, Fuckel and Saccardo, and on his reexamination of Saccardo Mycoth. Veneta n. 959 and Fuckel Fungi Rhen. Exs. 2685.

Thümen (1878: 87), however, doubted the synonymy of *Helotium vitigenum* and *H. hyalopes* because of differences in ascus length. However, this difference can easily be explained by the shrinking effect of the asci which Fuckel measured in the living state (126 µm) and Saccardo probably in the dead state (90–110 µm).

Fresh collections and molecular data are needed to clarify the taxonomic relationship of *Hymenoscyphus vitigenus* and its asserted synonym *Helotium hyalopes*. Dennis (1956: 92) described under *Helotium vitigenum* a British sample on unidentified twig, which he considered to agree well with Fungi Rhen. Exs. 2685. Contrary to his opinion, however, delimitation of *H. hyalopes* against *Hymenoscyphus subferrugineus* is easily accomplished by the presence of croziers in *H. subferrugineus* (a detailed restudy of the lectotype of that species will be presented in a separate paper). Possibly, the British sample belongs in the scope of that species. On the other hand, de-

limitation of *H. hyalopes* against *H. caudatus* (P. Karst.) Dennis seems more problematic: *H. caudatus* is a collective species on leaves of deciduous trees, being until now little understood. The name was applied to collections which obviously belong to different taxa, featuring scutuloid spores with a very different size and guttulation, differing also sometimes in the ascus base. However, collections on wood or bark so far appear never to have been referred to *H. caudatus*.

I never saw fresh material referable to *Hymenoscyphus vitigenus* or *Helotium hyalopes*. Like Dennis (*loc. cit.*), the following authors examined only a recent collection (under the name *Hymenoscyphus vitigenus*): Raitviir & Faizowa (1983, ?*Salix* twigs), Sacconi (1985, *Vitis vinifera* twigs), and Blank (1989, *Vitis vinifera* leaves). Blank's specimen (P.B. 689) was reexamined by me and found to be a mixture of two different species growing on different petioles, both with a similar range in spore size: (1) a sparse population with slightly scutuloid spores which represents the fungus illustrated by P. Blank, and which hardly differs from *H. caudatus* (H.B. 6015a, Fig. 62); (2) a more abundant population with strongly scutuloid spores, perhaps belonging in the scope of *H. caudatus* in a wide sense (H.B. 6015b, Fig. 63). Both possess euamyloid asci without croziers. Blank's drawing shows oblong ellipsoid-fusoid to clavate spores, but is obviously not accurate enough to recognize that the spores are predominantly heteropolar. His description includes also the macroscopy of the associated second taxon, and his remark "reddening with age" appears to refer to that species rather than *H. vitigenus*.

The present study indicates that *Vitis* hosts at least three different species of *Hymenoscyphus*: *H. macroguttatus* (Fig. 48), *H.* ?*caudatus* (Figs 60, 62–63), and *H.* ?*scutula* (Fig. 61). Whether *H. vitigenus s.* Saccardo (Fig. 64) belongs to *H. macroguttatus* or to *H. menthae* remains to be clarified. Even more important would be to locate the type of

