Hymenoscyphus serotinus and *H. lepismoides* sp. nov., two lignicolous species with a high host specificity

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Summary: *Hymenoscyphus serotinus* is a rather well-known and common species which, in its restricted sense, was so far recorded only within Europe, where it fruits exclusively in late autumn and early winter on externally blackened wood of twigs and thin branches of *Fagus*. Despite its rather characteristic, long and slender, curved (comma-shaped) ascospores, the species was not rarely confused in the past with other European lignicolous taxa: either with *H. calyculus*, from which it was thought to be insufficiently separated, or with an undescribed species that likewise fruits in late autumn on blackened wood though of *Carpinus*, and is here described as a new species, *H. lepismoides*. This differs from *H. serotinus* in longer and wider, straighter spores, which are provided by prominent terminal setulae, and also in the absence of croziers at the ascus base.
Apart from this and some other misinterpretations, *Hymenoscyphus serotinus* was considered by various authors as a foliicolous taxon, mainly outside Europe. One of these records, on unidentified skeletonized leaves from Jilin (China), was reinvestigated in the present study and considered to be related to, though not conspecific with, *H. vacini*, a European species confined to skeletonized leaves of *Acer*. The identity of this and other extra-European records remains to be resolved by future studies.

Keywords: Ascomycota, *Helotiales*, *Fagus*, *Carpinus*, croziers, setulae.

Introduction

Species diversity and delimitation within the genus *Hymenoscyphus* Gray is generally rather problematic because of the paucity of reliable morphological features. In addition to this, the neglect of characteristics of the living cells (Baral, 1992), or the croziers at the ascus base (Huhtinen, 1990: 66; Baral, 1996: 255) frequently evoked confusion in the past. For instance, in *H. serotinus* the remarkable spore curvature is diminished in the dead state, hence the separation from the similar *H. calyculus* and the here described *H. lepismoides* is obscured. *H. lepismoides* differs from the other two also in simple-septate ascus bases and larger spores. Similarly, *H. albidus* and *H. pseudoalbidus*, which are treated by us in a separate paper (Baral & Bemmann, in prep.), have been confused in previous light-microscopical investigations because they hardly differ in any morphological feature except for the absence vs. presence of croziers.

The main focus of the present paper is on the new species *H. lepismoides*, which was known to the senior author since 1988, though only from a single locality in the north of Luxembourg, where it regularly fruited in late autumn in a hedge of *Carpinus* on dead attached twigs of that tree. This species could not be identified with a published taxon, and seems to have been overlooked due to its rareness. Regrettably, fresh collections were available only during 1988–1989 (Fig. 7), and the here presented photographs all show the fungus in the dead state.

In the course of a clarification of misidentifications around *Hymenoscyphus serotinus* which grows on fallen twigs of *Fagus* in Europe, the species concept of extra-European authors who treated this species as predominantly foliicolous has been analyzed. When comparing the different European reports in the literature, it becomes obvious that Rehm's (1893) concept of *Helotium serotinum* gives much larger spore dimensions compared to other authors. According to our revision of the voucher specimens we also discovered that three famous discomycete researchers of the 19th century, L. Fuckel, H. Rehm and J. Feltgen, merged under the name *Helotium serotinum* also a different species, here newly described as *H. lepismoides*.

Materials and methods

Microscopy: Collections were examined preferably in the living state, but also from rehydrated herbarium material, using a Zeiss Standard 14 and a Zeiss Standard KF microscope equipped with achromat and planapochromat objectives. Tap water (H_2O) was used as a standard medium (Baral, 1992). The iodine reaction was tested with Lugol's solution (IKI = ~1% I_2, 2% KI, in H_2O), without KOH pre-treatment. Brilliant Cresyl Blue (CRB) added to a water mount was used for testing the presence of gel and the staining of vacuolar bodies (VBs). For observing the ascus base, fresh apothecia were sectioned free-hand, and sections were mounted without applying any pressure on the cover slip. In the case of herbarium specimens, hymenial fragments were rehydrated in H_2O, and a small drop of KOH and one of aqueous Congo Red (CR) was added. Waterman blue-black ink was applied for a better visibility of ascospore sheaths and setulae [1].

Photographic images (macro- and microphotos) were obtained using a Nikon Coolpix E4500 and a Nikon Coolpix 5000. Drawings were done free-hand.

Host identification: The identity of the host genus was evaluated from the wood anatomy (e.g., Hassler & Hirschmann, 1985), either from microscopic sections, or often by external view of the cross-broken wood. In the present case, *Fagus* can easily be distinguished from *Carpinus* by its very broad radial rays and abundant diffuse pores that tend to be aggregated in the early wood, whereas *Carpinus* has single-layered radial rays that are aggregated by simulating broad rays, and rather sparse pores that are often arranged in radial rows.

Distribution maps: Coordinates of collection sites were approximately evaluated using Google Earth and entered in a database (dBASE IV). Excerpts from this were exported to Microsoft® Excel, then transformed to a kml-file using the tool http://www.earthpoint.us/ExcelToKml.aspx, and finally displayed in Google Earth.

Abbreviations: * = living state, † = dead state, CR = aqueous Congo Red, CR_{SDS} = CR + sodium dodecyl sulfate, CRB = aqueous Cresyl Blue (~1%), IKI = Lugol's solution (~1% I_2, ~3% KI), KOH = potassium hydroxide (~10%), LB = lipid body, VB = vacuolar body, ø = no specimen preserved, n.v. = *non visus* (specimen or image not seen by us), d.v. = *documentum visus* (only microphotos/draw-

[1] Hengstmengel (1996) suggested the term *setula* (or bristle) to replace the previously used term "cilium", because cilia refer to the partly motile organelles of eucaryotic cells, e.g., those of the ciliates (*Ciliophora*).

ings/descriptions seen by us), *det.* = *determinavit* (identified [by another person]). {} = values in curled parenthesis refer to the number of collections that were examined; after the host plant and the associated species the curled parenthesis contains the number of certain and, after the dash, uncertain hosts.

Herbaria: Herbarium material was studied from the official herbaria of AH (Alcalá de Henares), HMAS (Beijing), KR (Karlsruhe), LUX (Luxembourg), M (München), S-F (Stockholm; FRE = Fungi rhenani exsiccati), and STU (Stuttgart). Further mentioned herbaria from which material was not examined are ATHU (Athens), BBF (Bagnères-de-Bigorre), BR (Meise, Brussel), CNF (Zagreb), K (Kew, London), LU (Luzern), MCVE (Venezia), O (Oslo), and PRM (Praha). Abbreviations of private herbaria are: A.F. = André Fraiture (Meise), B.P. = Branislav Perić (Podgorica), D.O. = Peter Dobbitsch (Bad Dürrheim), F.F. = Francis Fouchier (Marseille), G.C. = Gilles Corriol (Bagnères-de-Bigorre), G.G. = Guy Garcia (Bédarieux), H.B. = Hans-Otto Baral, H.H. = Hans Haas (†, Stuttgart, in STU), H.J. = Hermann Jahn (†, Detmold), J.C.S. = Jens Christian Schou (Denmark), L.S. = Lisa Samsø (Denmark), M.A.R. = Miguel-Angel Ribes (Madrid), M.B. = Martin Bemmann, M.T. = Marie-Thérèse Tholl (Doncols), N.V. = Nicolas Van Vooren (Lyon), R.A. = Reinhard Agerer (München), R.T. = Rudolf Thate (†, Neustadt/Weinstraße, in KR), S.Å.H. = Sven-Åke Hanson (Helsingborg), T.H.D. = Tove H. Dahl (Arendal; in O), T.R. = Torsten Richter (Rehna), U.G. = Ueli Graf (Baldegg, Luzern), W.Z. = Wen-ying Zhuang (Beijing), Y.M. = Yannick Mourgues (St. Germain de Teil).

Taxonomy

Hymenoscyphus serotinus (Pers. : Fr.) W. Phillips, *Man. Brit. Discom.*: 125 (1887), as *Hymenoscypha serotina*) — Fig. 1–5.

≡ *Peziza serotina* Pers., *Syn. meth. fung.*, 2: 661 (1801); Pers. : Fr., *Syst. mycol.*, 2 (1): 119 (1822).

≡ *Helotium serotinum* (Pers. : Fr.) Fr., *Summa veg. Scand., Sectio post.*: 355 (1849).

≡ *Lanzia serotina* (Pers. : Fr.) Korf & W.Y. Zhuang, *Mycotaxon*, 22 (2): 506 (1985).

?= *Helvella aurea* Bolton, *Hist. Fung. Halifax*, III: no. 118, pl. 98, fig. 2 (1789).

≡ *Peziza aurea* (Bolton) Sowerby, *Col. fig. Engl. Fung. Mushr.*, 2: 64, pl. 150 (1799), 3: 132, pl. 320 (1803), *nom. illegit.* [non *Peziza aurea* (Pers.) Fr., *Syst. mycol.*, 2(1): 156 (1822), sanctioned name; ≡ *Eustilbum aureum* (Pers.) S.E. Carpenter & Seifert, anamorph of *Bisporella resinicola* (Baranyay & Funk) S.E. Carpenter & Seifert], non *s.* Sowerby [= *Calycina citrina* (Hedw.) Gray (fide Saccardo 1889: 224, as *Helotium citrinum*)]

≡ *Calycina aurea* (Bolton) Kuntze, *Rev. gen. plant.*, 3: 448 (1898).

?= *Peziza ochracea* Cumino, *Mém. Acad. imp. Sci. Turin*, 13: 233, tab. 3, fig. 2 (1805), *nom. illegit.* [non *P. ochracea* Hoffm. 1796, *nec* (Schaeff.) Pers. 1800, *nec* Schumach. 1803, *nec* Grev. 1823, *nec* Schwein. 1832, *nec* (Fr.) P. Karst. 1869, *nec* Boud. 1875].

Etymology: The specific epithet *serotinus* refers to the late seasonal occurrence, *ochracea* refers to the brownish-yellow disc, and one of the German vernacular names ("Kommasporiger Becherling") describes the characteristic spore shape.

Epitype (designated here): Baden-Württemberg, Heidelberg, Königstuhl, branch of *Fagus sylvatica*, 24.XI.2012, Elvira Zur (KR-M-0036187, ex M.B. 010/2012, Fig. 1 e, h–m, Fig. 2 g–m, p).

Description: Apothecia fresh (0.5–)1–4(–7) mm diam., receptacle 0.3–0.4 mm thick, disc pale to deep (vividly) golden- to lemon- or sulphur-yellow but also not rarely white to cream, turning reddish-brownish with age, stipe short to very long (0.2–)0.5–4(–8) × 0.25–0.6(–0.9) mm, narrow, whitish, overall pubescent. **Asci** *120–145 × (8.5–)9.3–10 µm {2}, †110–135 × (6–)6.5–8(–9) µm {4}, IKI medium strongly blue (bb), *Hymenoscyphus*-type {3}, arising from croziers {12}. **Ascospores** *in situ* *(20–)21–28(–30) × 3.5–4(–4.3) µm {7}, †(18)21–28(–31) × (3–)3.2–3.6(–3.8) µm {10}, actual length */†~(22)24–30(–33) µm, strongly heteropolar, narrowly clavate-scutuloid, apex rounded to obtuse, with a more or less distinct hook on one side, from upper or middle part gradually strongly tapered

Key to the lignicolous European species of *Hymenoscyphus* being confused in the past with *H. serotinus* (taxa with scutuloid spores, whitish to yellow discs, and a tendency to long stipes)◊

1. Spores *(11–)13–22(–25.5) µm long, straight or ± inequilateral, gradually tapered from middle or lower part to the base; apothecia growing on twigs and branches, logs, and stumps 2
1. Spores *20–30(–40) µm long, inequilateral to slightly or strongly curved (especially in living state), gradually tapered from upper or middle part to the base, strongly heteropolar; apothecia growing on twigs and branches 5

2. Spores ± strongly heteropolar (distinctly scutuloid), *(16–)18–22(–25.5) × (3.5–)4–5(–5.5) µm, without setulae, lipid content rather low to high (2–5); asci arising from simple septa; on various angio- and gymnosperms ..... ***H. virgultorum***
2. Spores ± slightly heteropolar (indistinctly scutuloid); asci usually arising from croziers 3

3. Spores *(11–)13–16(–18) × 4–5 µm, without setulae, lipid content rather low (2–3); asci arising from croziers; on *Salix* ..... ***H. conscriptus***
3. Spores *(13–)15–21(–25) × (4–)5–6.5(–7) µm, lipid content high (4–5) 4

4. Spores without setulae; asci arising from croziers; on *Alnus glutinosa*, *A. incana*, *Fagus*, *Rosaceae*, etc. ..... ***H. calyculus s.l.*** (incl. *H. subferrugineus*)
4. Spores with 1–3 setulae at each end; asci arising from croziers, rarely from simple septa; on *Alnus viridis* and *A. incana* ..... ***H. trichosporus***

5. Spores *(28–)33–37(–40) × (4.5–)6–7.5(–8) µm, inequilateral to often slightly, rarely medium curved, with (1–)2–3 setulae at each end; asci *165–200 × 14–15 µm (†115–160 × 9.5–15 µm), arising from simple septa; on *Carpinus betulus* ..... ***H. lepismoides***
5. Spores *(20–)21–28(–30) × 3.5–4(–4.3) µm, slightly to strongly curved (arcuate), without setulae; asci *120–145 × 8.5–10 µm (†110–135 × 6–9 µm), arising from croziers; on *Fagus sylvatica* ..... ***H. serotinus***

◊ The data in this key are derived from personal observations.

Fig.1 – *Hymenoscyphus serotinus* (on twigs and branches of *Fagus sylvatica*). a–d. fresh apothecia; e. asci and paraphyses; f–h, k–l. mature ascospores (arrow: detached sheath); j. overmature ascospore with septum and anastomosis; i. ascus apices with euamyloid apical ring (*Hymenoscyphus*-type); m. croziers at ascus base. – Living state: e, g–h, l; dead state: f (in H_2O), i (in IKI), j–k (in KOH), m (in KOH+CR). – a: 11.XI.2012 (Asturias, phot. E. Rubio); b: 15.X.2012 (Rehna, phot. T. Richter); c: 29.X.2009 (Kaiserslautern, phot. P. Behrens); d, f: 31.X.2010 (Wienerwald, phot. M. Mann), e, h–m: M.B. 010/2012 (Heidelberg, epitype, M. Bemmann); g: X.2006 (Lozère, phot. M. Hairaud).

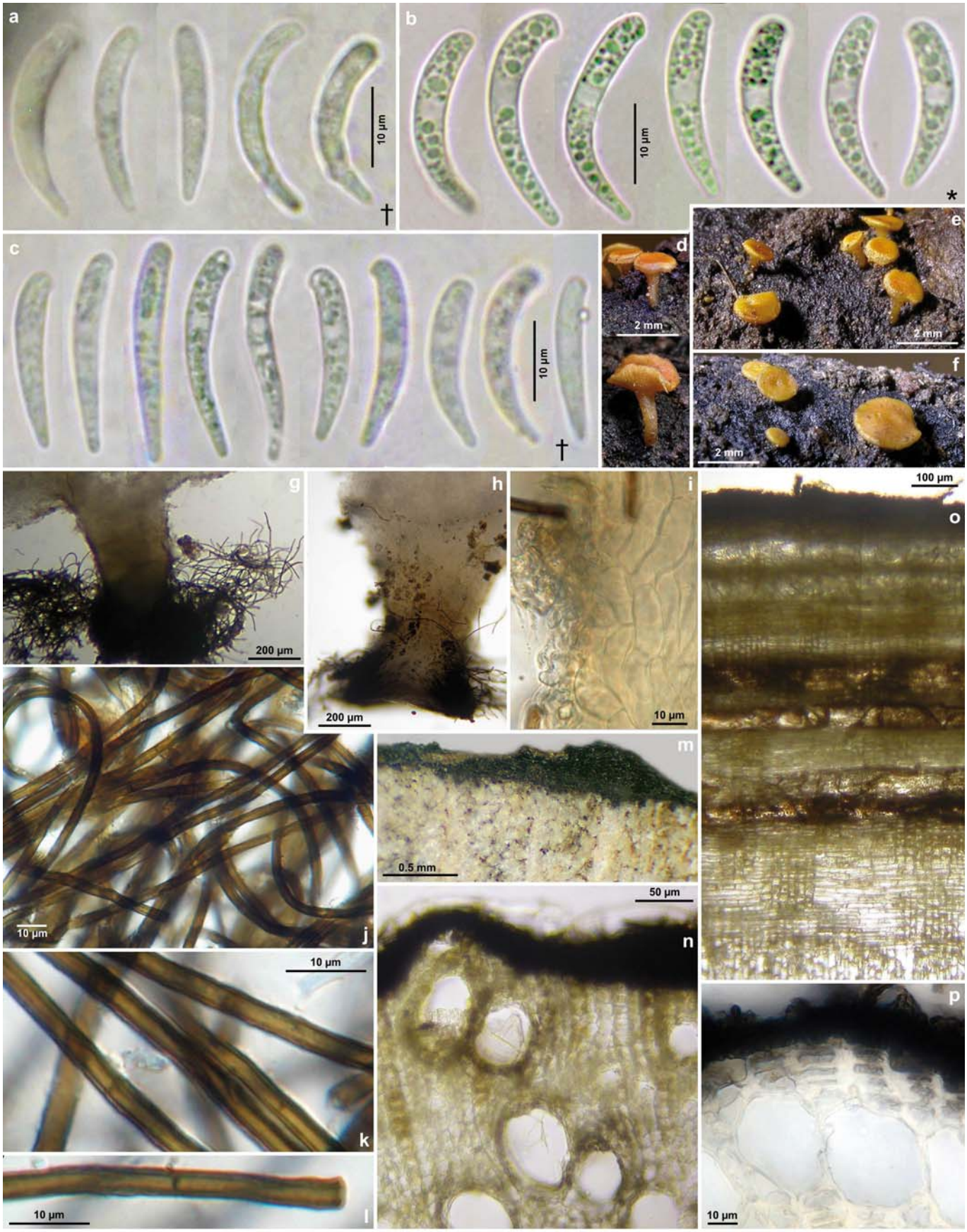

Fig. 2 – *Hymenoscyphus serotinus* (on twigs and branches of *Fagus sylvatica*). a–c. ascospores; d–f. apothecia (rehydrated), g–h: stipe of apothecia (g: in section, h: in external view, with ochre-brown exudate and blackish-brown hyphae); i: ectal excipulum of stipe in median section; j–l: blackish-brown hyphae; m: cross section of twig, with blackened surface; n, p: dto. (n: vascular bundles with olive-brown border); o: longitudinal section of twig (surface and vascular bundles black-brown). – Living state: b; dead state: a, c (in KOH). – a. S-F227299 (Rheingau, FRE 1157); b. 11.XI.2012 (Asturias); c–f. S-F227298 (Spessart); g–m, p: M.B. 010/2012 (Heidelberg, epitype); n–o: H.B. 2995 (Tübingen). – Phot. a, c–f, n–o: H.O. Baral; b: E. Rubio; g–m, p: M. Bemmann.

towards base, slightly to strongly curved (arcuate), setulae absent but with a delicate sheath detaching from the spore after ejection {2}; containing many small and a few medium-sized LBs {9}, lipid content 3.5–4.5; overmature spores 1-septate. **Paraphyses** cylindrical, *2.5–3.5 µm wide {2}, †2–2.5 µm, containing numerous small, medium refractive guttules (VBs) {4} that fill the upper part of the paraphyses at a length of 30–50 µm. **Medullary excipulum** hyaline, of *textura intricata*, hyphae †1.5–3 µm wide, medium sharply delimited from ectal excipulum by a parallel, 40–50 µm thick layer of *textura porrecta*. **Ectal excipulum** hyaline, from base of receptacle to margin of *textura prismatica*(-*porrecta*), 60–70 µm thick at lower flanks, cells †(11–)15–30(–40) × (4–) 6–8(–9) µm, oriented at a 0–30° angle to the surface (at 60–80° near stipe), 30–40 µm thick near margin, oriented at a 10–40° angle; stipe bearing ~25–50 µm long, slightly flexuous, hyaline hairs; crystals absent in complete tissue. **Anamorph** unknown.