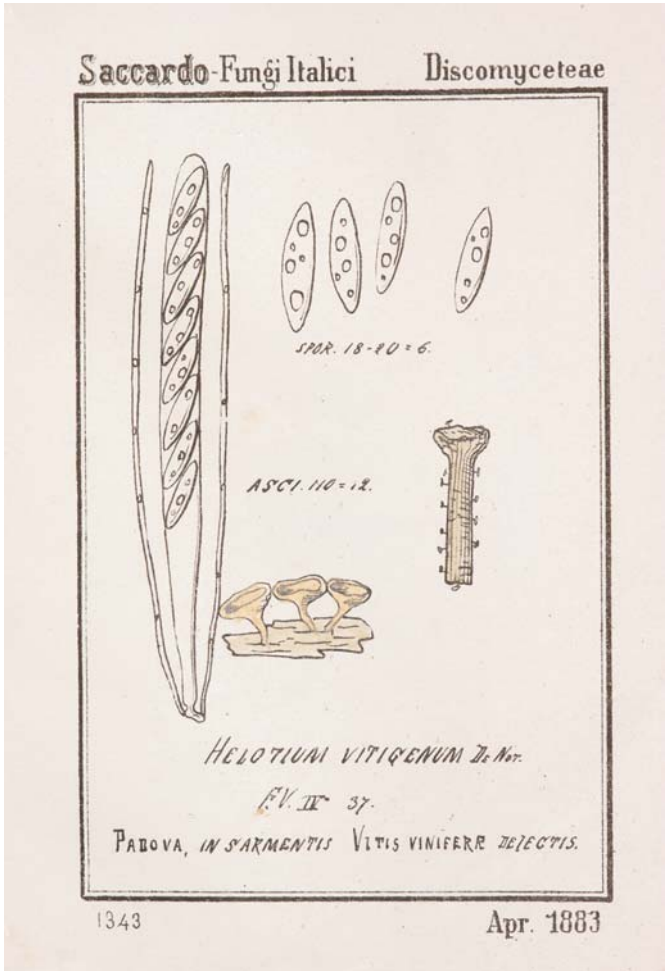


Fig. 64. *Hymenoscyphus vitigenus* (Venetia, twigs of *Vitis vinifera*), in the interpretation of Saccardo (1883: pl. 1343). – Identity not clarified, perhaps *H. menthae* or *H. macroguttatus*?

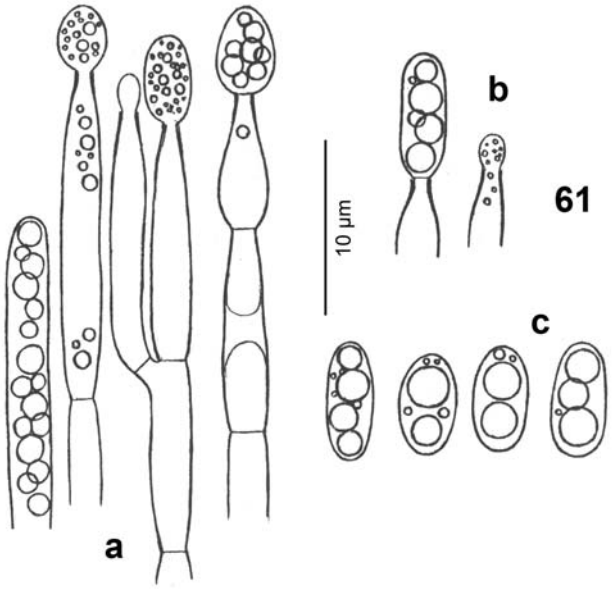


Fig. 65. ?*Acremonium* sp., intrahymenial parasite of *H. menthae*. – a, b. Conidiophores producing guttulate conidia among the still-living, guttulate paraphyses (left) of the host. c. Mature phialoconidia. – All in living state.

H. vitigenus and to find out whether it might represent an earlier synonym of *H. macroguttatus* or *H. menthae*.

Lizoň & Kučera (2014) accepted a name change by Kuntze (1898) from *hyalopes* to *hyalopus*, but I feel there is no reason for doing so because the prefix *hyalo-* is both Greek and Latin and can, therefore, be used in compositions of *pes* as well as *pus*.

Specimens examined (*H.* cf. *vitigenus*): **Germany: Hessen**, ~6 km NW of Mainz, around Budenheim, ~100 m, branch of *Vitis vinifera*, on bark, undated (autumn), L. Fuckel (Fuckel Fungi Rhen. Exs. 2685, M, syntype of *Helotium hyalopes*, H.B. 6010b ø [mixture with *H.* ?*scutula*, H.B. 6010a]). – **Switzerland: Schaffhausen**, 6.3 km NE of Schaffhausen, 1.2 km NW of Thayngen, Geiger (vineyard), 460 m, leaves of *Vitis vinifera*, on petioles, 15.XI.1987, P. Blank (P.B. 689, H.B. 6015a ø [mixture with *H.* ?*scutula*/*caudatus*, H.B. 6015b]).