Habitat: in shady, planar to montane beech forests on slightly acidic or mostly alkaline, often calcareous soil that is moist or rarely waterlogged (at banks of streams), on corticated or decorticated, (2–)5–12(–20) mm thick twigs and branches (exceptionally logs?) of *Fagus sylvatica* {108/5}, *F. sylvatica* f. *purpurea* {1}, *F. sylvatica* subsp. *moesiaca* {1/1}, indet. tree {4}, lying on or sticking in moist ground, partly covered by litter, on medium rotten wood {34}, when corticated then seemingly erumpent through the bark. **Assoc.:** none observed. **Phenology:** (Sept.–)Oct.–Nov.(–Dec.)((–Jan.)). **Desiccation tolerance:** not tested, but apparently intolerant. **Altitude:** 45–800 m in Northern Europe, 220–1250 m in Central Europe, 550–1600 m in Southern Europe. **Geology:** acidic: paragneiss {2}, Devonian slate {1}, Buntsandstein (Lower Triassic) {2}; alkaline: Knollenmergel (Upper Triassic) {2}, basalt {3}, loess (Pleistocene) {2}, Lias (Jura) {6}, Malm (Jura) {2}. **Vegetation:** in temperate beech forests, mainly basophilic: *Hordelymo-Fagetum*, *Galio-Carpinetum primuletosum*, *Galio odorati-Fagetum*, *Fraxino-Aceretum pseudoplatani*, *Abieti-Fagetum*, but also more acidophilic: *Carici-Fagetum*, *Carici remotae-Fraxinetum*, *Luzulo-Fagetum*; also in oro-Mediterranean, predominantly basophilic beech forests, mixed with *Abies*, *Castanea*, *Ostrya*, *Prunus*, *Pyrus*, *Quercus*, *Ulmus*, etc.

General remarks

Hymenoscyphus serotinus was among the first collections made by the senior author when he started studying ascomycetes in 1973 (examples of drawings are given on Fig. 3l–m). Although the species appeared to be well defined and easily recognizable by its characteristic ascospores, a good name for it could not be found in the available literature at that time, since it was not included, e.g., in Dennis' *British Ascomycetes* (1978). The correct species epithet became clear when the first author got access to Dennis' *Revision of the British Helotiaceae* (1956) and Rehm's work (1883–96) on the Central European discomycetes.

Peziza serotina was originally described from an unlocalized, certainly European collection, with rather large, vividly yellow apothecia with a thin and flat disk and a short stalk, fruiting on dry twigs at steep, semi-shaded paths in late autumn (Persoon, 1801). The taxon was later interpreted by various European authors in the sense of a fungus with the following features: (1) rather long and narrow ascospores (16–30 × 3–4 µm) being basally gradually tapered and apically beaked (scutuloid), moreover slightly to strongly curved (falcate, comma-shaped = virguliform), (2) more or less yellow cups with whitish stipes of very variable length, (3) growing exclusively on blackened wood of twigs and branches of *Fagus sylvatica*, (4) occurring in temperate to mountainous European regions between September and December (Fuckel, 1870: 313; Saccardo, 1883, pl. 1345; Rehm, 1893: 781; Lagarde, 1906: 231; Killermann, 1935: 275; Velenovský, 1934: 189, pl. 20 fig. 16; Schieferdecker, 1954: 90, pl. 13 fig. s; Dennis, 1956: 81; Jahn, 1979: 46, 1990: 48; Sacconi, 1983: 205; Svrček, 1985: 177, pl. 20 fig. 6; Ellis & Ellis, 1985: 128; Baral & Krieglsteiner, 1985: 136; Plomb, *in* Keller *et al.*, 1985: 147; Pop & Fouchier, 1999; Rubio *et al.*, 2010: 228; Carbone, 2010; Delivorias *et al.*, 2010).

Spore size and curvature

Reports on the length of strongly curved spores are problematic if the method of measuring, i.e., along the curvature (actual length) or just from the tip to the base (*in situ*) is not stated by the authors. However, due to variation in the actual spore length the difference in the result between both methods is not striking.

Generally, our spore measurements refer to the *in situ* values, if not otherwise stated, while in the above description we have indicated both methods separately. These values are in good concordance with the data of, e.g., Schieferdecker (22–28 × 3.5–4 µm), Dennis (18–28 × 3–4 µm), Jahn (21–30 × 3–4 µm), Svrček (20–29 × 3–4 µm), Breitenbach & Kränzlin (1981: 182, as *H. calyculus*, 16–24 × 3–4 µm), Sacconi (26–28 × 3 µm), Pop & Fouchier (23–27 × 3–3.5 µm), and Delivorias *et al.* [(18–)21–26(–29) × 2.9–3.5(–4) µm].

For his collection on *Fagus* twigs (*Fungi Rhen. Exs.* 1157), Fuckel (1870) reported the spores as curved, 20–24 × 4 µm. The present re-examination of a duplicate in S yielded slightly to strongly curved spores of 22–28 × 3.2–3.7 µm (Fig. 2a). Handwritten notes by Rehm on the label of the Spessart specimen (Fig. 10a) concern "mostly curved" spores up to 27 × 3.5 µm, with 3–4 globose guttules. The present re-examination (Fig. 2c–f) revealed abundant free spores of 21–27 × 3.2–3.8 µm which are slightly (rarely strongly) curved.

The spore size of 25–33(–36) × 4–4.5 µm given by Plomb (*loc. cit.*) appears to refer to the actual spore length: according to the scale bar on the enclosed drawing (Fig. 3k) a spore size of 25–29 × 3.8–4.4 µm *in situ* can be evaluated which, however, still means an extraordinary spore width. Similarly wide spores were observed by M. Hairaud (pers. comm.) in a non-preserved specimen from the department of Lozère (Fig. 1g): *21.5–28.5 × 3.7–4.2(–4.6) µm as evaluated from the scale bar. In both finds the lipid content is about 2–3, which is distinctly lower than in the typical collections.

The absence of sickle-shaped spores in some of the reports is partly due to the dead state of the spores, according to our observations. When applying KOH or other lethal agents to a water mount of living spores of *H. serotinus*, the spores show a distinct tendency to be less curved [compare Fig. 1h, l (*) with 1j–k (†), also Fig. 2b (*) with 2a, c (†)] though strongly curved spores are also sometimes seen in old herbarium material. As a consequence, dead spores tend to be slightly longer than living spores when measured in situ, but also narrower. Differences in spores size and curvature in the literature are partly due to this effect, which is seen also when rehydrating old herbarium material in water, i.e., it does not primarily depend on the mounting medium.

Particularly Dennis' (1956: 81, fig. 73) sketches of a Slovakian (fig. 73B) and a British (fig. 73C) specimen (both on twigs of *Fagus*) show straight or only slightly, rarely basally medium curved spores (Fig. 3g). The Slovakian sample concerns an exsiccatum of Bäumler (*in* Zahlbruckner, 1912), and possibly this is the same specimen that Bäumler (1897) reported from the Gemsenberg near Pressburg (= Pozsony), Hungary, which is today Bratislava in Slovakia. Despite the lack of strongly curved spores, both samples undoubtedly concern genuine *H. serotinus*.

Ascus iodine reaction

The apical ring in *H. serotinus* reacts blue (bb) in a medium of Lugol's solution as defined in "Methods" above. Delivorias *et al.* (2010) reported and figured for their finds a hemiamyloid reaction of the apical ring: "in Lugol's solution staining reddish brown prior to KOH, blue after KOH". On a colour plate sent to us by P. Delivorias, the unpretreated ring looks indeed dirty red. This, on the first glance, surprising result is provoked by an unusually strong concentration (5%) of iodine in the Lugol's solution used in their laboratory (P. Delivorias, pers. comm.), while the presented microphotos, though showing only dead elements, undoubtedly concern genuine *H. serotinus*.

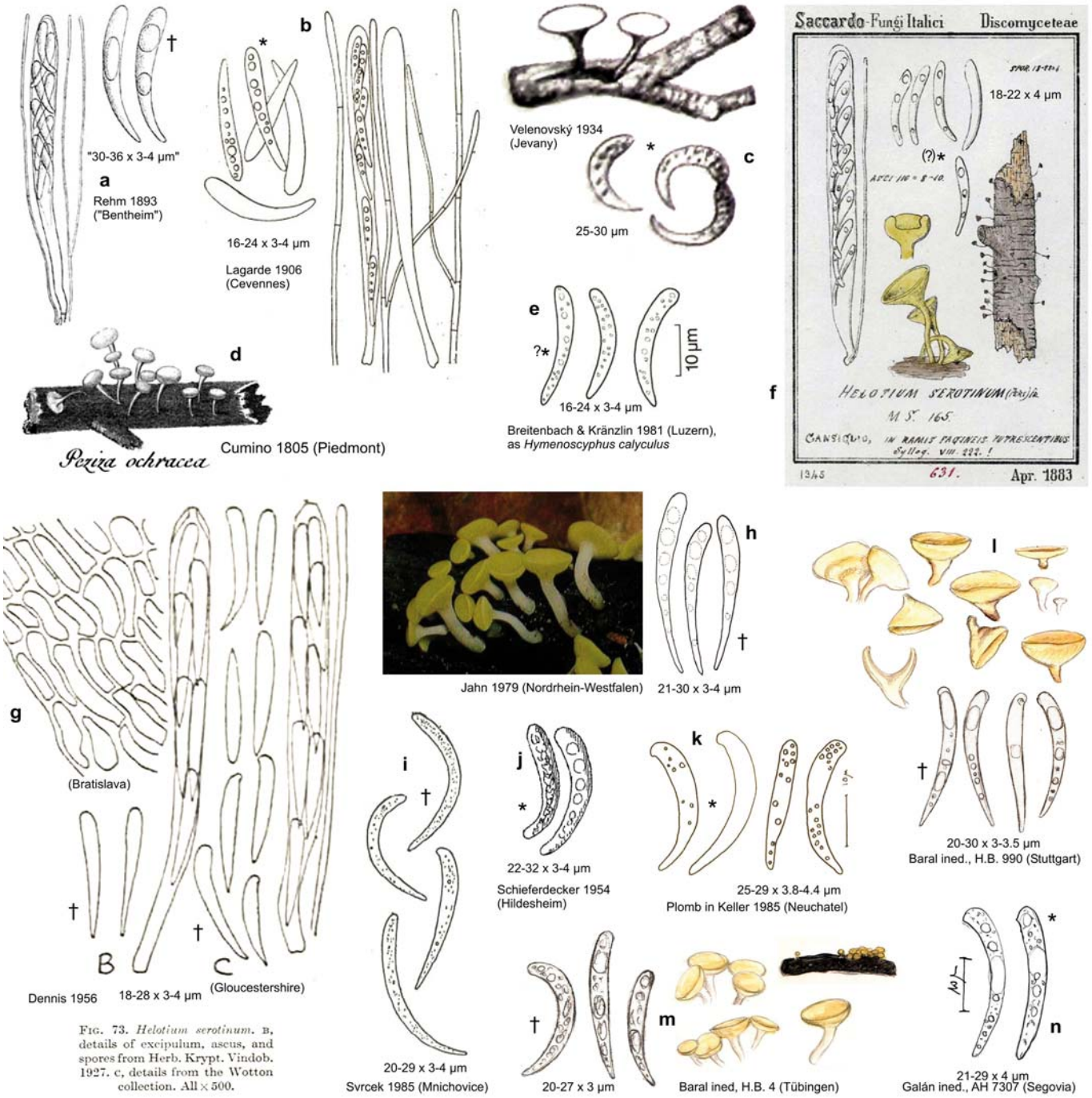

Fig. 3 – Illustations of correctly identified records of *Hymenoscyphus serotinus* in the literature and from unpublished studies, with the exception of Cumino's uncertain report that lacks microscopic data, and Rehm's drawing (a) of two spores which seems to be a copy of the Bentheim collection of *H. lepismoides* (Fig. 10b), though influenced by the narrower and stronger curved spores of genuine *H. serotinus*. – The signs * and † were added by us in order to indicate the living vs. dead state.

Ecology

H. serotinus appears to be restricted to twigs and branches of *Fagus sylvatica*, with a branch diameter not exceeding 2 cm. The strict occurrence on *Fagus* was emphasized by Fuckel (1870), Lagarde (1906), Velenovský (1934), Schieferdecker (1954), Jahn (1979), Svrček (1985, 1986: 13), Ellis & Ellis (1985), Baral & Krieglsteiner (1985), Deny (2002), and Krieglsteiner (1999, 2004). The present study confirms this restriction. The twigs are partly covered by a layer of fallen leaves or even buried in the soil. The fungus was mainly found in shady forests that prevent desiccation, and it occurs also on wet or swampy soil, but also in more thermophilous woods.

The wood surface is always blackened by a mycelium of dark brown hyphae that may form a felted mat of varying thickness over the surface (Fig. 2g–h, j–p), but may also occur in the peripheral vascular bundles (Fig. 2o). The consistent association with this blackish hyphal network was also stressed by Jahn (1979: 31; 1990: 34), Baral & Krieglsteiner (*loc. cit.*) and Runge (1981). Whether the hyphae belong to the fungus (what we believe) or to an unrelated hyphomcete remains to be clarified. In any case, conidia have not been observed on these hyphae.

The present map (Fig. 4) comprises all those records which we have either seen ourselves, or which appear to us trustable according to published or unpublished illustrations or notes. The species is undoubtedly common in most temperate to montane areas where beech occurs, but we did not try a comprehensive inventory of the known records, including all the deposited herbarium materials.

According to the present data, *H. serotinus* was exclusively found in autumn, from September until December, exceptionally in January. However, Krieglsteiner (*in* Baral & Krieglsteiner, 1985) mentioned an unexpected record made in 23 June 1983. The species is found in various associations of beech forests on alkaline but also acidic soils. The present data comprise altitudes between 65 and 1600 m. In southern countries the beech forests are found at higher altitude (550–1600 m) compared to Central (140–1250 m) and Northern Europe (65–160 m).

In the Northern European countries, *H. serotinus* appears to be restricted to their southernmost parts and to prefer more subcontinental than atlantic climate regions. For Norway only a single record in the southeast came to our notice. In Skåne (Southern Sweden), the species is frequent, according to S. Åke-Hanson (pers. comm.). Also in the east and northeast of Denmark, the species is quite common on *Fagus* twigs (T. Laessøe, pers. comm., http://www.svampe.dk). In Great Britain, *H. serotinus* is seemingly rare: Dennis (1956) saw only one record, Clark's (1982) single report from Worcestershire requires re-examination (host unidentified, microdata lacking) and P. Thompson (pers. comm.) never found true *H. serotinus* in southern parts of England, while his single record in the Fungal Database of Britain and Ireland, though recorded on *Fagus*, appears to concern *H. virgultorum* (Vahl) W. Phillips.

For the Netherlands a few records on *Fagus* are seen on the online distribution map (http://www.verspreidingsatlas.nl/622220), but published reports with a characterization of the fungus are unknown to us, and S. Helleman (pers. comm.) never found the species in his observed area in Noord-Brabant. Also in Belgium and Luxembourg only a few records are known (A. Fraiture, B. Declercq, G. Marson, M.T. Tholl, pers. comm.). Within France, the accessible records are not frequent and concern central, eastern and southern regions.

A very different situation is noted within Germany. Although the planar regions of Northern Germany are largely devoid of records, especially towards the western, more atlantic regions, the fungus is said to be common in Schleswig-Holstein (Lüderitz, 2001), and to the south the species becomes rather frequent. A distribution map of *H. serotinus* for West Germany with a rather dense occurrence in several regions is presented in Baral & Krieglsteiner (1985: 140) and Krieglsteiner (1993, pl. 783). Krieglsteiner (1999: 243; 2004: 606) reported one record of *H. serotinus* in the Main-Spessart area, but 29 in the Rhön area. He considered the species as showing affinities to mountainous beech forests and mentioned different plant associations depending on the soil characteristics (acidity, nutritional richness). The above summary of the vegetation is mainly taken from his data. The few records from Switzerland and Austria are probably not representative of the actual distribution. Within Eastern Europe only a few collections came to our notice. For instance, records of *H. serotinus* from Southern Poland are unknown to P. Perz (pers. comm.), and also from Czechia data are sparse. However, the checklist of Polish larger ascomycetes (Chmiel, 2006) lists several references, though the substrate includes besides twigs of *Fagus* also those of *Betula*.

In the whole area of Slovenia, Croatia and Bosnia-Herzegovina settled with *Fagus sylvatica* as a forest component, however, the species is very frequent, and a detailed paper on its occurrence is in progress (N. Matočec & I. Kušan, pers. comm.). Three of these records were included in the present distribution map. Also within Spain *H. serotinus* is found to be relatively common in Asturias (Cantabrian Mountains), according to E. Rubio (pers. comm.), but it occurs also in central parts of Spain where *Fagus*-dominated natural forests exist in small isolated areas (known records are those from the Sierra de Guadarrama near Segovia). Similarly, *H. serotinus* was recorded in mountainous beach forests in Northern Italy (Sacconi, 1983; M. Carbone, B. Fellmann, F. Fouchier, pers. comm.), in Southwestern Bulgaria (mountains of Vitosha, Rila, Sredna Gora, Rhodopes; Dimitrova & Baral, 2005), and also in Thessaly, Greece (Delivorias *et al.*, 2010).

Typification and possible synonyms

According to Dennis (1956), "no material of *Peziza serotina* now remains in the Persoon herbarium". Also Dumont (1981: 72) was unable to locate a type, and Lizoň (1992: 48) stated that type material is unlikely to have survived. Consequently, many workers referred to Fuckel's exsiccatum FRE 1157 as reference specimen.

M. Filippa (pers. comm.) drew our attention to the fact that *Peziza serotina* is a sanctioned name. According to art. 9.2 of the Melbourne Code, "For sanctioned names, a lectotype may be selected from among elements associated with either or both the protologue and the sanctioning treatment [...]". Fries (1822: 119) cited in his sanctioning work a single illustration, Bolton's (1789) plate 98 fig. 2 of *Helvella aurea* Bolton, which is also shown in the German translation of Bolton & Willdenow (1799: 12, pl. 98 fig. 2). In Bolton *et al.* (1820: 148) *H. aurea* was synonymized with *Peziza serotina* by C.G. and T.F.L. Nees von Esenbeck.

Bolton's drawing shows merely a piece of substrate (probably a twig) with apothecia up to ~6 mm diam., with a stalk ~4–6 times longer than wide, and the description includes a golden hymenial colour. The substrate is mentioned as "sticks, stalks of plants, etc. in moist and watery places in woods". A few of Bolton's basidiomycetous specimens were rediscovered in the Kew Herbarium (Roberts & Legon, 2003), therefore, it cannot be excluded that a specimen of his *Helvella aurea* has survived.

Bolton's illustration might well concern *Hymenoscyphus serotinus*. However, the substrate is unknown and the seasonal occurrance not stated. Until authentic material of *Helvella aurea* might be detected at Kew, Bolton's illustration is here designated as **lectotype** of *H. serotinus*. In order to settle the taxonomic confusion in regard to the uncertainty about this lectotype and to the different interpretations of the name *H. serotinus*, we here designate the specimen from Heidelberg (KR-M-0036187, ex M.B. 010/2012) as **epitype** of *Hymenoscyphus serotinus*.

Peziza ochracea Cumino (1805) was listed in Traverso (1910: 842) as a possible synonym of *Helotium serotinum*. Similar as with Persoon's (1801) taxon, the original description of *P. ochracea* is devoid of any microscopic data (see Fig. 3d). The apothecia are described with a yellow disc and a white underside and stipe, growing in autumn on rotten twigs of *Fagus*. Cumino's remark "*supra putridos Fagi truncos*" suggests trunks, logs or perhaps stumps. However, the drawing shows a twig with a blackish surface which suggests identity with *Hymenoscyphus serotinus*, although it could as well belong to the plurivorous *H. subferrugineus* which may occur on *Fagus*. *P. ochracea* is also listed in Colla (1837: 177), who iterated Cumino's original description. The specimen concerns a find in the Valle Pesio (Cuneo, Piedmont, Italy) where he first lived as a monk in Certosa di Pesio and later as the director of the botanical garden of Cuneo (Soma, 2003). We have taken up this record in our list of trustworthy specimens, although it should be recollected in that region of the Alps to ascertain its occurrence. Cumino's drawing might provide the first illustration of the species.

Specimens included

(all on *Fagus sylvatica* = *F.s.*, except for a few cases of uncertain or unidentified hosts)

NORWAY: Eastern Norway, Vestfold, 15 km N of Larvik, 4.5 km E of Kvelde, S of Brånakollane, 160 m, on wood of twigs of *F.s.*, 16.X.2011, T.H. Dahl & K. Homble (T.H.D. 347/2011, O, d.v.).

SWEDEN: Skåne, Ekeby, 16 km ESE of Helsingborg, 1.8 km NW of Ekeby, 80 m, twig of *F.s.*, 3.XI.2001, S.Å. Hanson (S.Å.H. 01-332, n.v.). – NÄSUM, 9 km SSW of Olofström, 3 km N of Näsum, 65 m, twig of *F.s.*, 7.XII.2001, S.Å. Hanson (ø, n.v.). – Baldringe, 7.5 km WNW of Tomelilla, 3.5 km N of Baldringe, 83 m, twig of *F.s.*, 10.X.2007, I. Månsson, *det.* S.Å. Hanson (ø, n.v.).

DENMARK: Jylland, 6.5 km SW of Hobro, 2.5 km SSE of Brøndum, Trinderup Krat, 45 m, twig of *F.s.*, on wood, 27.X.2011, J.C. Schou (J.C.S. 2011-425467, d.v.). – 8 km SE of Silkeborg, 2.5 km NE of Rodelund, Sønderskov, 85 m, twig of indet. woody plant, 4.XI.2012, L. Samsø (L.S. 2012-487401, d.v.).

GREAT BRITAIN: Gloucestershire, Wotton-under-Edge, ~150 m, twig of *F.s.*, 10.XI.1948, collector not cited (K, Dennis, 1956: fig. 73C).

Fig. 4 – Distribution of *Hymenoscyphus serotinus* based on list of included specimens.

BELGIUM: Wallonia, Luxembourg, 10 km WNW of Arlon, 2 km NNE of Hachy, Kripsenbachnusch, 403 m, branch of *F.s.*, on wood, 11.XI.1991, A. Fraiture (A.F. 1542, n.v.). – 22 km W of Arlon, 1.7 km SSE of Tintigny, bois de la Prise, 365 m, twig of *F.s.*, 23.X.1992, A. Fraiture (A.F. 1753, n.v.).

LUXEMBOURG: L'Oesling, Ardennes, 7 km W of Wiltz, Doncols, rue de village, 465 m, on wood of twig of *F.s.* f. *purpurea*, 8.XI.1993, M.T. Tholl (M.T. 922, n.v.); – Gutland, 5 km SSW of Luxembourg, N of Kockelscheier, Weier, 300 m, on wood of branch of *F.s.*, 18.X.1989, G. Marson & J. Häffner (ø).

GERMANY: Mecklenburg, 8 km SW of Rehna, 2.7 km NE of Dechow, Staatsforst Rehna, 60 m, branches of *F.s.*, 15.X.2012, T. Richter (T.R.). – Niedersachsen, Oberharz, 10 km ESE of Goslar, 2 km S of Bad Harzburg, Schmalenbergsklippe, ~370 m, *F.s.*, 30.X.1984, K. Wöldecke (Wöldecke, 1998, n.v.). – Rhön, near Fulda, L. Krieglsteiner (Krieglsteiner, 2004, n.v.). – Nordrhein-Westfalen, ~6 km ENE of Lemgo, ~1 km W of Dörentrup, Lemgoer Wald, ~200 m, branch of ?*F.s.*, 9.X.1972, H. Jahn, M.A. Jahn & G. Dreier (H.J., n.v.). – Teutoburger Wald, ~5 km S of Detmold, near Berlebeck, ~350 m, branches of ?*F.s.*, X.1974, H. Jahn & M.A. Jahn (H.J., n.v.). – Paderborner Land, 17 km SSW of Paderborn, 7.5 km ENE of Büren, SE of Altenböddeken, 340 m, branch of *F.s.*, 15.X.1994, K. Siepe (ø, n.v.). – Hochsauerlandkreis, 5 km SW of Marsberg, 1.5 km NW of Giershagen, Giershagener Wald, Klus Kapelle, 300 m, branch of *F.s.*, 6.X.2007, K. Siepe (ø, n.v.). – 11 km SW of Brilon, 3.5 km SW of Olsberg, Haardtkopf, 380 m, branch of *F.s.*, 3.X.2003, F. Kasparek & K. Siepe (ø, n.v.). – Thüringen, near Bad Salzungen, L. Krieglsteiner (Krieglsteiner, 2004, n.v.). – 20 km NW of Sonneberg, 2 km E of Goldisthal, Wurzelberg, 800 m, twigs of *F.s.*, 31.X.07, P. Püwert & I. Wagner (ø, n.v.). – 0.8 km WSW of Sonneberg, Stadion, 375 m, on twig of (?)*F.s.* (as *Corylus avellana*), 7.XII.2008, I. Wagner (ø, d.v.). – Hessen, Rheingau, 6.3 km NE of Gersfeld, 2.2 km SSW of Ehrenberg-Wüstensachsen, 700 m, twigs of *F.s.*, 1.XI.2004, L. Krieglsteiner (KR-M-0022268, n.v.). – ~10 km NE of Bingen, ~N of Oestrich, ?400 m, on wood of twig of *F.s.*, undated (< 1870), L. Fuckel (FRE 1157, Barbey-Boissier 1219, S-F227299, H.B. 9751ø). – Rheinland-Pfalz, Eifel, ~20 km W of Mayen, ~5 km S of Adenau, Nürburgring, ~600 m, twig of *F.s.*, 20.X.1976, R. Thate (R.T.). – ~15 km NW of Bingen, ~4 km NE of Rheinböllen, ~450 m, on wood of branch of *F.s.*, 29.IX.2007, M. Carbone (MCVE 25664, n.v.). – Pfälzer Wald, 8 km SE of Kaiserslautern, 3 km W of Waldleiningen, 355 m, twigs of *F.s.*, on wood, 29.X.2009, P. Behrens (ø, d.v.). – 15 km WNW of Neustadt/Weinstr., 4.5 km N of Esthal, SW of Schwarzsohl, 470 m, indet. tree, 30.X.1966, R. Thate (ex R.T. 473, KR-M-0036367). – 3.7 km N of Neustadt/Weinstr., 1.5 km NW of Gimmeldingen, Silbertal, 240 m, twig of *F.s.*, 19.XI.1967, R. Thate (R.T.). – ~11 km W of Landau, Annweiler, 220 m, twig of *F.s.*, 20.XI.1974, R. Thate (ex R.T., KR-M-0036369). – Baden-Württemberg, Heidelberg, 5.5 km ESE of Heidelberg, Königstuhl, Oberer Sandweg, 435 m, on wood of branch of *F.s.*, 24.XI.2012, E. Zur (KR-M-0036187, ex M.B. 010/2012, epitype). – 10 km ESE of Heidelberg, 1.5 km N of Wiesenbach, Herrenwald, 257 m, on wood of twig of *F.s.*, 1.XI.2010, D. Bandini (ø). – Stuttgart, 6 km NW of Stuttgart, 1.5 km SSW of Weilimdorf, Frauenholz, 365 m, twig of *F.s.*, 6.X.1976, H.O. Baral (ø). – 5.5 km NW of Stuttgart, 1.8 km S of Weilimdorf, Hasenbrünnele, 360 m, twig of *F.s.*, 10.X.1976, H.O. Baral (ø). – *ibid.*, Sperberklinge, 390 m, on wood of branch of twig of *F.s.*, 21.XI.1973, H.O. Baral (H.H. 10343, H.B. 3ø). – 6 km SW of Stuttgart, 1.5 km E of Büsnau, Pfaffenwald, 440 m, twig of *F.s.*, 21.X.1975, H.O. Baral (H.B. 7ø). – *ibid.*, 460 m, twig of *F.s.*, 28.X.1974, H.O. Baral (H.H. 10344, H.B. 990ø). – Schwäbisch-Fränkischer Wald, 1 km of Welzheim, Friedhof, 515 m, branch of indet. tree, 9.XI.1982, H. Maser (ø, d.v.). – Schönbuch, 4.8 km NW of Tübingen, 1.8 km NNE of Hagelloch, Arenbach E of Becklesgartenhütte, 400 m, *F.s.*, 30.XI.1976, H.O. Baral (ø). – 5.8 km N of Tübingen, 1.6 km NW of Bebenhausen, Kohlhau, 470 m, twig of *F.s.*, 10.X.1978, H.O. Baral (ø). – 6.7 km NNE of Tübingen, 2.7 km NE of Bebenhausen, Langer Rücken, N of Bärlochhütte, 480 m, twig of *F.s.*, 14.XI.1978, H.O. Baral (ø). – 5.5 km NNW of Tübingen, 2.3 km WNW of Bebenhausen, Tellerklinge, 400 m, *F.s.*, 2.XII.1976, R. Agerer (R.A. 6856). – 4 km N of Tübingen, WSW of Bebenhausen, Goldersbach, 360 m, twig of *F.s.*, 26.X.1976, H.O. Baral (ø). – 1.3 km ESE of Bebenhausen, Kirnberg, N of Olgahain, 455 m, *F.s.*, 31.X.1978, H.O. Baral (ø). – 6 km N of Tübingen, 2 km N of Bebenhausen, NE of Brühlweiher, 420 m, twig of *F.s.*, on wood, 31.X.1978, H.O. Baral (H.B. 2995). – 3 km NW of Pfrondorf, Mauterswiese, 420 m, *F.s.*, 31.X.1978, H.O. Baral (ø). – 8 km NE of Tübingen, 4 km N of Pfrondorf, Eisenbachhain, 485 m, twig of *F.s.*, 3.XI.1973, H. Haas (H.H. 10340, H.B. 2ø). – *ibid.*, 480 m, branch of *F.s.*, 20.X.1974, H.O. Baral (H.H. 10339, H.B. 4ø). – 1.5 km NNE of Pfrondorf, Brand, 460 m, *F.s.*, 16.XI.1986, H.O. Baral (ø). - E of Pfrondorf, Tiefenbach, 385 m, on wood of twig of *F.s.*, 15.X.2000, H.O. Baral (ø). – Schwäbische Alb, 12.5 km SSE of Reutlingen, 2 km WNW of Engstingen, Greuthau, 780 m, twig of *F.s.*, 17.XI.1976, P. Hausmann (ø). – ~8.7 km WSW of Münsingen, WSW of Gomadingen, Sternberg, 800 m, on wood of twigs of *F.s.*, 24.IX.1988, H.O. & O. Baral (ø). – 8 km ENE of Metzingen, E of Neuffen, Burg Neuffen, 700 m, *F.s.*, 17.XI.1974, collector unknown (H.H. 10342, H.B. 6ø). – 3 km SE of Nürtingen, Johannes-Sonn-Hütte, 320 m, twig of *F.s.*, 1.XI.1974, H.O. Baral (H.H. 10341, H.B. 5ø). – 8 km ENE of Heidenheim, 1.3 km E of Nattheim, Nattheimer Viereckschanze, 610 m, *F.s.*, 2.XI.1980, O. Baral (KR-M-0001714). – ~15 km E of Heidenheim, Dischingen, ~500 m, *F.s.*, 16.X.1983, L.G. Krieglsteiner (ø). – Schwarzwald, 9.5 km ENE of Freiburg, 2.5 km NW of Eschbach, Conventwald, ~800 m, twig of *F.s.*, 21.X.1974, D. & P. Laber (ø). – *ibid.*, 15.X.1995 (KR-M-0001950). – 4 km N of St. Märgen, Bannwald Zweribach, ~750 m, twig of *F.s.*, undated, P. Dobbitsch (D.O. 808). – Bodensee, 8 km W of Radolfzell, Kaltbrunn, 450 m, "log" of *F.s.*, 21.X.1960, R. Thate (R.T. 360, KR-M-0036368). – Bayern, Unterfranken, Rhön, near Bad Kissingen, L. Krieglsteiner (2004, n.v.). – Main-Spessart, 35 km NW of Würzburg, ?W of Lohr, forest near Rechtenbach, ?400 m, on wood of branch

of *F.s.*, X.1877, H. Rehm (S-F227298, H.B. 9750ø). – 26 km NW of Würzburg, 1.5 km WSW of Karlburg, Lange Lage, 280 m, twigs of *F.s.*, on wood, 22.X.1993, L. Krieglsteiner (ø, Krieglsteiner, 1999, n.v.). – Niederbayern, Bayerischer Wald, 20 km E of Regen, 7 km NNE of Spiegelau, Waldhäuser, Aufstieg zum Rachelsee, 1060 m, on wood of twig of *F.s.*, 31.X.1988, N. Luschka, det. E. Weber (REG 253, d.v.). – Schwaben, ~5 km SW of Günzburg, NE of Kissendorf, Bubesheimer Wald, 490 m, *F.s.*, 13.X.1979, M. Enderle (ø).