General comments

Shrinking effect. Ascus and spore size were found to be comparatively variable characters. Although there are tendencies for different mean values of length, width, and l:w-ratio between the species treated here, such data gained from a single collection helps little in species identification. Variation may even occur within single collections. F. ex., in the type material of those names here referred in synonymy with *H. menthae*, ascus length and width were often found to be very different from Svrček's data. Likewise, spore length in *H. menthae* may vary between 15–19 and 18–24 µm depending on the collection.

In addition to this variation, the shrinking effect of the asci (difference in size when comparing living with dead asci, Baral, 1992: 345), which is a general feature of ascomycetes, is very remarkable in the genus: asci shrink ca. 15–20% in length and ca. 8–20% in width, therefore, they lose up to about half of their volume (the same shrinkage takes place during active spore discharge). In comparison to this, shrinkage of ascospores is comparatively unimportant: ca. 1–2% in length and ca. 2–5% in width. Size differences in relation to the mounting medium (H_2O, KOH, MLZ, CB etc.) are quite unimportant when dealing with dead elements.

Iodine reaction of ascus apex. The intensity of the iodine reaction as well as its colour (eu- or hemiamyloid) is usually a relatively constant feature within a species. Different observations gained

from the same material occurred, however, for instance in the types of *H. repandum* var. *rumicis* and *H. stramineum* between Svrček's and my data. Possibly this was a result of different reagents, although hemiamyloid reactions which cause such divergences were not observed in the species treated here. The shape of the apical apparatus is highly consistent within the genus *Hymenoscyphus*. It therefore does not aid species distinction, but it permits recognition of misplaced taxa: for instance, *Calycina herbarum* (Pers.) Gray has for a long time been treated in *Hymenoscyphus*.

Croziers. The ascus base is currently neglected with regard to the presence or absence of croziers because in squash mounts the detection of this character needs a higher amount of patience and often the use of KOH in combination with Congo Red. However, in not too thin median sections of living material mounted in water, the character is usually very promptly seen.

White (1942, 1943, 1944) carefully examined and depicted the ascus base and ascogenous hyphae for simple septa and croziers as a species marker of *Hymenoscyphus* (as *Helotium*). In spite of these excellent and at that time new observations, White's knowledge was not taken up by most later workers. Only in recent times the character received due consideration, either at the species level (e.g., Hengstmengel, 1996; Baral *et al.*, 2013; Baral & Bemmann, 2013, 2014), or variety level (Huhtinen, 1990). French workers, e.g. Berthet (1964), often use the equivalent terms 'pleurorhynque' (for croziers) and 'apo-rhynque' (for simple septa).

In my studies on the *Helotiales* after ca. 1987 I began to examine ascus bases for the presence or absence of croziers, stimulated by White's studies. This character turned out to provide a useful species marker in many genera, allowing clear separation between taxa which were previously considered to be difficult. It proved also very helpful in the genus *Hymenoscyphus* which is evident in the treatments by White (*loc. cit.*), Hengstmengel (1996), Baral (1997), Baral *et al.* (2013) and Baral & Bemmann (2014).

Hengstmengel's (1996) important paper deals with some species related to *H. scutula*, most of them with scutuloid spores but, in contrast to *H. scutula*, all being characterized by having croziers. The presence of croziers turned out to be a rather rare character state in species of *Hymenoscyphus* with scutuloid spores, while species having asci arising from simple septa are in the majority (Hengstmengel, 1996: 192; Baral, 1997: 255).

White and Hengstmengel predominantly worked with dead herbarium material. Essential with such material is to swell the elements in KOH or NH_4OH. Staining with CR noticeably increases contrast of cell walls, and is obligatory in badly preserved material. Croziers are clearly visible in side view only, but are easily taken for simple septa if in the opposite position; thus orientation can obscure croziers and give the impression of variation within a single apothecium (Huhtinen, 1990: 66).

When studying living material, croziers and simple septa are usually rapidly seen due to the transparency of the cytoplasm. It is advantageous to study median sections in which the elements are still in situ. Working with herbarium specimens is actually more difficult and time-consuming in this respect, which seems to be one reason why the character has most frequently been neglected by workers.