SWITZERLAND: Schaffhausen, 8.5 km N of Schaffhausen, 1.5 km N of Merishausen, Osterberg, 700 m, on wood of twigs & branches of *F.s.*, 11.XI.1989, H.O. Baral & P. Blank (ø). – 2.7 km NW of Schaffhausen, E of Griesbacherhof, Hohlenbaum, 550 m, *F.s.*, 15.XI.1985, P. Blank (ø). – 2.5 km NE of Schaffhausen, 1.8 km W of Gennersbrunn, Rheinhardt ("Solenberg"), 480 m, twig of *F.s.*, 21.XI.1986, H.O. Baral (ø). – 7 km NE of Schaffhausen, 1 km ENE of Thayngen, Flüheweg, 530 m, on ?*F.s.*, 20.XI.1987, H.O. Baral (ø). – Luzern, 22 km N of Luzern, 2.2 km ESE of Aesch, Bachtale, 630 m, twig of *F.s.*, 10.XI.2010, U. Graf (1011-10 U.G. 2, d.v.). – ~4 km NNE of Hochdorf, ~2 km NNW of Hohenrain, Ibenmoos, ~650 m, branch of *F.s.*, 16.X.1979, F. Kränzlin (LU 1610-79, Breitenbach & Kränzlin, 1981, as *H. calyculus*, d.v.). – St. Gallen, 16 km ENE of Rapperswil, 5 km W of Wattwil, Chrüzegg, 1250 m, on wood of twig of *F.s.*, 24.X.2010, T. Flammer (M.B. 02/2013). – Neuchâtel, ~6 km ENE of Couvert, Creux-du-Van, Val de Travers, ~900 m, on wood of branch of *F.s.*, 7.X.1982, G. Plomb (*in* Keller, 1985, d.v.).

AUSTRIA: Niederösterreich, Wienerwald, 20 km SSW of Wien, 2.5 km E of Gaaden, Steinwandlgraben, 580 m, twig of *F.s.*, 31.X.2010, M. Mann (ø, d.v.).

CZECHIA: Central Bohemia, 27 km SE of Praha, Mnichovice, ~370 m, twig of *F.s.*, XI.1926, J. Velenovský (PRM 148179, d.v.). 30 km ESE of Praha, Jevany, ~450 m, twigs of *F.s.*, 14.X.1922 & 16.XI.1923, J. Velenovský (PRM, Svrček, 1985, d.v.), – Plseň, 26 km SSE of Plseň, ~5 km S of Blovice, Chejlava, ~550 m, twig of *F.s.*, 25.X.1981, M. Svrček (Svrček, 1986, n.v.). – 32 km SE of Pilsen, Brdy mt., Chyninské buky, ~650 m, twig of *F.s.*, 24.X.1981, M. Svrček (Svrček, 1986, n.v.).

SLOVAKIA: Bratislava, ~4 km NNW of Bratislava, Cesta na Kamzík ("Gemsenberg"), ~400 m, on twigs of *F.s.*, date unknown (autumn), J.A. Bäumler (Kryptog. exs. Vindob., Cent. XX, n. 1927, as "Hungaria, prope Pozsony", Dennis, 1956: fig. 73B).

FRANCE: Centre, Loiret, 13 km NE of Orléans, 3.8 km WNW of Rebréchien, 140 m, *F.s.*, 10.XI.1985, A. Reynaud, *det.* A. Péricouche (ø, n.v.). – Lorraine, Vosges, 4.5 km ESE of Gérardmer, Saint-Jacques-de-la-Bresse, 1060 m, twig of *F.s.*, 17.X.1988, J. Deny (ø, n.v.); – 4.5 km SE of Gérardmer, Grouvelin, la Roche des Bioquets, 1025 m, twig of *F.s.*, 1.XI.1991, J. Deny (ø, n.v.); 13 km ENE of Gérardmer, le Tanet, 1225 m, twig of *F.s.*, 13.X.1993 and 4.X.1994, J. Deny (ø, n.v.). – Franche-Comté, Doubs, 23 km S of Besançon, 1.8 km SSE of Malans, vallon du Bief Tard, 510 m, twigs of *F.s.*, 29.X.2009, G. Moyne (ø, d.v.). – Rhône-Alpes, Haute-Savoie, 31 km E of Genève, 4 km SSE of Bellevaux, ESE of La Clusaz, 1055 m, twig of *F.s.*, on wood, 2.X.2010, N. Van Vooren (N.V. 2010.10.04, d.v.). – Ardèche, 8.5 km ESE of Pradelles, 3 km ENE of Lavillatte, 1250 m, on wood of twigs & branches of *F.s.*, 21.IX.1990, I. Collin (ø).– Provence-Alpes-Côte d'Azur, Vaucluse, mont Ventoux (northern part), 1400–1600 m, wood of *F.s.*, X.1901, collector not cited (Lagarde, 1902: 373, n.v.). – Alpes-Maritimes, 4.3 km SE of Puget-Théniers, 1.2 km W of La Penne, cime de Borrel, 1000 m, twigs of *F.s.*, 24.X.1998, P. Collombon (F.F. 98093, Pop & Fouchier, 1999, d.v.).– Languedoc-Roussillon, Lozère, Mende, unlocated, ~1000 m, *F.s.*, ~30.X.2006, collector unknown, *det.* M. Hairaud (ø, d.v.). – 29 km ESE of Mende, 6 km SSW of Altier, forêt du Cougnet, 1485 m, branch of *F.s.*, on wood, 5.IX.1998, G. Corriol (G.C. 98100501, d.v.). – 12.5 km W of Marvejols, 3.8 km NNW of Salces, E of étang de Bellecombe, 1375 m, twig of *F.s.*, 23.IX.2007, Y. Mourgues (Y.M. HS071, n.v.). – Midi-Pyrénées, Aveyron, 16 km NW of Bédarieux, 3 km S of Mélagues, col de Thalis, 900 m, twig of ?*F.s.*, 19.XI.2004, G. Garcia (G.G. 04111901, d.v.). – 29 km ESE of Millau, 4.5 km ESE of Saint-Jean-du-Bruel, Croix de la Guérite, 1020 m, on *F.s.*, 15.XI.2011, C. Hannoire, *det.* M. Ferrières (ø, n.v.). – Hautes-Pyrénées, 1.4 km ESE of Bagnères-de-Bigorre, NNW of Gerde, Castet, 620 m, branch of *F.s.*, on wood, 20.X.2012, G. Corriol (G.C. 12102019, BBF, d.v.). – around Gavarnie, ~1500 m, on indet. tree, 8.X.1972, F. Candoussau (?ø, n.v.). – Gard, Cévennes, forêt de l'Aigoual, ~1000 m, *F.s.* (Lagarde, 1906: 231, d.v.).

SPAIN: Asturias, 1 km N of Pola de Somiedo, on wood of twigs of *F.s.*, 703 m, 21.XI.1998, E. Rubio (Rubio *et al.*, 2010, ø, d.v.). – 2.3 km SE of Pola de Somiedo, SW of Coto de la Buenamadre, Hayedo de Mumián, 1107 m, twig of *F.s.*, 11.XI.2012, E. Rubio (ø, d.v.). – Castilla y León, Sierra de Guadarrama, 66 km ENE of Segovia, 4.5 km SE of Riofrio de Riaza, Puerto de la Quesera, 1600 m, on wood of twigs of *F.s.*, 21.XI.2000, V. González *et al.* (AH 7326, H.B. 8022, sq. DQ431168). – *ibid*., 21.XI.2000, R. Galán *et al*. (AH 7307, H.B. 8023, sq. DQ431173, FJ005155). – *ibid*., 30.X.2002, *leg*. O. Rodriguez & F. Esteve-Raventós (sq. DQ431178). – Huesca, 10 km E of Sabiñánigo, 4 km NE of Yebra de Basa, Santa Orosia, SE of Collado de las Tres Cruces, 1498 m, twigs of *F.s.*, on wood, 10.X.2009, F. Pancorbo, J.C. Campos, J.C. Zamora *et al.* (M.A.R. 101009 10, d.v.).

ITALY: Piedmont, ?18 km SE of Cuneo, Valle Pesio, ?900 m, twigs of *F.s.*, autumn, U. Cumino (ø, d.v.). – Veneto, 45 km NNE of Treviso, ~15 km SE of Belluno, bosco del Cansiglio, 1000 m, twig of *F.s.*, 1.X.1981, S. Sacconi (Sacconi, 1983, d.v.). – Toscana, 30 km NW of Arezzo, 10 km SW of Poppi, Pratomagno, 1390 m, on wood of branch of *F.s.*, 2.X.2007, B. Fellmann (ø). – Umbria, 13.5 km ENE of Gubbio, 2.5 km NE of Costacciaro, Monte Cucco, Pian delle Macinare, twigs of *F.s.*, on wood, 15.X.2012, F. Fouchier (F.F. 12061, n.v.). – Molise, ~11 km NW of Campobasso, near Castropignano, ~550 m, on wood of branch of *F.s.*, 15.IX.2010, M. Carbone (MCVE 26329, n.v.).

CROATIA: Hrvatsko Zagorje, 11.5 km N of Zagreb, Mt. Medvednica, 2 km NE of Sljeme (peak), Medved graba near Horvatove stube stairways, 740 m, twig of *F.s.*, 7.XI.1998, N. Matočec (CNF-2/4108, n.v.). – Gorski kotar, 22 km NNE of Rijeka, 12.5 km NE of Klana, Mt. Risnjak, Klanska polica, 1190 m, twig of *F.s.*, 30.IX.2002, N. Matočec (CNF-2/5921, n.v.). – Lika, 12 km E of Jablanca, Mt. Velebit, Štirovača, Mrkvište, 1260 m, twig of *F.s.*, 6.X.2008, N. Matočec (ø, n.v.).

MONTENEGRO: 80 km NNW of Podgorica, 2.7 km WSW of Žabljak, Durmitor, Mlinski potok, 1440 m, twigs of ?*F.s.* subsp. *moesiaca*, 6.X.2012, B. Perić (B.P., C7D-06-10-12, d.v.). – 37 km NE of Podgorica, 9 km ESE of Verusa, Massif Komovi, Planinica mt., below Bijela voda, 1425 m, branch of *F.s.* subsp. *moesiaca*, on wood, 20.X.2012, B. Perić (B.P., C7D-20-10-12, d.v.).

GREECE: Thessaly, 28 km WSW of Karditsa, 3 km W of Mt. Zygourolivado, 1550 m, twigs and branches of *F.s.*, 14.XI.1999, P. Delivorias (ATHU–M 5854, 5855, 5856); – *ibid*., 15.X.2000, P. Delivorias (ATHU–M 5857, 5858); – *ibid*., 29.X.2000, P. Delivorias (ATHU–M 5859); – *ibid*., 10.XI.2002, P. Delivorias (ATHU–M 5860); – *ibid*., 10.X.2009, P. Delivorias & A. Bonetti (ATHU–M 6304, 6305) (Delivorias *et al*., 2010, d.v.).

Deviating applications of the epithet *serotinus*

Despite a rather precise and conform characterization of *Hymenoscyphus serotinus* by various authors mentioned above, some European but also American and Asian authors applied the taxon in a wider and mostly different sense. This is obvious from the given substrates which include host genera other than *Fagus*, and besides wood or branches also leaves and fruits. Considering the undoubtedly pronounced host specificity of *H. serotinus*, we conclude that all records from deviating substrates are most probably misidentified. Misidentifications of host trees, or unidentified hosts complicate the situation. Also a deviating phenology or a more tropical occurrence suggests that the authors follow a deviating species concept.

European records

Within Europe, indications for the different application of the epithet *serotinus* trace back to Albertini & Schweinitz (1805: 331), who reported both leaves and branches as a substrate, rarely also a terrestrial habitat, wet places (often close to water), as well as the months May, June, and July in regard to phenology. Fries (1822: 119) drew attention to this discrepancy by separating Albertini & Schweinitz's report as "var. *verna*". Although Phillips (1887: 125) cited Fuckel (FRE 1157, twigs of *Fagus*) as exsiccata, he specified the ecology as "on dead leaves and branches in water". Also Saccardo (1889: 222), Massee (1895: 241), and Gillet (1879: 156) included leaves as substrate, apparently influenced by Albertini & Schweinitz. Schröter (1908: 81), copied by Migula (1913: 1188), described a fungus with short-stalked, vividly golden yellow apothecia and almost straight ("flattened at one side"), fusiform spores of 16–20 × 3–4 µm, growing especially on leaves and fruit capsules of *Quercus*, also on leaves of *Betula* and on twigs, in autumn but also late spring. Schröter's concept of *Helotium serotinum* might include *Hymenoscyphus epiphyllus* and *H. monticola*, whereas the drawing in Migula (*loc. cit*., pl. 178 fig. 5–8) appears to be influenced by Rehm's illustration of *Helotium serotinum* (Fig. 3a) which appears to be a mixture of *Hymenoscyphus lepismoides* and genuine *H. serotinus*.

Fuckel and Rehm included also collections on *Carpinus*, described below under the name *H. lepismoides*, in their species concept of *Helotium serotinum*. However, the authors were unaware of this substrate: in one of his specimens from Oestrich (Rheingau), Fuckel misidentified that host as *Fagus*, while Rehm did not identify any host genus in the collection from Bentheim (Münster, Westfalen).

Rehm's (1893: 770, fig. 3–4, 781) description and drawing under the name *Helotium serotinum* predominantly originate from the Bentheim specimen and concern *Hymenoscyphus lepismoides* on *Carpinus* (Fig. 8a–f, h–i, 9b). The furthermore cited sample from Spessart (on *Fagus*, S-F227298) represents *H. serotinus* in the present sense.

Velenovský (1934) once observed a "similar form" on branches of *Juglans*, but Svrček (1985) found the substrate to be "surely *Fagus*".

Although Lizoň (1992: 47) treated almost exclusively European specimens on *Fagus* branches, he included in *H. serotinus* a specimen collected in August on *Acer* petioles in Indiana (U.S.A.), for which he figured a nearly straight, basally widened rather than tapered spore (Lizoň, *loc. cit.*: fig. 2). Besides these substrates he mentions also twigs of *Carpinus betulus*, but this host does not appear in his list of examined specimens. That record might concern *H. lepismoides*, but from which source it was taken remains obscure.

Galán & Ortega (1983) report under the name *Hymenoscyphus serotinus* a fungus on twigs of two Mediterranean species of *Quercus* with coriaceous leaves (*Q. rotundifolia*, *Q. faginea*). The spores are said to be straight or only slightly curved, scutuloid, 18–30 × 3.4 µm. However, the spores are drawn much broader than typical of *H. serotinus* (4–5 µm according to the scale), and the identification was changed to *H. scutula* (Pers.) W. Phillips by R. Galán on the personally submitted separatum. Similarly, Milekhin & Prokhorov (2008) report rather wide spores (20–25 × 4–5 µm, without mention of a curvature) for their collections on wood of *Quercus* and *Populus*. For a collection of *H. serotinus* reported in Tănase *et al.* (1999: 124) from Alpes-de-Haute-Provence the host is erroneously cited as *Quercus* (F. Fouchier, pers. comm.). The same collection is described by Pop & Fouchier (1999), and there the host is correctly given as *Fagus* ("hêtre").

Helotium serotinum var. *obesum* Bres. *in* Schulzer (1885) was recorded in Slavonia (eastern part of Croatia) in August and September on wood and leaves of *Quercus*. The description is too brief to permit recognition of its identity. A close relation to *Hymenoscyphus serotinus* seems improbable since the spores were described as oblong, subfusiform, 14–16 × 3 µm, apparently straight.

Records from America

Seaver (1951: 118) reported *Helotium serotinum* for North America "on fallen leaves and branches of different kinds", following a remark of Saccardo (1889) that is possibly based on the short note of *Peziza serotina* on leaves from North Carolina by Schweinitz (1822: 95), while Seaver saw only a single specimen from Ohio, determined by B. Kanouse. This record and one under the name *H. serotinus* from Idaho on stems of *Cornus stolonifera* (Glawe n. d., Shaw, 1973: 44; Farr *et al.*, 1989: 740) require reexamination.

In their paper on *Hymenoscyphus caudatus* (P. Karst.) Dennis and related species from tropical America, Dumont & Carpenter (1982: 575f.) included under the name *H. serotinus* various collections, mainly on leaves (often unidentified, e.g., on midveins, on petioles of *Inga*, on a fern), also on unidentified herbaceous stems, rarely on woody substrates such as twigs, branches and logs. The authors stressed the great variability in size and colour of the apothecia among the specimens, with the larger ones (up to 5 mm diam.) occurring on woody substrates. Nevertheless, they united all under one name, based on the high microscopical similarity. Their species concept was circumscribed by ascospores being strongly beaked above, tapering gradually towards the base, moderately curved when outside asci, lacking setulae, and measuring (16–)18–23(–30) × 3–3.5(–4.5) µm. In the dead state the spores of genuine European *H. serotinus* may indeed resemble those illustrated by Dumont & Carpenter (*loc. cit.*: fig. 4D; Colombia, Dpto. Cauca, on wood, CO-1316; see Fig. 5d).

Dumont (1981: 72) considered *H. fastidiosus* (Peck) Arendh. (on leaves of *Alnus*) as a probable synonym of *H. serotinus*. However, according to White's (1942: 165, fig. 9) precise analysis of the type material, the spores of *H. fastidiosus* are predominantly straight or only apically curved, and the asci arise from simple septa. Dumont is apparently in error when stating that they are produced from small croziers: according to Dumont & Carpenter (1982), the asci in all of their tropical collections of the seven species treated are said to arise from croziers, including *H. caudatus*, for which the authors report a high number of collections on leaves (rarely herbaceous stems) from tropical America. Since *H. caudatus* was found to lack croziers in most of the European as well as North American specimens (White, 1943: 151; Baral, ined.), and Dumont & Carpenter (*loc. cit.*) did not il-

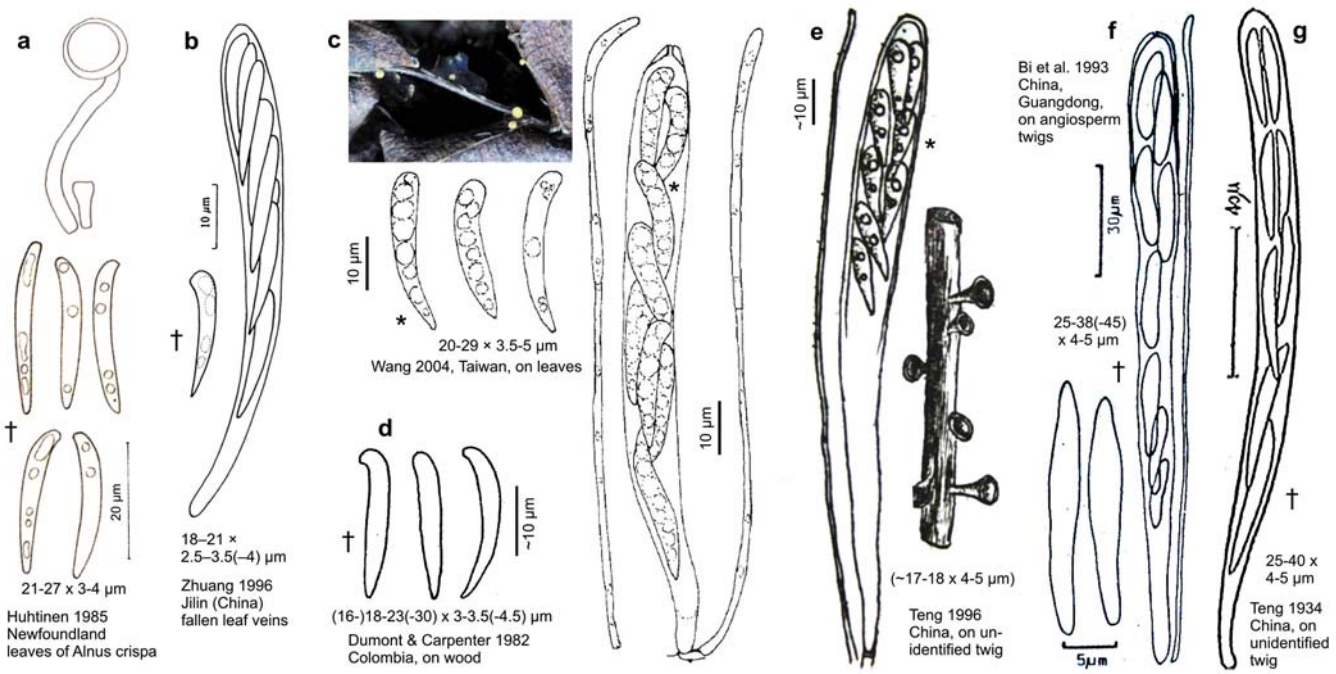

Fig. 5 – Published illustations of extra-European records under the name *Hymenoscyphus serotinus* or *Helotium serotinum*. Based on the deviating substrate (leaves or unidentified wood) and partly also a different spore size and shape, these records represent different species: a: *Hymenoscyphus* ?*fastidiosus*/*denticulatus*; b. *H.* aff. *vacini*; c. *H.* aff. *caudatus*; d–e. *H.* ?*virgultorum*; f–g. (?)*Dicephalospora rufocornea*.

lustrate the feature in any of their drawings, their descriptions seem to be untrustworthy in this respect, at least this is obvious in the above-mentioned *H. fastidiosus*. Those samples on woody substrata should be compared with European *H. virgultorum*, a taxon here interpreted as plurivorous lignicolous species in which the asci arise from simple septa (Baral, ined.).

Huhtinen (1985: 516, fig. 70) described under the name *Hymenoscyphus serotinus* a collection from Newfoundland (Canada) on leaves of *Alnus crispa*, with spores very similar to typical specimens on *Fagus* twigs, but almost straight or only slightly curved, and the apothecia with up to 0.5 mm diam. comparatively small (see Fig. 5a). Regrettably, the presence of croziers was not tested. Huhtinen compared his record with *H. fastidiosus*, which he excluded because of its larger spores. His record should also be compared with *H. denticulatus* (Velen.) Svrček: Dennis (1956: 81) considered long- and slender-spored foliicolous specimens, which he regarded on page 82 as a possible form of *Helotium caudatum*, as similar to the lignicolous *Helotium serotinum*. This unnamed foliicolous taxon was considered by Svrček (1985: 142) as most probably identical with *H. denticulatus*, a species that seems to differ from *H. caudatus* in narrower spores and a crenulate margin.

Records from Asia

Under the name *Helotium serotinum* Thind & Singh (1971: 303, fig. 3) described a specimen on angiosperm wood, collected in August from mountainous India (Himalaya), with almost straight, scutuloid spores 25–32 × 4.2–5 µm. Sharma (1991: 169, pl. V fig. 5–7) added under the name *Hymenoscyphus serotinus* further records from this area, collected during June–September on angiosperm twigs and fern stipes, with spores (22–)23–29 × 3.5–6 µm. The provided drawing is almost the same as in 1971. Especially the broad spores exclude genuine *H. serotinus*.

Korf & Zhuang (1985) studied several foliicolous collections from Sichuan, China, which they referred to *H. serotinus* based on a similar apothecial morphology. However, the authors wondered why Dumont & Carpenter retained the species in *Hymenoscyphus*, since they observed not infrequently a very evident stroma in the host tissue. Consequently, they transferred the taxon to the *Sclerotiniaceae*, as *Lanzia serotina*. No description or illustration was provided by Korf & Zhuang, who also expressed their belief (without examination of a type specimen) that *Helotium vacini* Velen. is a later synonym of Persoon's taxon. Zhuang (1993) obtained a dark stroma in a Chinese ascospore isolate identified as *Lanzia serotina* (W.Z. 238), and thus saw her previous perception confirmed that the species is sclerotiniaceous. Later, Zhuang & Liu (2007) retransferred the taxon to *Hymenoscyphus* based on their molecular analysis.

Zhuang (1993, 1996) and Wang (2004) reported various collections from China (Jilin, Sichuan, Yunnan, Taiwan) under the name *Lanzia serotina*, all on unidentified leaves or leaf veins. The provided illustrations of microscopic characters differ somewhat among each other: Wang (*loc. cit.*, TNM F8314, Taiwan) figured slightly to moderately curved, comparatively large spores (see Fig. 5c), whereas Zhuang (1996: fig. 22, HMAS 61897 = W.Z. 803, Jilin) figured smaller, only very slightly curved spores (Fig. 5b). This latter drawing was also reproduced in Zhuang & Liu (2007: fig. 9), but was there erroneously said to be copied from Zhuang (1998) and to have the number HMAS 75941 (W.Y. Zhuang, pers. comm.).

Zhuang (1996) and Wang (2004) reported the apothecia of *Lanzia serotina* as white to yellow or yellowish, respectively, with a dark or black stipe base. Its diameter varied between 0.5–1 mm (Wang), (0.5–)1–2.3 mm (Zhuang, 1993), and 0.4–1(–4) mm (Zhuang, 1996). No mention of croziers or simple septa was made concerning any of these Chinese specimens, which should be compared with European *Hymenoscyphus vacini* and *H. caudatus*.

Although the spore drawings in Dumont & Carpenter (*loc. cit.*) and Wang (*loc. cit.*) from tropical specimens concur rather well with those from European *H. serotinus*, their conspecificity is quite improbable. Any lignicolous, herbicolous and foliicolous material from America and China requires re-examination, e.g., concerning the presence of croziers, but also concerning spore guttulation. The reported differences in spore size and curvature suggest that different taxa are involved, even within the foliicolous specimens.

One of Zhuang's specimens (HMAS 61896 = W.Z. 801 = H.B. 5830, from the temperate province of Jilin, northwest of China) was re-examined in 1997 by the senior author (Fig. 6). It was collected on unidentified leaves in the northeast of China at the same date and locality as the above-mentioned HMAS 61897. Indeed, the specimen resembles in many details, including the skeletonized leaves, *H. vacini*, a species re-described in a separate paper (Baral & Bemmann, in prep.). However, the asci and spores are distinctly smaller, particularly narrower, when comparing measurements in the dead state. The apothecia are distinctly smaller as well (rehydrated 0.35–0.5 mm diam.). Similar as in *H. vacini*, the netveins of the leaves in HMAS 61896 are brown, not blackened (Fig. 6d). Contrary to *H. vacini*, the entire stipe is pale greyish, without a blackish base. It seems most likely that this specimen represents a species of its own, different from *H. vacini*. In both species the asci arise from simple septa. A few overmature, light brownish, rough-walled spores were seen inside some asci (Fig. 6a).

Zhuang & Wang (1998: 27) and Zhuang (1998: 26) stated that the description of *Helotium serotinum* by Teng (1963, 1996, on fallen twigs in woods of Hainan, Southern China), resembles *Ciboria peckiana* (Cooke) Korf, a taxon considered to be a synonym of *Tatraea*

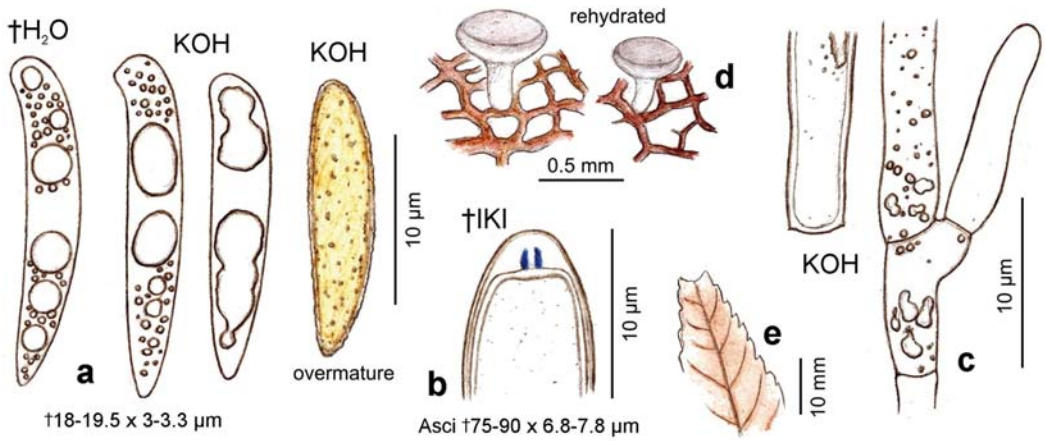

Fig. 6 – *Hymenoscyphus* aff. *vacini*. a. ascospores (from inside asci, containing LBs); b. ascus apex with euamyloid apical ring (*Hymenoscyphus*-type); c. ascus bases arising from simple septa; d. apothecia emerging from netveins; e. part of skeletonized leaf. – All in dead state. – CHINA: JILIN, ~40 km ENE of Jilin, ~32 km NW of Jiaohe, Liudaohe, former Jiaohe Experimental Forestry Farm, 700 m, skeletonized leaves of indet. angiosperm, 1.IX.1991, W.Y. Zhuang (HMAS 61896, W.Z. 801, as *Lanzia serotina*; H.B. 5830ø). – *Del.*: H.O. Baral.

macrospora (Beck) Baral (see Baral *et al.*, 1999). Two years earlier, however, Zhuang (1996: 36) wrote that Teng's and Tai's (1979) records of *H. serotinum* concern the tropical species *Dicephalospora rufocornea* (Berk. & Broome) Spooner, based on specimens deposited in HMAS. According to Zhuang (pers. comm.), this contradiction is due to the fact that different specimens were re-examined and found to belong to different species.

These two taxa are characterized by fusoid, homopolar ascospores of a length of ~25–35 µm, which fit the illustration in Teng (1934, see Fig. 5g) but not that in Teng (1963, 1996, see Fig. 5e). The latter drawing shows clavate, strongly heteropolar spores, which have a distinctly lower length:width ratio (~17–18 × 4–5 µm when using the given ascus size), reminiscent of a *Hymenoscyphus*, perhaps *H. virgultorum*. Despite the two very different illustrations, the description in Teng (1996: 189) is the same as in Teng (1934: 455) and seems to concern *D. rufocornea* because of an orange hymenium and spores being "clavate-fusoid, often slightly curved, continuous, 25–40 × 4–5 µm".

Also the specimens reported by Bi *et al.* (1993: 30 , pl. 2 fig. 18–20) on angiosperm twigs from Guangdong (Southern China) might represent *D. rufocornea*, according to the "aurantiacous to scarlet" apothecia and "falciform to fusiform" spores of 25–38(–45) × 4–5 µm. Yet, the drawing shows almost homopolar, straight spores with a size of 21–23 × 3 µm (evaluated from the scale bar, but 19–27.5 × 3.5–5.5 µm for those inside the ascus, see Fig. 5f).

Taxa which were named after *H. serotinus*

Two taxa referring to the name *serotinus* in their specific epithet have been described. The tropical *H. subserotinus* (Henn. & E. Nyman) Dennis is characterized by homopolar, fusoid spores. It was considered to be a synonym of *Lanzia rufocornea* (Berk. & Broome) Dumont by Dumont (1980), which was combined as *Dicephalospora rufocornea* (Berk. & Broome) Spooner by Spooner (1987). *H. microserotinus* (W.Y. Zhuang) W.Y. Zhuang was erected by Zhuang (1996) in the genus *Lanzia* based on specimens recorded on unidentified herbaceous stems and particularly leaves (petioles and veins) from mountainous sites in Anhui and Sichuan (China). Its strongly heteropolar (scutuloid), almost straight spores closely resemble those of Zhuang's likewise mainly foliicolous "*L. serotina*" (Fig. 5b), but are distinctly shorter (11–18.3 × 2.5–3.8 µm). A similar fungus was quite frequently recorded in Europe (mainly Germany) on *Fagus* leaves, with scutuloid spores (*12–16.5 × 3–4.5 µm) and asci arising from simple septa (Baral, ined.). It might well be that this represents *H. microserotinus*. British specimens on leaves of *Alnus* and *Fagus* identified in Ellis & Ellis (1987: fig. 334) as *H. albopunctus* might concern the same species, whereas North American specimens including the type show only slightly scutuloid, partly almost homopolar spores (White, 1942, 1943).

Phylogenetic relationship

H. serotinus is closely related to *H. calyculus* (Sowerby) W. Phillips, as was also stated by Dennis (1956) who regarded it as "perhaps no more than a form" of that species. However, *H. calyculus* has shorter, rather straight, basally only slightly tapered spores (see Dennis, *loc. cit.*: 83). Breitenbach & Kränzlin (1981: pl. 182) shared Dennis' doubts by giving their sample of genuine *H. serotinus* the name *H. calyculus*, following Dennis (1978) who did not mention *H. serotinus* at all.

For genuine *H. serotinus* three sequences of ITS rDNA (DQ431168, DQ431173 = H.B. 8023, DQ431178) and one of LSU (FJ005155) are presently available in GenBank. All of them derive from specimens collected on *Fagus* twigs in the Sierra de Guadarrama near Segovia (Spain). These three sequences show 100% similarity among each other. In a phylogenetic tree based on this gene region (Baral *et al.*, 2006) they are found in the genus *Hymenoscyphus* sister to *H. scutula* and *H. macroguttatus* Baral, Declercq & Hengstm., which demonstrates that the species is not a member of the genus *Lanzia* Sacc. (*Rutstroemiaceae*) as suggested by Korf & Zhuang (1985).

In an unpublished molecular analysis on sequences gained from various species of *Hymenoscyphus* (Queloz *et al.*, unpubl.), Spanish *H. serotinus* (H.B. 8023) is found within a group comprising *H. virgultorum*, *H. fructigenus* (Bull.) Gray and others. The used sequence was recently obtained by V. Queloz from the apothecia, and shows full identity with the three sequences in GenBank, except for a deviation at the transition from ITS to LSU: the beginning of LSU starts here with TGACCT, which is the general signature in fungi, while in the three above-mentioned sequences it is TGGACCT, which is obviously an error.

The single available extra-European sequence concerns a foliicolous Chinese collection under the name *Lanzia serotina* (HMAS 82122, AY348592), which was considered by W.Y. Zhuang (pers. comm.) as conspecific with the one studied here (Fig. 6). The sequence clustered in the genus *Hymenoscyphus* in a study by Zhang & Zhuang (2007), and a BLAST places it in the vicinity of *H. brevicellulus* H.D. Zheng & W.Y. Zhuang, *H. microserotinus*, and *H. microcaudatus* H.D. Zheng & W.Y. Zhuang (92–95% similarity), whereas genuine *H. serotinus* does not show up at all. Although Zheng & Zhuang (2013) mentioned *H. serotinus* from Segovia (DQ431168) in their list of ITS sequences, the species was not included in the phylogenetic tree.

Description of *Hymenoscyphus lepismoides*

Hymenoscyphus lepismoides Baral & Bemmann, sp. nov. – MB 805225 – Fig. 7–11

Holotype: Luxembourg: Wiltz, Doncols, twigs of *Carpinus betulus*, on wood, 14.I.1989, M.T. Tholl, G. Marson & H.O. Baral (ex H.B. 3656, M).

Etymology: derived from the similarity of the ascospores with *Lepisma saccharina* (silverfish).

Diagnosis: Apothecia 1–4 mm diam., with yellow disc and paler exterior, short- to long-stipitate. Asci *165–200 × 14–15 µm, with euamyloid apical ring, arising from simple septa. Ascospores *33–37 × 6–7.5 µm, distinctly heteropolar and inequilateral (scutuloid), straight to slightly curved, with one or several prominent setulae at each end, multiguttulate. Paraphyses containing refractive vacuolar bodies (multiguttulate). Habitat on more or less blackened wood of twigs and thin branches of *Carpinus*, usually attached though not far from the ground, in late autumn.