The genetical background of croziers is still obscure. Huhtinen (*loc. cit.*) and Hengstmengel (1996: 192) gave a comprehensive account of the morphology and taxonomic value of croziers and simple septa. Usually, the character occurs in combination with additional features and supports the taxonomic validity of a taxon. The relative DNA-content seemed to be correlated with the presence or absence of croziers, based on results published in Bresinsky *et al.* (1987: 311). Six species of *Lachnaceae* were measured in this study: two of them had approximately a double relative DNA-content (77–90, ploidy level 4×) compared to the other four (37–45, ploidy level 2×). Although these samples have never been studied for the ascus base, I knew from different collections that the first two species have croziers, whereas the latter four had simple septa. However, further examination of similar pairs of species by Weber (1992) could not confirm such a correlation.

The relative DNA-content of *H. menthae* was 57 (ploidy level 3×, Weber, 1992: 122, as *H. consobrinus*). The method of measuring the DNA content requires fresh collections, and such were not available during this study for *H. macroguttatus* and other species treated here.

Ascospore shape. The two main character states of spores, homo- and heteropolar, are not sharply delimited in the genus *Hymenoscyphus*. In *H. macroguttatus* most spores are homopolar, i.e., it is impossible to determine the upper end of an ejected spore. A few spores in some collections were found to be very slightly scutuloid: the upper end is then quite well recognizable (Fig. 32a, right spore). In species with scutuloid spores nearly all spores feature a well-recognizable upper (rounded) and lower (pointed) ends. Due to the bilateral symmetry of scutuloid spores, their oblique apex and unilateral flattening is visible only in side view and, therefore, seemingly absent in ca. 50% of the spores.

Homopolar spores are more primitive compared to heteropolar spores, and scutuloid (bilateral-symmetrical) spores represent a higher specialized type compared to the more simple clavate spore shape. It seems, therefore, imaginable that *H. menthae*, *H. repandus* and *H. macroguttatus* represent an ancient group compared to the core of *Hymenoscyphus* around the type species *H. fructigenus*. However, unpublished phylogenetic results indicate that this is only true for the former two species, whereas *H. macroguttatus* belongs near species with scutuloid spores. *Cyathicula coronata* (Bull.) P. Karst., on the other hand, has almost the same type of ascospores as *H. menthae* in regard to shape, size, and guttulation, and even the apical apparatus of the asci is indistinguishable. It differs in an ectal excipulum of strongly gelatinized *textura oblita* and in long marginal teeth. However, collections of what seems to be *C. coronata* were seen in which the marginal teeth were completely absent (e.g., H.B. 9971, Cataluña, L. Sánchez). Genetically, *C. coronata* is rather distant to *H. menthae*, though both cluster in the family *Helotiaceae* as currently circumscribed.

Ascospore guttulation. Spore guttulation is frequently neglected by workers, for two reasons: the guttules (oil drops = lipid bodies = LBs) are more or less invisible (masked) when mounting living or dead spores in MLZ or CB, or often also when mounting dead spores in H_2O; they are well visible when mounting living spores in water, or likewise when mounting dead spores in KOH or NH_4OH. When studying dead spores, however, the guttules show a very high variation in size and shape among the spores, if the lipid content is medium or high. This variation is caused by coalescence in some or most of the spores. Further variation is due to the developmental stage of the spores: immature spores have few or smaller oil drops while they again decrease by consumption during the first stages of germination. For a correct interpretation of guttules in dead material, such secondary changes, as well as immature and overmature stages of spore development, must be disregarded. These effects have misled workers into disregarding cell contents, despite their high taxonomic value in living material. Lipid patterns in spores probably indicate differences in adaption concerning the first phase of colonization.

The taxonomic value of the guttule or lipid pattern (size and arrangement of the oil drops in spores) can hardly be overestimated. Nevertheless, it is frequently neglected in descriptions due to its seemingly high variation within a single preparation. As I have shown elsewhere (Baral, 1992), this variation is the result of (1) living vs. dead spores, and (2) different developmental stages of the spores. When mature living material is mounted in water, highly constant lipid patterns are observed if the attention is focused on living spores, either within the turgescent mature asci, or when recently forcibly ejected. Secondary changes of lipid bodies (oil drops = LBs) such as coalescence (fusion, e.g., Fig. 9a1 – a2 or Fig. 59a1 – a2), or degradation after septum formation and during germination (Figs 10a, 11a2, 40a2, 58a2) can easily be recognized in fresh living

apothecia. In fact, such altered spore contents do not occur inside living asci, but only inside asci which have lost their turgor some hours or days ago, or when they were ejected prior to that time.