Description: Apothecia fresh (0.5–)1–4(–5) mm diam., receptacle 0.4–0.5(–0.7) mm thick, singly or often fasciculate (partly from a common stipe); disc more or less round, light to bright yellow to yellow-ochre when fresh, turning red-bown with age, slightly concave to flat, eventually also strongly convex, margin smooth to finely crenulate or fimbriate, 10–25 µm protruding, exterior whitish to pale yellow or greyish-brownish, distinctly pubescent; stipe 0.3–2.5(–4) × 0.3–0.7 mm, pale yellow, at base or sometimes entirely red-brown, erumpent from beneath periderm (stipe partly to entirely hidden); in dry state disc deep yellow, but after ~20–100 years turning light to deep ochraceous or (reddish-)brown, stipe pale cream-ochraceous. **Asci** *165–200 × 14–15 µm {T}, †(115–)125–150(–160) {7} × (9.5–)11–14(–15) µm {9}, clavate, 8-spored, spores (†) obliquely biseriate, *pars sporifera* †100–115 µm long; apex (†) strongly conical, dome †2–3.2 → 0.8–1.7 µm thick, lower 2/3–3/4 of apical ring deep blue in IKI (bb) {5}, *Hymenoscyphus*-type (ring also well visible in KOH), entire ascus wall bright pinkish-red in CR except for uppermost apex; base gradually narrowed in a long stalk arising from simple septa {6}. **Ascospores** *(28–)33–37(–40) × (4.5–)6–7.5(–8) µm {3}, †(25–)28–35(–39)((–41)) × (5–)5.5–7(–7.5)((–8)) µm {8}, strongly heteropolar, clavate-scutuloid, apex obtuse, partly with a more or less distinct hook on one side, gradually strongly attenuated from upper or middle part towards base, (*/†) almost straight (inequilateral) to often slightly, rarely medium curved (comma-.shaped); with

(1–)2–3 usually more or less curved setulae 1–2 µm or up to 3(–4) µm long {9}, those at upper end usually laterally inserted at the beak but also terminal, those at the base often more or less reflexed but also converging, often with remnants of a delicate sheath, particularly at the base, setulae also lacking in some spores, wall CRB negative; containing numerous medium-sized LBs (0.5–)0.8–2(–2.5) µm diam. and many small ones (0.4–0.5 µm) {2} (multiguttulate), lipid content 5 {9}; overmature spores 1–3-septate, germ tube always basally formed. **Paraphyses** cylindrical, with apically rounded terminal cell *~42–48 × 3–4 µm {2}, †2–3(–3.5) µm wide {2}, lower cells †1.5–2 µm wide, containing medium to strongly refractive, more or less hyaline, small to large, globose VBs in upper 20–45 µm {2}, VBs staining light redbrown in IKI, also a few minute, pale orange-yellow LBs. **Medullary excipulum** hyaline, of loose *textura intricata*, hyphae *2.5–3.5 µm wide, sharply delimited from ectal excipulum by a parallel, 25–50 µm thick layer of *textura porrecta*. **Ectal excipulum** hyaline, from base of receptacle to margin of thin-walled *textura prismatica*(*-porrecta*), cells *11–30 {1} × 5–10(–15) {2} µm, 120 µm thick at lower flanks, oriented at a 30–45° angle to the surface; 40–50 µm thick near margin, oriented at a 10–30° angle to the surface; exterior overall covered by a 10–30 µm thick layer of 3–4 µm wide hyphae, their ends protruding as 30–75 µm long, septate, hair-like, partly agglutinated hyphae that contain low-refractive VB-guttules; crystals absent in complete tissue. **Anamorph** unknown.

Habitat: on entirely or partly corticated, 1.5–10 mm thick twigs and branches of *Carpinus betulus* {11}, attached (0.3–1.2 m above ground) or lying on the ground, on medium decayed, moderately to strongly blackened wood {11}, often erumpent from small holes or

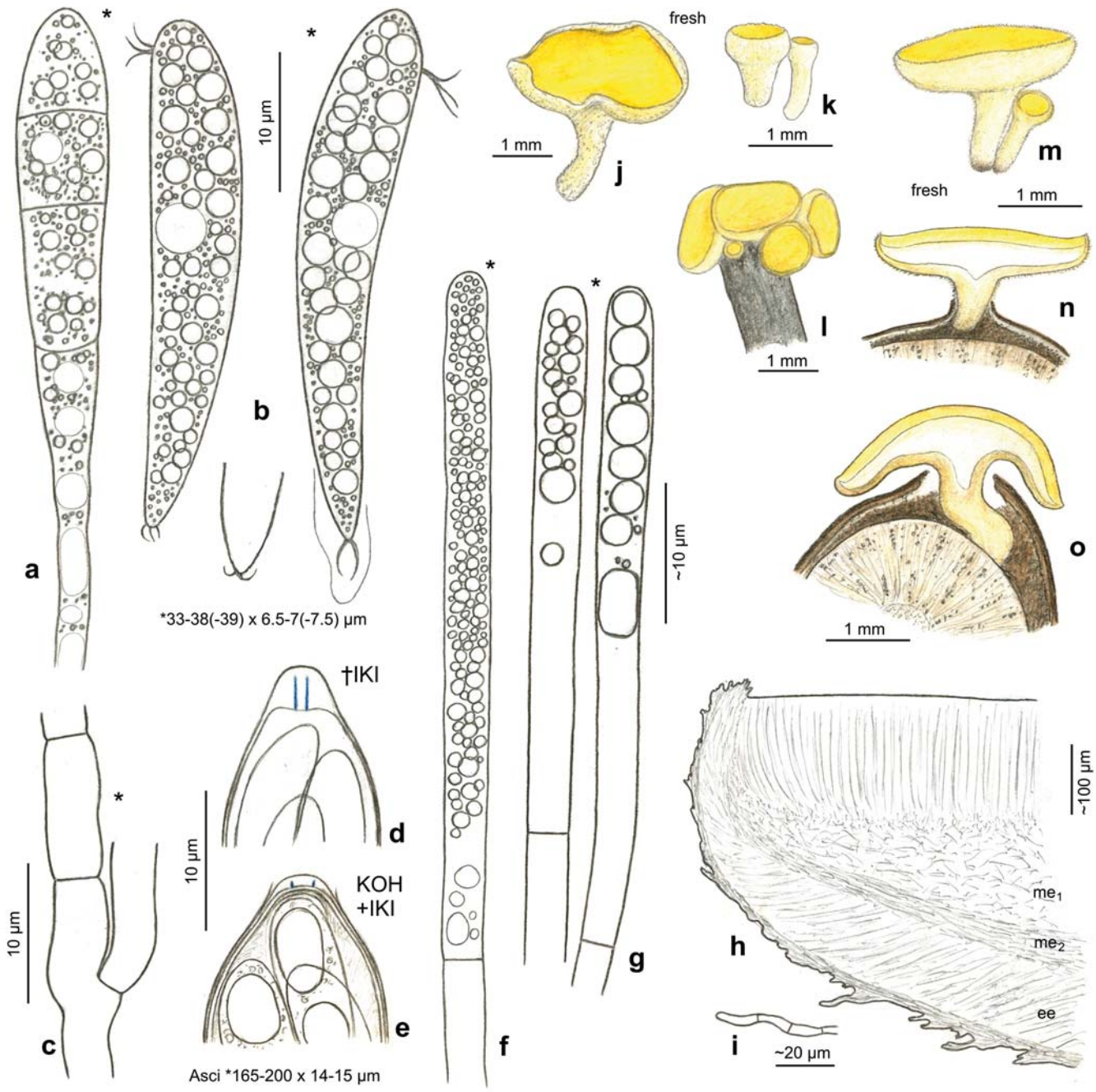

Fig. 7 – *Hymenoscyphus lepismoides* (on twigs of *Carpinus betulus*). a–b. ascospores (containing LBs, with terminal setulae), a: overmature (germinating), b: mature (freshly ejected); c. simple-septate ascus base; d–e. ascus apices with euamyloid apical ring (*Hymenoscyphus*-type); f–g. paraphyses (containing VBs); h. median section of apothecium (m1 =); i. hair-like hyphae emerging from cortical layer of ectal excipulum at flanks; j–o. apothecia erumpent from beneath bark (n–o: in median section). – Living state except for d–e. – a, c–d, g, j–k: H.B. 3618 (topotype); b, e–f, h–i, l–o: H.B. 3656 (holotype). – *Del*.: H.O. Baral.

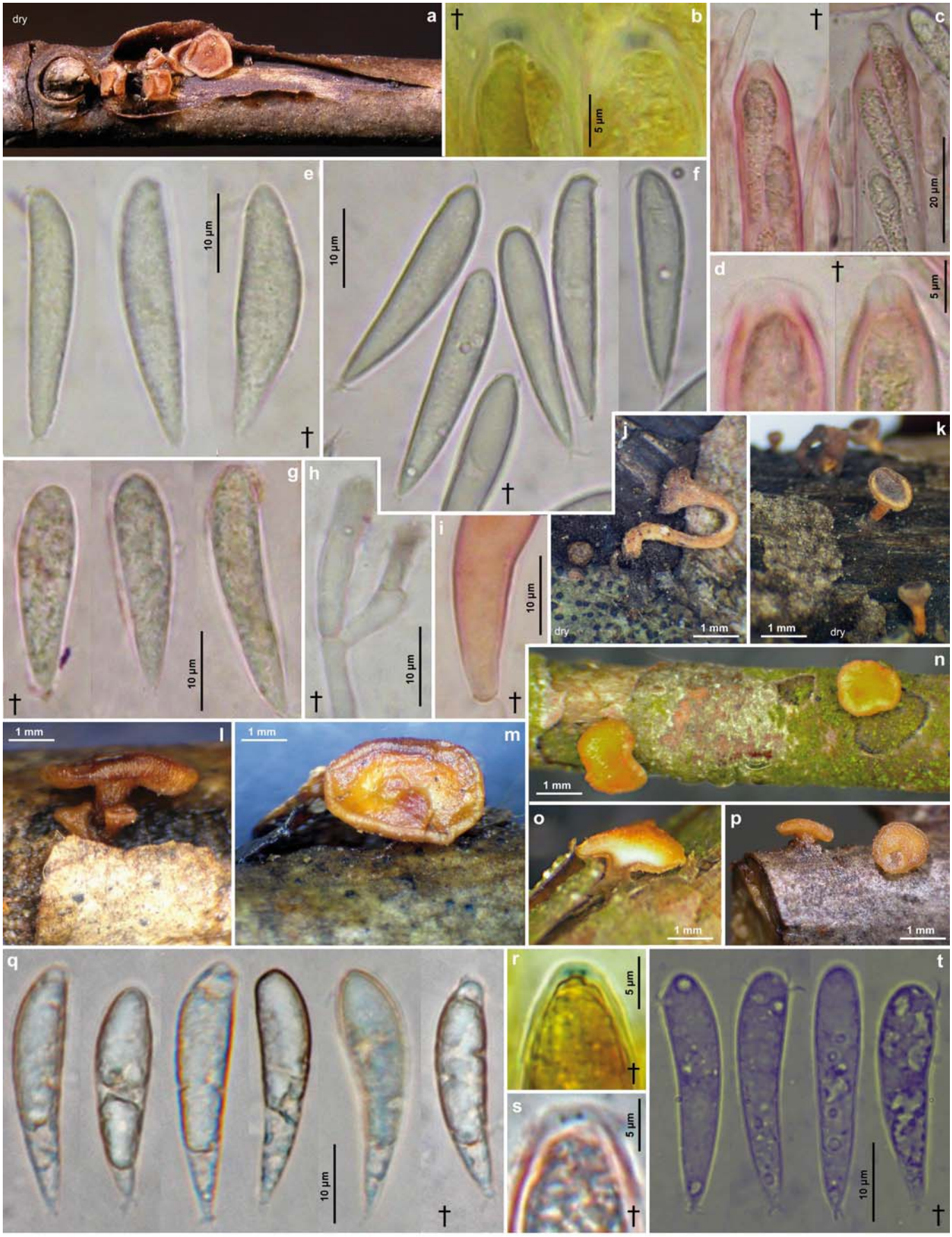

Fig. 8 – *Hymenoscyphus lepismoides* (on twigs of *Carpinus betulus*). a, j–k. dry apothecia on twigs of *Carpinus betulus*; l–p. dto. (rehydrated); b–d, r–s. ascus apices with apical ring and in d (left) with periascus; e–g, q, t. ascospores; h–i. simple-septate ascus bases. – All in dead state: f, q (in H_2O), b, r (in IKI), t (in Waterman blue-black ink), e (in KOH), c–d, g–i, s (in KOH+CR or CR_{SDS}). – a–f, h–i. S-F (Spessart); g. S-F227300 (Oestrich); j–k, r, t. LUX 42882 (Reckinger Barrière); l–m. LUX 42881 (unlocalized); n–o. 4.II.2013 (Doncols); q, s. LUX 42884 (Reckenthal). – Phot.: a–i: H.O. Baral; j–t: M. Bemmann.

in broad cracks of bark. **Assoc.:** *Calycina italica* {1}, *Graphis scripta* {1}, *Porina aenea* {1}. **Phenology:** Nov.–Jan. **Desiccation tolerance:** not tested but probably tolerant. **Altitude:** 50–465 m. **Geology:** Devonian slate {2}, Silurian shale {1}, Bentheim Sandstone (Cretaceous) {1}, Luxembourg Sandstone (Lower Lias) {3}, Hettangian marl (Lower Lias) {1}. **Vegetation:** *Pulmonario-Carpinetum* {1}.

General remarks

Macroscopically *H. lepismoides* closely resembles *H. serotinus*. Both species have yellow, stipitate apothecia of a very similar size (1–4 mm diam.), and fruit in late autumn on twigs and branches, the former on *Carpinus*, the latter on *Fagus*. *H. lepismoides* differs from *H. serotinus* in much larger, especially wider asci that arise from simple septa, in much larger ascospores that are on average much less curved in the living state, and in the presence of prominent setulae at the spore ends for which the spores resemble a silverfish. Moreover, the apothecia are apparently desiccation-tolerant, judging from the fact that they partly fruited on attached twigs and branches, in contrast to *H. serotinus*.

In both species the spores are surrounded by a sheath. While in *H. serotinus* the sheath separates from the spore after ejection and can hardly be observed in herbarium material, that in *H. lepismoides* may remain attached, particularly to the spore base, as was seen in the dried specimen from Sjöbo (Fig. 9e). In the holotype the sheath enclosed the setulae (Fig. 7b), whereas in the specimen from Sjöbo the setulae emerged externally from the sheath, which suggests that the spore wall separated into two layers.

The species was previously called *Hymenoscyphus thollianus* nom. prov., named after Marie-Thérèse Tholl. Under that name it appears also in an unpublished key on the genus *Hymenoscyphus* by B. Declercq, who suggested there the here chosen specific epithet *lepismoides*.

H. lepismoides was collected and documented in the fresh state during 1988–1989 (Fig. 7). Although the species resembles the caulicolous *Hymenoscyphus scutula* in spore shape and presence of setulae, its other features were not found to be in accordance with any published description. *H. lepismoides* differs from *H. scutula* in much larger spores with often more than one setula at each spore end, smaller oil drops in the spores, a bright yellow apothecial disc, and a stipe emerging from blackened wood instead of non-stromatized herbaceous stems. Similar as in *H. scutula*, the apical setulae are often laterally inserted at the projecting beak. In *H. trichosporus* Dougoud (Dougoud, 2001: 11), on branches of *Alnus viridis*, the

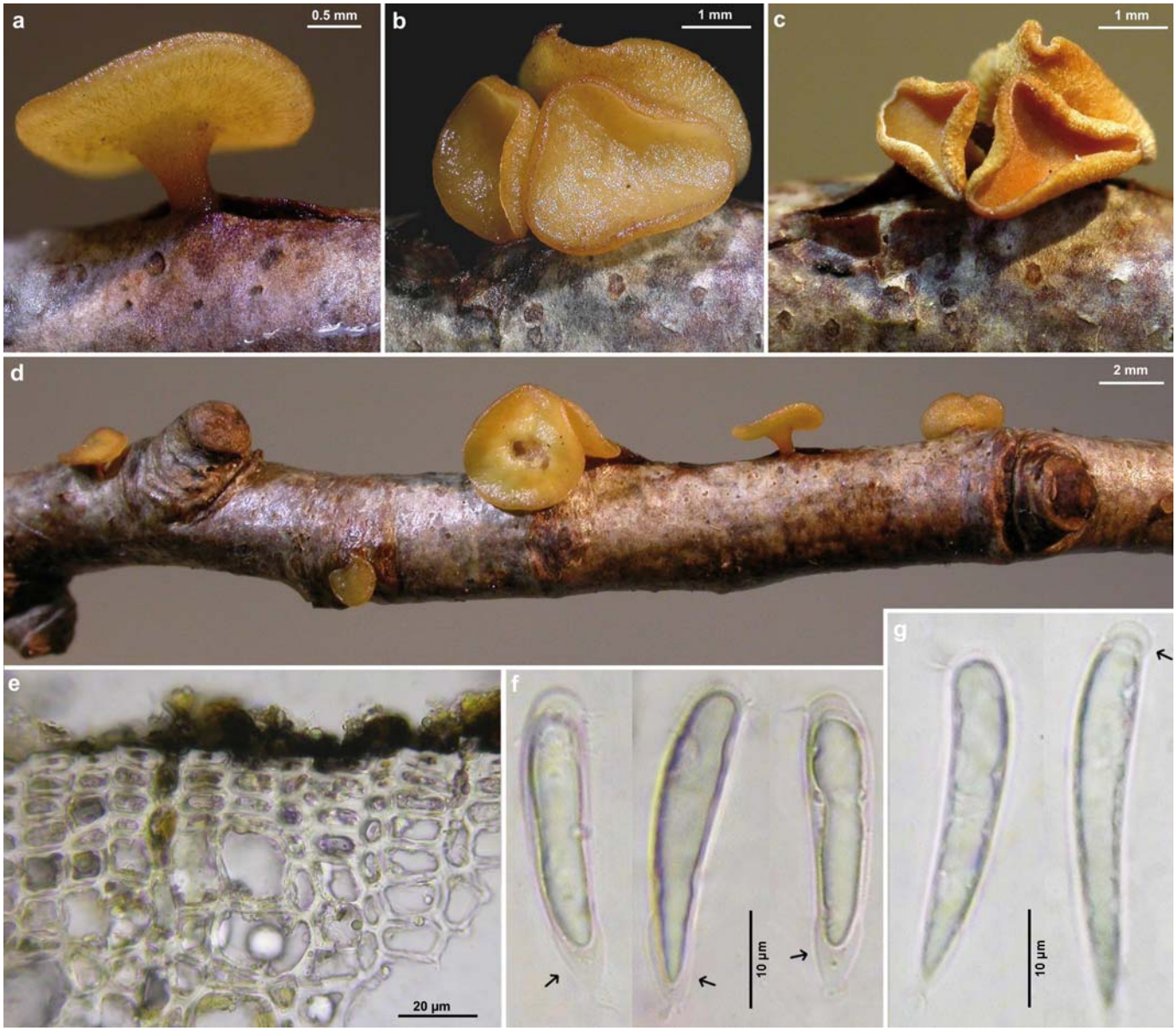

Fig. 9 – *Hymenoscyphus lepismoides* (on twigs of *Carpinus betulus*). a–b, d. rehydrated apothecia (almost 9 years after being collected); c. dry apothecia; e. cross section of decorticated part of twig with blackened surface; f–g. ascospores (dead state, f in KOH+CR, g in KOH), with inconspicuous setulae, arrow showing remnant of spore sheath at the base or sometimes apex. – a–g. H.B. 9832 (Skåne), phot. H.O. Baral.

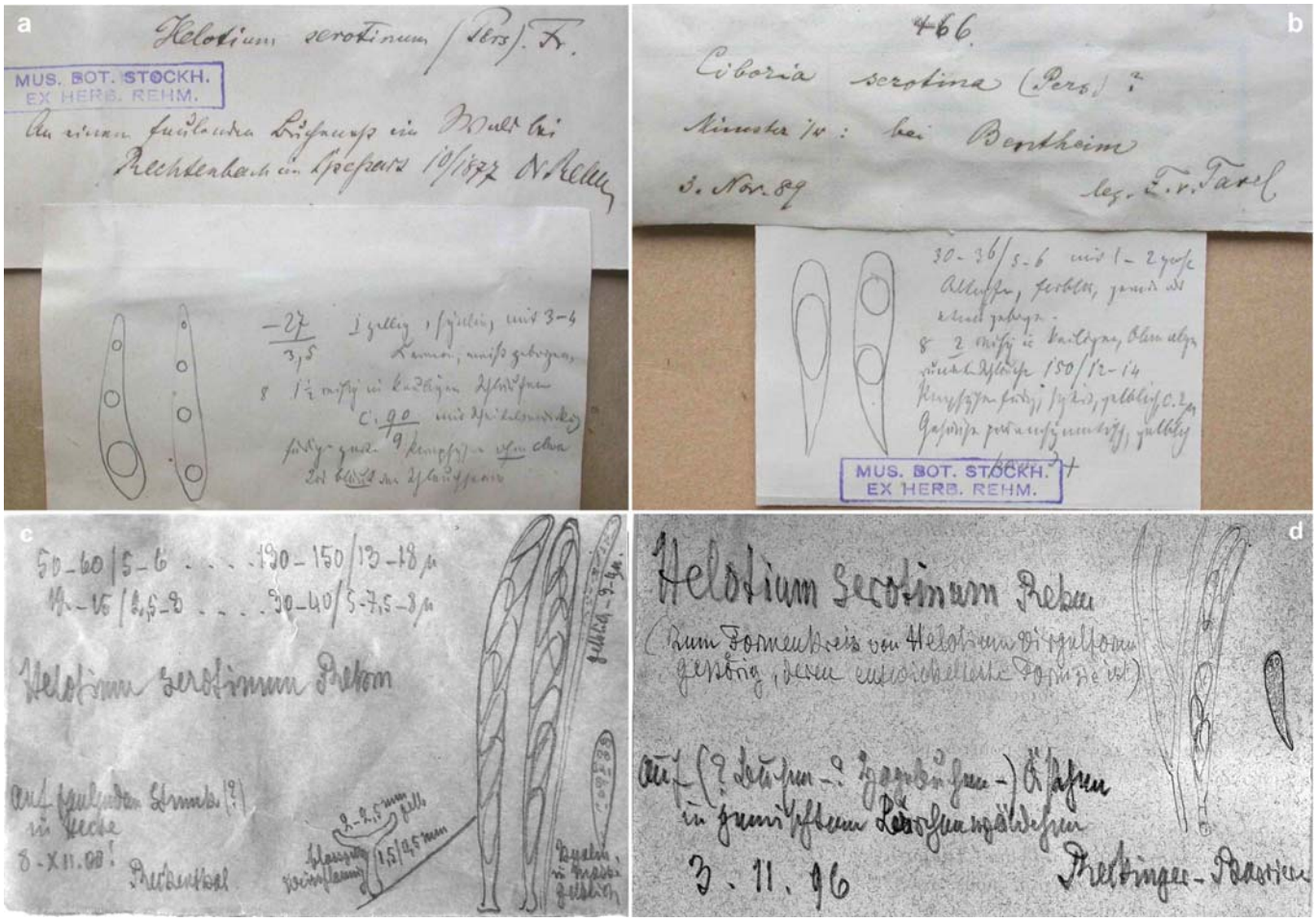

Fig. 10 – Sketches by Rehm (a–b) and Feltgen (c–d) on herbarium labels of specimens identified as *Helotium serotinum* (a: = *Hymenoscyphus serotinus* [on *Fagus*], b–d: *H. lepismoides* [on *Carpinus*]). – a. from Spessart (Unterfranken, S-F227298); b. from Bentheim (Nordrhein-Westfalen, S-F, Tavel 466); c. from Reckenthal (Luxembourg, LUX 42884); d. from Reckinger Barrière (Luxembourg, LUX 42882).

apothecia also have a yellow-orange disc and the spores possess 1–2(–5) setulae at each end, but the spores are almost homopolar (cylindric-ellipsoid) and much shorter, also the asci arise from croziers. However, two records on *A. viridis* and *A. incana* showed asci arising from simple septa (Baral, ined.).

Confusion with *H. serotinus* by previous authors

As already stated above, Fuckel, Rehm, and Feltgen overlooked the existence of *Hymenoscyphus lepismoides* as a species distinct from *H. serotinus*. We detected this confusion when revising specimens under the name *Helotium serotinum* from the herbaria of these authors. Also a report by Dimitrova (2002: 257) from Bulgaria (Sredna Gora Mts, Mt. Lozenska) under the name *H. serotinus* (on wood of *Carpinus* twigs, SOMF 13490) possibly concerns *H. lepismoides*, but no description is given.

Although Rehm considered *Helotium serotinum* to be well characterized by its large, partly long-stalked, vividly yellow apothecia growing on blackened wood of *Fagus* twigs, with long, elongate-clavate, mostly slightly curved spores, the given spore size of 30–36 × 4–6 µm already indicates that he was dealing with a species different from genuine *H. serotinus*.

The examination of two specimens of Fuckel (from Oestrich) and two of Rehm in S (from Bentheim and Spessart) revealed that both authors merged the two species under the name *Helotium serotinum*: one specimen of each author concerns typical *Hymenoscyphus serotinus* on wood of *Fagus* (Oestrich, FRE 1157, S-F227299; Spessart, S-F227298), whereas the other belongs to *H. lepismoides* and grew on wood of *Carpinus* (Oestrich, S-F227300; Bentheim, Tavel 466). Fuckel perhaps did not examine that collection with the microscope when he misidentified the twigs as *Fagus*, otherwise he would not have overlooked the much larger spores. In contrast, Rehm (1893: 770 fig. 3–4, 781) mainly reported the characteristics of *H. lepismoides* by omitting the smaller spore size of *H. serotinus*.

In Fuckel's specimen of *H. lepismoides* (Oestrich, undated, S-F227300, on twigs of *Carpinus*) the asci were found to measure 150 × 12 µm and the spores 25–34(–36) × (5–)5.5–7(–7.5) µm (Fig. 8g). The spores are almost straight and possess 1–2 inconspicuous, 1–2 µm long setulae at each end. Ascus and spore size thus turned out to be much larger than indicated by Fuckel (1870: 313). The values given there (128 × 6 µm, 20–24 × 4 µm) actually fit the other specimen (FRE 1157) which represents true *H. serotinus*.

Rehm (1893: 770, fig. 3–4, 781) did not clearly specify the origin of his description and illustration, but his diagnosis and spore sketch on the specimen from Bentheim (Fig. 10b, Tavel 466, spores 30–36 × 5–6 µm, with 1–2 large oil drops, host unidentified) indicate that this was the main though not the only source of his presentation. The Bentheim specimen turned out to grow on *Carpinus* and to represent *H. lepismoides* (Fig. 8a–f, h–i), which explains the discrepancy in Rehm's (1893) description concerning the large spore size in combination with *Fagus* as substrate. The other two cited collections (FRE 1157 and the specimen from Spessart, both on *Fagus*) influenced his description only marginally.

It appears mysterious why Rehm refrained from including in his description the rather small measurements of asci and spores which he had documented on the label of the Spessart collection made in 1877, which represents genuine *H. serotinus*. Rehm's (1893: 770, fig. 4) spore drawing actually seems to be a modification of his original sketch on the Bentheim specimen by giving the spores a stronger curvature. Rehm apparently tried to include the Spessart collection,

though in both specimens his spore sketch does not show such a strong curvature. Also he modified the description by including a spore width of 4 µm and an oil drop number of up to four. In the Bentheim collection, *Calycina italica* (Sacc.) Baral is present as a mixtum, partly with *H. lepismoides* on the same twig fragment. It has subsessile apothecia and much smaller, septate ascospores (†8–11.5 × 2–2.8 µm), but Rehm did not mention an associated species on the label.

Although Rehm did not find essential differences between *Helotium serotinum* on twigs of *Fagus* and *H. virgultorum* on twigs of *Alnus*, *Fraxinus*, *Quercus* and *Ilex*, he kept the two taxa as separate species. Because Rehm (1893: p. 770, fig. 1–2) stated "alder twigs" in the legend to *Helotium serotinum*, his illustration of a twig with apothecia might in fact belong to *H. virgultorum* (*loc. cit.*: fig. 5).

Rehm listed *Helvella umbelliformis* Pers. and *Helvella aurea* Bolt. as synonyms of *Helotium serotinum*. *H. aurea* was synonymized with *Peziza serotina* already by Fries (1822: 119) who did not mention *H. umbelliformis*, however. The purely macroscopic description of *H. aurea* in Bolton (1789, 1799) indeed recalls *Hymenoscyphus serotinus*, though neither the host tree nor the seasonal occurrence is indicated. Therefore, *H. aurea* should be considered as *nomen dubium*. The same applies to *H. umbelliformis*, which was very briefly described by Persoon (1822: 346) as *Helotium umbelliforme*, who listed *Helvella aurea* as a synonym, but did not at all compare or mention his *Peziza serotina*.

Massee (1895: 241) described the spores of *Helotium serotinum* as "25–35 × 4–6 µm, usually slightly curved", very similar in size and shape to Rehm's statements. Although Rehm's and Massee's spore width does not fit at all *H. serotinum* as described by Fuckel, Rehm mentioned this discrepancy only in regard to spore length, and he also did not comment on the much wider asci he had observed (100–150 × 10–12 µm). Rehm's different concept of *H. serotinum* might explain why he believed that the fungus illustrated by Saccardo (1883, see Fig. 3f) is not conspecific. But also Bäumler (1897) confirmed Rehm's opinion on Saccardo's illustration, although he studied genuine *H. serotinus*, according to the drawing by Dennis (1956) from his material.

Feltgen (1901: 59) reported collections under the name *Helotium serotinum* from Luxembourg on stubs of *Fagus* and *Carpinus*. However, his specimens can hardly be conspecific with typical *Hymenoscyphus serotinus*, considering the rather large measurements of asci (170–195 × 10–15.5 µm) and spores (26–36 × 4–8 µm), and the spore sketches on his labels (Fig. 10c–d). The present re-examination of five specimens in LUX by the junior author, representing four collections, revealed that all concern *H. lepismoides* (Fig. 8j–m, p–s). According to his labels, Feltgen gained the above-mentioned measurements from the specimen from Fort Olizy, while he found shorter and wide asci (130–150 × 13–18 µm) and longer spores (30–40 × 5–8 µm) in that from Reckenthal. The spore measurements gained in the present re-examination concur very well with Feltgen's: when summarizing the data from all five specimens, a spore size of †(26–)29–35(–40) × (5–)5.5–7(–8) µm is obtained. Ascus length (†125–140 µm) was measured only in the specimen from Reckenthal, while ascus width is rather consistently in the range of †(10–)11–13(–13.5) µm. The original sketches on the labels all show dead asci, but Feltgen's rather large measurements might include also some living asci.

In two of Feltgen's collections the branches were evidently lying on the ground, which can be concluded from the attached grains of sand. In that from Fort Olizy Feltgen wrote "on dry branch of...", which argues for an exposed, perhaps attached branch. The host tree was given by him only for the specimen from Mersch as "?beech-?hornbeam" and for the unlocalized one as "Alnus". According to the wood anatomy, the host tree is *Carpinus* in all five specimens.

Ecology

H. lepismoides appears to be a rare species. The few presently known sites suggest a rather local, perhaps disjunct distribution, given that further reports of this species under a different name do not exist. Since its host tree is very common in Europe, we presume that *H. lepismoides* also shows some climatic or geological preferences. The presently known records suggest a subatlantic distribution and a preference for acidic but also slightly calcareous soils.

H. lepismoides was detected by M.T. Tholl about 25 years ago in her home village Doncols in the north of Luxembourg (Oesling). During the past years she repeatedly observed the species at the type locality, a ~100 years old and about 2 m tall hornbeam hedge that surrounds her house. The apothecia grew here always on attached twigs of *Carpinus* in the lower part of the hedge. Apart from this locality, the species was detected in recent years only in Sjöbo (Skåne, Sweden), again at a single locality, where the apothecia occurred in great abundance (S.Å. Hanson, pers. comm.). The geology in Doncols (Ardennes) is Devonian slate, therefore, the soil is rather acidic. A similar geology can be assumed for the German site near Oestrich (Taunus) where Fuckel collected. The three known locations from which Feltgen's specimen derive, are on slightly calcareous Luxembourg Sandstone (Lower Lias). At the Belgian site near Villers-sur-Semois the geology is a slightly calcareous Hettangian marl (Lower Lias) with some indication of slight acidity, and the vegetation a *Pulmonario-Carpinetum* with *Quercus* and *Carpinus* as dominant trees (A. Fraiture, pers. comm.). The specimen from Münster (Nordrhein-Westfalen) was probably over slightly calcareous Bentheim Sandstone (Lower Cretaceous), and that from Sweden (Sjöbo) on rather neutral Silurian shale covered by glacial sediments.

Specimens examined

(all on *Carpinus betulus* = *C.b.*):

SWEDEN: Skåne, Sjöbo, 4.2 km NE of Sjöbo, 3.5 km SE of Brandstad, 100 m, on twigs of *C.b.*, on wood, 2.XII.2004, S.Å. Hanson (S.Å.H. 04-426, 04-442, 04-443, H.B. 9832ø).

BELGIUM: Wallonia, Luxembourg, 18 km W of Arlon, 1 km SE of Villers-sur-Semois, 340 m, on wood of *C.b.*, 9.XII.1994, A. Fraiture (BR5020029815367, ex A.F. 2373, d.v.).

LUXEMBOURG: L'Oesling, Ardennes, 7 km W of Wiltz, Doncols, rue de village, 465 m, on wood of twigs of *C.b.*, 15.XII.1988, M.T. Tholl (M.T. 621, n.v.); – *ibid.*, ~25.XII.1988 (H.B. 3618). – *ibid.*, 14.I.1989, M.T. Tholl, G. Marson & H.O. Baral (M, ex H.B. 3656, holotype). – *ibid.*, 4.II.2013, M.T. Tholl (M.B. 1/2013). – Gutland, 3.7 km W of Mersch, Reckinger Barrière, 320 m, on wood of branch of *C.b.*, 3.XI.1896, J. Feltgen (LUX 42882, 42883, as "*Helotium serotinum*, ?*Fagus*-?*Carpinus*"). – 3.3 km WNW of Luxembourg, Reckenthal, 300 m, on wood of branch of *C.b.,* 8.XII.1900, J. Feltgen (LUX 42884, as "*H. serotinum*, log"). – 0.8 km NE of Luxembourg, Fort Olizy, 310 m, on wood of branch of *C.b.*, 18.XI.1900, J. Feltgen (LUX 42885, as "*H. serotinum*, dry branch"). – unlocalized, on wood of branch of *C.b.*, undated, J. Feltgen (LUX 42881, as "*H. serotinum*, *Alnus*").

GERMANY: Nordrhein-Westfalen, ~50 km NW of Münster, around Bentheim, ~50 m, on wood of twigs of *C.b.*, 3.XI.1889, F. v. Tavel, *det.* H. Rehm (S-F, Tavel 466, as "*Ciboria serotina* (Pers.)?", H.B. 9749ø). – HESSEN, Rheingau, ~10 km NE of Bingen, [?N of] Oestrich, ?200 m, on wood of twigs of *C.b.*, undated (autumn), L. Fuckel (S-F227300, as "*Helotium serotinum*, *Fagus*", H.B. 9752ø).

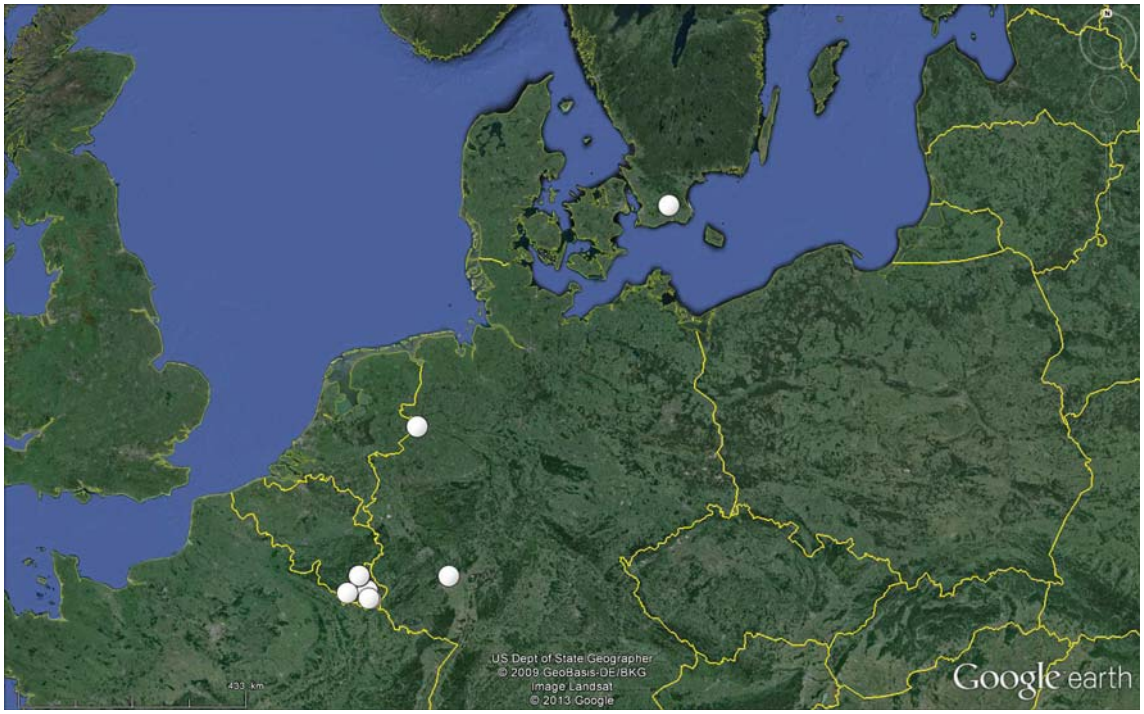

Fig. 11 – Known distribution of *Hymenoscyphus lepismoides*.