Lipid patterns were found to be highly consistent in virtually all of the freshly ejected spores of a preparation. This character allows a clear and rapid distinction between *H. menthae* and *H. macroguttatus*, but only if fresh specimens are at hand. Similar closely related species that differ markedly in this way occur in many groups of ascomycetes. The spores of such species contain a comparable amount of lipid but differ in size and number of single drops. For example, *Aleuria cornubiensis* (Berk. & Broome) J. Moravec (= *Melastiza chateri* W.G. Sm.) differs from *A. aurantia* (Pers.) Fuckel in multiguttulate vs. biguttulate spores, whilst dead spores are biguttulate in either species (Baral, 1992: figs 15–16). Likewise, *Ascocoryne cylichnium* (Tul.) Korf differs from *A. sarcoides* (Gray) J.W. Groves & D.E. Wilson with a similar consistency in the same way. This species pair is remarkable because its spores resemble those of *H. menthae* and *H. macroguttatus* in all respect.

Multiguttulate spores easily turn oligoguttulate by coalescence (fusion) of the small LBs when treated with chemicals such as lactophenol, or when heating a slide. Those large drops characteristic of *Aleuria aurantia*, *Ascocoryne sarcoides*, or *H. macroguttatus* are not formed by fusion but, like the small drops of multiguttulate spores, increase in size during spore ontogeny. This means that, under natural condition, fusion of oil drops does not take place. Large oil drops in living mature spores develop from one privileged minute drop out of a few LBs in the immature spore, the other LBs remaining more or less small. During growth the LBs always keep their perfectly globose shape. In dead spores, on the contrary, the lipid content often forms elongate drops or aggregations, and often shows a variable and asymmetrical pattern (see Baral, 1992: 357).

Spores that show the original lipid pattern of the living state can often be detected in old herbarium material, even in species with a high lipid content which shows a stronger tendency to fuse. However, sometimes all spores show more or less distorted lipid contents, e.g., when mounted in KOH. This was the case, e.g., in the specimen illustrated on Fig. 41, in which I noticed in the fresh state that the spores had 2–4(–6) large globose LBs, and where I failed to make a drawing at that time. In specimens that were carefully collected and preserved, the regular original guttule pattern is conserved in most of the spores, especially those inside the asci. This was found to be the case in all of the type and some other herbarium specimens studied here, even in those being older than 100 years (compare Figs 11–17, 38–40, 52–58, 60–61).

On the other hand, a distorted lipid pattern is frequently seen in fresh material as well. Often a small number of dead, mainly free spores are found on the hymenium. Uncritical workers often describe spores with variable contents of oil drops in a single collection and consequently consider spore guttulation as being of little taxonomic value. As an example, Hengstmengel (1984: 114) described the spores of *H. consobrinus* "with 1–4 relatively large guttules and/or a certain number of small guttules, later granulose to non-granulose". Apart from the fact that the observed variation is not a true one, the asserted development from a few large drops to many small droplets is actually impossible, and lacks any evidence.

Mountants such as MLZ or CB which contain lethal ingredients, but also water in the case of dead spores, often mask the lipid contents of cells. This further explains why authors who describe spores frequently disregard internal guttules. Contradictory reports in the literature about spore guttulation are frequently the result of this masking effect. Reviewers of preserved collections often wondered why they could not see any guttules inside the spores, although the descriptor of the fresh sample reported conspicuous oil drops. Even if both used water as mounting medium, they will arrive at contradictory results. In order to be sure about the presence of intracellular lipid in herbarium specimens, mounting in KOH or NaOH (ca. 1–5%), or NH_4OH is obligatory. These alkaline mountants considerably diminish refractivity of the cytoplasm but do not affect lipid contents.

The frequent presence of undistorted lipid in dead spores can be explained by the fact that spores of recently dried herbarium material are often still alive. This is easily seen when rehydrating the spores in water. Such rehydrated living spores are usually indistinguishable from those of the fresh state. Desiccation-tolerance of spores is indeed common in ascomycetes. Spores survive in a dormant state: the cytoplasm is completely dehydrated and the spores collapse due to water loss (in thick-walled spores of mainly non-helotialean fungi, de Bary bubbles are formed instead). When spores are rehydrated after a period of time which they do not survive, and they still show their original guttule pattern, it can be concluded that they lost viability in the dry state during storage in the herbarium. Coalescence of lipid bodies appears to require a hydrated cytoplasm, therefore, no coalescence took place in the dry spores. Irreversible distortion happens when the spores die in the hydrated state, either in the field during senescence of an apthecium, during prolonged storage in a moist box, when treating a water mount by chemicals or heat, or during drying by means of hot air. Therefore, the lipid pattern which we see in KOH-mounted herbarium material strongly depends upon the circumstances during the desiccation process.

Coalescence of LBs in hydrated cytoplasm can sometimes be observed in a water mount and is the first visible sign of injury to a living cell. I have demonstrated in a video film at the IMC 4 (1990, Regensburg) that the application of CB or MLZ to living hydrated multiguttulate spores of a *Pezicula* induces complete coalescence of the LBs within a few seconds. Interestingly, no or only slight coalescence of the LBs occurs when KOH is added to the living spores. KOH-provoked coalescence I have repeatedly noticed in herbarium specimens: in water the dead spores still showed a rather undistorted guttule pattern, while a certain degree of fusion of the oil drops happened when KOH was added. Furthermore, the LBs may become elongated by forces of the contracting cytoplasm. This is especially apparent when applying KOH to living asci of taxa in which the asci are multiguttulate when immature.

Hypothesis on the biological sense of guttule patterns: Lipid bodies in spores undoubtedly serve as a reserve substance that supplies energy and carbon during the first phase of germination (for literature see Baral, 1992: 357). Drought tolerance of spores is not linked to their lipid content, since dry dormant spores do not show metabolism at all. This is obvious from the fact that the LBs are still present in full size in herbarium specimens, hence they were not in the least consumed during storage.

Since constant differences in guttule patterns between closely related species occur rather frequently in ascomycetes, the biological function of LBs in spores should be of some importance in regard to the colonization of substrate. The differences in spore guttulation can be represented by two parameters: (1) the absolute lipid content of the spores, and (2) the size of the oil drops. These two parameters are supposed to function in the following way.

(1) A high lipid content seems to indicate that the nutritive conditions in the field during spore germination are frequently poor. The high amount of reserve substances accomplish optimal growth in the first phase of colonization. Species which are adapted to better conditions for germination refrain from storing high amounts of lipid in their spores. Because of the rather high consistency within a species, the two parameters are obviously genetically fixed.

(2) Many small lipid bodies are more rapidly consumed by enzymes during germination than a few large LBs, since the total surface area of all LBs is distinctly higher in a multiguttulate spore. A species with a multiguttulate spore is advantaged in substrate colonization over one with a few large drops, for instance, during short periods of humidity.

The disadvantage of the multiguttulate pattern lies in the fact that in a spore of a given volume more lipid can be stored when a few large LBs are formed. The tendency to store as much lipid as possible

in ascospores is very obvious in various groups, for example, in species of *Geoglossaceae* and *Leotiaceae*, *Discinella*, *Helvellaceae*, or *Octospora/Lamprospora*. In these taxa the largest LBs have a diameter not much below the width of the spore, while smaller LBs occupy the remaining space in the most optimal way except for the small nuclear region.

H. menthae and *H. macroguttatus* inhabit similar ecological niches, which makes it difficult to explain their different spore guttulation. A hypothesis to understand this striking difference might work as follows: depending on the seasonal weather, one of the two taxa is advantaged over the other in the speed of colonization. The much higher frequency of *H. menthae* in Central Europe might indicate that rapid ascospore germination is obligatory in the colonized habitats of this area. *H. repandus*, a species very similar to *H. menthae* in external as well as microscopical appearance (cf. Engel, 1987, color plate 55, figs 210 and 211; Baral & Marson, 2005) inhabits comparable habitats but deviates in considerably smaller spores with a low relative oil content. Macroscopically it is virtually indistinguishable from *H. menthae*, and it seems to represent a further ecological variant exploiting the advantage of a small and therefore possibly more efficiently transported propagule which needs minimum energy supply for its production.

Ascospore septation: One of Hengstmengel's (1984: 116; also in Arnolds *et al*., 1984: 313) characters of *H. consobrinus* which distinguishes it from *H. scutula* was the frequently seen 1-septate spores. However, his observations were mainly derived from herbarium material, in which it is nearly impossible to distinguish between mature and overmature spores. I have never detected septate spores inside living asci in any species of *Hymenoscyphus s.l.*, and forcibly discharged spores were also seen to be aseptate when studied immediately after discharge (except for two unpublished species in which the living asci regularly contain 1- or 3-septate spores).

Ascospore pigmentation: Overmature spores were found to become pale brown in some collections of *H. menthae*. As pointed out in Galán & Baral (1997), this is quite a common feature in *Hymenoscyphus*, though occurring inconsistently within a species. Such a delayed spore pigmentation is not uncommon in various groups of *Helotiales* and is, therefore, not useful for separating the genus *Phaeohelotium* as was done by some authors (the recent acceptance of the genus by Baral *et al.* (2013) is based on other features). The amount of brown spores in a preparation depends mainly on the senescence of the apothecia. For some other reason, perhaps unfavourable field conditions, some populations produce many such brown spores when senescent, while in others none or only a few can be found (compare, e.g. the rareness of brown spores in *H. fraxineus*, Baral & Bemmann, 2014). In any case, brown spores have never been seen inside living asci of the genus *Hymenoscyphus*, therefore, freshly ejected spores are always hyaline.

Paraphysis guttulation (refractive VBs). All species in this study examined from living material contain very similar, more or less refractive guttules (vacuolar bodies, VBs) in the terminal cells of paraphyses (see Baral, 1992: 363f). VBs usually cannot be seen in herbarium material, also they disappear instantly when mounted in lethal media such as KOH or MLZ, therefore, they are frequently absent in descriptions. Since some *Hymenoscyphus* species possess vacuoles of very low or even absent refractivity, VBs are of taxonomic interest and should be examined whenever fresh collections are available. Usually also the cortical cells of the ectal excipulum contain them, at least near the margin. Under vital staining with CRB, VBs yield a homogeneously, finally deep turquoise stain which confirms their vacuolar nature, while in non-refractive vacuoles CRB precipitates to form a few small, globose, dark blue MCs (metachromatic bodies, Baral, 1992: fig. 1c). In his unpublished identification key to the species of *Hymenoscyphus* recorded in Belgium, B. Declercq used ascospore shape, excipular cell shape, and VBs as entry criteria, which underlines the taxonomic value of VBs.

Apothecial colour. The yellow colour of the receptacle of *H. menthae* originates from minute carotenoid-containing LBs close to the septa in the cells of the subhymenium and lower part of paraphyses. This pigment fades away with the years during storage in the herbarium.

In contrast to lipid-bound pigments, the yellowish-cream to red-brown colour change of the originally white apothecia of *H. macroguttatus* and *H. subferrugineus* is due to the presence of VBs in the paraphyses and cortical cells. When VBs disappear in dead cells of senescent material, they are replaced by a slightly refractive cytoplasm of very irregular structure which shows a secondary pigmentation due to an oxidation process. The red-brown macroscopic colour of senescent apothecia was considered by some authors to be characteristic of *H. subferrugineus*, perhaps without being aware of the fresh apothecial colour which was whitish or pale yellowish in the present collections. Recognition of living cells at 400–1000× is necessary to avoid misinterpretations of apothecial colours. Red-brown hydrated apothecia like those of senescent *H. subferrugineus* may look sound in external view, but under the microscope hardly any living cells can be found.

Boudier (1909: 284, pl. 488) figured the upper instead of lower part of the paraphyses of *H. menthae* with a homogeneous yellow colour (Fig. 30), but described them as "remplies de granulations jaunes". However, he illustrated these droplets smaller and not as densely packed as in the present illustrations (Figs 1b, 26b, 27a), therefore, their yellow colour might originate from a colour change due to oxidation of the distorted VBs.

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