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References

Albertini I.B. (von) & Schweinitz L.D. (von) 1805. — *Conspectus fungorum in Lusatiae superioris Agro Niskiensi crescentium*. Lipsiae.

Bäumler J.A. 1897. — Beiträge zur Cryptogamen-Flora des Pressburger-Comitates. Die Pilze. *Verhandlungen des Vereins für Natur- und Heilkunde zu Presburg*, 9: 33–110 .

Baral H.-O. & Krieglsteiner G.J. 1985. — Bausteine zu einer Askomyzeten-Flora der Bundesrepublik Deutschland: In Süddeutschland gefundene inoperkulate Diskomyzeten – mit taxonomischen, ökologischen, chorologischen Hinweisen und einer Farbtafel. *Beihefte zur Zeitschrift für Mykologie*, 6: 1–160.

Baral H.-O. 1992. — Vital versus herbarium taxonomy: morphological differences between living and dead cells of ascomycetes, and their taxonomic implications. *Mycotaxon*, 44: 333–390.

Baral H.-O. 1996. — *Hymenoscyphus seminis-alni*, a new species of the *H. fructigenus*-complex. *Mycotaxon*, 60: 249–256.

Baral H.-O. & Bemmann M. (in prep.). — *Hymenoscyphus pseudoalbidus* vs. *Hymenoscyphus albidus*. A comparative light-microscopical study on the causal agent of European ash dieback and related foliicolous, stroma-forming species.

Baral H.-O., Galán R., Krisai-Greilhuber I., Matočec N. & Palmer J.T. 1999. — *Tatraea dumbirensis*, new records of a rare leotialean discomycete in Europe. *Österreichische Zeitschrift für Pilzkunde*, 8: 71–82, pl. V.

Baral H.-O., Galán R., López J., Arenal F., Villarreal M., Rubio V., Collado J., Platas G. & Peláez F. 2006. — *Hymenoscyphus crataegi* (*Helotiales*), a new species from Spain and its phylogenetic position within the genus *Hymenoscyphus*. *Sydowia*, 58 (2): 145–162.

Bi Z., Zheng G. & Li T. 1993. — *The macrofungus flora of China's Guangdong province*. Hong Kong, Chinese University Press.

Bolton J. 1789 (1788–1791). — *An History of Fungusses, growing about Halifax*. Vol. III. Huddersfield.

Bolton J. 1799. — *Geschichte der merkwürdigsten Pilze*. III. Theil, aus dem Englischen mit Anmerkungen von Carl Ludwig Willdenow. Berlin.

Breitenbach J. & Kränzlin F. 1981. — *Die Pilze der Schweiz*. Band 1 Ascomyceten. Luzern, Mykologia.

Carbone M. 2010. — *Hymenoscyphus trichosporus*, prima segnalazione Italiana. *Ascomycete.org*, 2 (3): 19–26.

Chmiel M.A. 2006. — *Checklist of Polish larger ascomycetes*. Biodiversity of Poland, vol. 8. W. Szafer Institute of Botany, Polish Academy of Sciences, 152 p.

Clark M.C. 1982. — Further discomycetes in Britain. *Bulletin of the British Mycological Society*, 16 (1): 60–66.

Colla A. 1837. — *Herbarium Pedemontanum juxta methodum naturalem dispositum, additis nonnullis stirpibus exoticis ad universos ejusdem methodi ordines exhibendos*. Vol. 7: 1–672. Turin.

Cumino U. 1805. — Fungorum vallis Pisii specimen. *Mémoires de l'Académie imperial des Sciences de Turin*, 13: 202–269.

Delivorias P., Dimitriadis I., Gonou-Zagou Z. & Kapsanaki-Gotsou E. 2010. — Some interesting species of *Hymenoscyphus* from Greece. *Mycologia Balcanica*, 10: 87-92.

Dennis R.W.G. 1956. — A revision of the British *Helotiaceae*. *Mycological Papers*, 62: 1–216.

Dennis R.W.G. 1978. — *British Ascomycetes*. Vaduz, J. Cramer.

Deny J. 2002. — *Helotiales recoltées dans les environs de Gérardmer*. (available on www.ascofrance.com/uploads/forum_file/291.doc)

Dimitrova E.G. 2002. — Discomycetous fungi of the *Leotiales* found on the *Betulaceae* in Bulgaria. *Turkish Journal of Botany*, 26: 253–258.

Dimitrova E.G. & Baral H.-O. 2005. — Chechlist of Bulgarian *Helotiaceae* (Ascomycetes). *Flora Mediterranea*, 15: 57–72.

Dougoud R. 2001. — Un ascomycète alnicole nouveau, *Hymenoscyphus trichosporus* sp. nov. *Documents mycologiques*, 30 (120): 11–14.

Dumont K.P. 1980. — *Sclerotiniaceae* XVI. On *Helotium rufo-corneum* and *Helotium fraternum*. *Mycotaxon*, 12: 255–277.

Dumont K.P. 1981. — *Leotiaceae* III. Notes on selected temperate species referred to *Helotium* and *Hymenoscyphus*. *Mycotaxon*, 13 (1): 59–84.

Dumont K.P. & Carpenter S.E. 1982. — Los Hongos de Colombia–VII: *Leotiaceae* IV. *Hymenoscyphus caudatus* and related species from Colombia and adjacent regions. *Caldasia*, 13 (64): 567–602.

Ellis M.B. & Ellis J.P. 1987. — *Microfungi on land plants, an identification handbook*. New enlarged edition. Slough, Richmond Pub.

Farr D.F., Bills G.F., Chamuris G.P. & Rossman A.Y. 1989. — *Fungi on plants and plant products in the United States*. St. Paul, Minnesota, APS Press.

Feltgen J. 1901. — *Vorstudien zu einer Pilz-Flora des Großherzogthums Luxemburg*. I. Theil, Ascomycetes, Nachträge II. Luxemburg.

Fries E. 1822. — *Systema mycologicum*. Vol. II, sect. 1. Lundae.

Fries E. 1849. — *Summa vegetabilium Scandinaviae. Sectio posterior*. Holmiae & Lipsiae.

Fuckel L. 1870 [1869]. — Symbolae mycologicae. *Beiträge zur Kenntnis der rheinischen Pilze. Jahrbücher des Nassauischen Vereins für Naturkunde*, 23–24: 1–459.

Galán R. & Ortega A. 1983. — Contributión al estudio de los *Helotiales* en la Península Ibérica (I). *Anales de la Universidad de Murcia (Ciencias)*, 41: 325–337.

Gillet C.C. 1879-1887. — *Champignons de France. Les discomycètes*. Alençon, E. de Broise.

Glawe D. A. (n.d.) – *Pacific Northwest Fungi Database*. Puyallup, Department of Plant Pathology, Washington State University. Retrieved August 6, 2013, from :
http://pnwfungi.wsu.edu/programs/searchFungusResultDetail.asp?fungusID=1832

Hassler U. & Hirschmann F. 1985. — Hilfsschlüssel zur mikroskopischen Bestimmung einheimischer Gehölze. *In*: Kaiser F. (ed.). *Neue Erkenntnisse in der Pilzkunde* (Abh. Naturhist. Ges. Nürnberg), 40: 47–55.

Huhtinen S. 1985. — Mycoflora of Poste-de-la-Baleine, northern Québec Ascomycetes. *Le Naturaliste canadien*, 112: 473–524.

Huhtinen S. 1990 [1989]. — A monograph of *Hyaloscypha* and allied genera. *Karstenia*, 29 (2): 45–252.

Jahn H. 1979. — *Pilze die an Holz wachsen*. Herford, Busse.

Jahn H. 1990. — *Pilze an Bäumen*. Berlin, Patzer. (2nd edition of Jahn 1979, revised by H. Reinartz and M. Schlag).

Keller J. 1985. — Studientagung der Wissenschaftlichen Kommission in Les Cernets, unter Mitarbeit von F. Lüthi, G. Plomb, H. Göpfert, M. Jaquenoud, R. Hotz, D. Laber, J.R. Chapuis, G. Lucchini. *Schweizerische Zeitschrift für Pilzkunde*, 63(8): 146–164.

Killermann S. 1935. — Bayerische Becherpilze 2. Teil. *Kryptogamen Forschungen*, 2(3): 255–296, pl. 4–5.

Korf R.P. & Zhuang W.-Y. 1985. — A synoptic key to the species of *Lambertella* (*Sclerotiniaceae*), with comments on a version prepared for TAXADAT, Anderegg's computer program. *Mycotaxon*, 24: 361–386.

Krieglsteiner G.J. 1993. — *Verbreitungsatlas der Großpilze Deutschlands (West)*. 2. Schlauchpilze. Stuttgart, Ulmer.

Krieglsteiner L. 1999. — Pilze im Naturraum Mainfränkische Platten und ihre Einbindung in die Vegetation. — *Regensburger Mykologische Schriften*, 9: 1–905.

Krieglsteiner L. 2004. — Pilze im Biosphären-Reservat Rhön und ihre Einbindung in die Vegetation. *Regensburger Mykologische Schriften*, 12: 1–770.

Lagarde J. 1902. — Champignons du massif du Ventoux. *Bulletin de la Société mycologique de France*, 18: 328–378.

Lagarde J. 1906. — Contributions à l'étude des Discomycètes charnus (suite). *Annales Mycologici*, 4(3): 203–256.

Lizoň P. 1992. — The genus *Hymenoscyphus* (*Helotiales*) in Slovakia, Czechoslovakia. *Mycotaxon*, 45: 1–59.

Lüderitz M. 2001. — *Die Großpilze Schleswig-Holsteins - Rote Liste*. Band 1: Grundlagen und Schlauchpilze (Ascomycetes). Flintbek.

Massee G. 1895. — *British Fungus-Flora*. A Classified text-book of mycology. Vol IV. London, G. Bell & Sons.

Migula W. 1913. — *Kryptogamen-Flora von Deutschland, Deutsch-Österreich und der Schweiz*. Band III. Pilze. 3. Teil. 2. Abteilung. Ascomycetes. Gera.

Milekhin D.I. & Prokhorov V.P. 2008. — Widespread species of family *Leotiaceae* from forest parks of Moscow. *Moscow University Biological Sciences Bulletin*, 63 (4): 178–183.

Persoon C.H. 1801. — *Synopsis methodica fungorum*. Pars prima. Göttingen.

Persoon C.H. 1822. — *Mycologia Europaea*. Sectio prima. J.J. Palmius, Erlangen.

Phillips W. 1887. — *A manual of the British discomycetes* with description of all the species of fungi hitherto found in Britain, included in the family and illustrations of the genera. London, Kegan Paul, Trench & Co.

Pop A. & Fouchier F. 1999. — *Crepidotus epibryus*, *Hymenoscyphus serotinus* et *Psathyrella fulvescens* var. *brevicystis*. Taxons récoltés aux Journées Mycologiques FAMM-FMDS à Annot. *Bulletin de l'AEMBA*, 32: 13–19.

Rehm H. 1893. — *Die Pilze Deutschlands, Oesterreichs und der Schweiz*. III. Abteilung: Ascomyceten: Hysteriaceen und Discomyceten. Leipzig, E. Kummer.

Roberts P.J. & Legon N.W. 2003. — Fungal specimens of James Bolton at Kew. *Kew Bulletin*, 58: 759–761.

Rubio E., Miranda M. A., Linde J. & Sánchez J.A. 2010. — *Biodiversidad Fúngica del Parque Natural de Somiedo*. Fundación Biodiversidad & Ayuntamiento de Somiedo.

Runge A. 1981. — Die Pilzflora Westfalens. *Abhandlungen aus dem Landesmuseum für Naturkunde zu Münster in Westfalen*, 43 (1): 3–135.

Saccardo P.A. 1883. — *Fungi Italici autographice delineati*. [pl. 1281-1440]. Patavia.

Saccardo P.A. 1889. — *Sylloge Fungorum*. Vol. 8: i–xvi, 1–1143. Patavia.

Sacconi S. 1983. — *Polydesmioideae* e *Helotioideae* (famiglia delle *Helotiaceae*). *Bollettino del Gruppo micologico G. Bresadola*, 26: 195–208.

Schieferdecker K. 1954. — *Die Schlauchpilze der Flora von Hildesheim*. Hildesheim, G. Gerstenberg.

Schroeter J. 1908. — *Die Pilze Schlesiens, zweite Hälfte*. Breslau, J.U. Kern.

Schulzer von Müggenburg S. 1885. — Einige neue Pilz-Spezies und Varietäten aus Slavonien. *Hedwigia*, 4: 129–151.

Schweinitz L.D. (von) 1822. — Synopsis fungorum Carolinae superioris, edita a D. F. Schwaegrichen. *Schriften der naturforschenden Gesellschaft zu Leipzig*, 1: 20–132.

Seaver F.J. 1951. — *The North American Cup-fungi (Inoperculates)*. New York, Hafner Publishing.

Sharma M.P. 1991. — Diversity in the Himalayan *Hymenoscyphus* S.F. Gray: an overview. *In*: S.P. Khullar & M.P. Sharma (eds.). *Himalayan botanical researches*. New Delhi, Ashish Publishing House: 107–211.

Shaw C.G. 1973. — Host fungus index for the Pacific Northwest - I. Hosts. *Washington Stat) Agricultural Experiment Station, Bulletin*, 765: 1-121 (not seen).

Somà V. 2003. — Ugo Maria Cumino: certosino, botanico e micologo della fine del '700. *Revue Valdôtaine d'histoire naturelle*, 57: 107-114.

Spooner B.M. 1987. — *Helotiales* of Australasia: *Geoglossaceae*, *Orbiliaceae*, *Sclerotiniaceae*, *Hyaloscyphaceae*. *Bibliotheca Mycologica*, 116: 1–711.

Svrček M. 1985 [1984]. — A taxonomic revision of inoperculate discomycetes described by J. Velenovský in the genus *Helotium*, preserved in National Museum, Prague. *Acta Musei Nationalis Pragae*, XL, B (3–4): 129–215.

Svrček M. 1986. — Discomycetes from West Bohemia. *Folia musei rerum naturalium Bohemiae occidentalis - Botanica*, 24: 1–29.

Tănase C., Pop A. & Manic Ş. 1999. — Des espèces des macromycètes collectées des différentes régions Françaises. *Analele Ştiinţifice ale Universităţii "Al. I. Cuza", Iaşi, Biologie Vegetală, Ser. IIa*, 45: 123–131.

Tai F.L. 1979. — *Sylloge fungorum sinicorum*. Beijing, Science Press, Academica Sinica, 1527 p. (not seen).

Teng S.C. 1934. — Notes on discomycetes from China. *Sinensia*, 5 (5–6): 431–465.

Teng S.C. 1963. — *Fungi of China*. Beijing, Science Press, 808 p. (in Chinese).

Teng S.C. 1996. — *Fungi of China*. Ithaca, Mycotaxon Ltd, 586 p.

Thind K.S. & Singh H. 1971. — The *Helotiales* of India – XV. *Journal of Indian botanical Society*, 50: 301–308.

Traverso J.B. 1910. — *Sylloge Fungorum*. Vol. 19 (Index iconum fungorum A-L): i–xi, 1–1158.

Velenovský J. 1934. — *Monographia discomycetum Bohemiae*. Pars II. Praha.

Wang Y.Z. 2004. — Two species of *Lanzia* new to Taiwan. *Fungal Science*, 19: 31–34.

White W.L. 1942. — Studies in the genus *Helotium*, I – A review of the species described by Peck. *Mycologia*, 34: 154–179.

White W.L. 1943. — Studies in the genus *Helotium*, III - History and diagnosis of certain European and North American foliicolous species. *Farlowia*, 1 (1): 135–170.

Wöldecke K. 1998. — Die Großpilze Niedersachsens und Bremens. *Naturschutz und Landschaftspflege in Niedersachsen*, 39: 1–536.

Zahlbruckner A. 1912. — Schedae ad "Kryptogamas exsiccatas" editae a Museo Palatino Vindobonensi, Centuria XX. *Annalen des K. K. Naturhistorischen Hofmuseums*, XXVI: 155–182 (–242).

Zheng H.D. & Zhuang W.-Y. 2013. — Four new species of the genus *Hymenoscyphus* (fungi) based on morphology and molecular data. *Science China Life Sciences*, 56 (1): 90–100. doi: 10.1007/s11427-012-4429-1

Zhuang W.-Y. 1993. — *Lanzia serotina* in culture. *Acta Mycologica Sinica*, 12 (1): 85–86.

Zhuang W.-Y. 1996 [1995–1996]. — The genera *Lambertella* and *Lanzia* (*Sclerotiniaceae*) in China. *Mycosystema*, 8-9: 15–38.

Zhuang W.-Y. 1998. — *Flora Fungorum Sinicorum*. Vol. 8. *Sclerotiniaceae* et *Geoglossaceae*. Beijing, Science Press (in Chinese, not seen).

Zhuang W.-Y. & Liu C.-Y. 2007. — Taxonomic reassessment of two taxa of helotialean fungi. *Mycotaxon*, 99: 123–131.

Zhuang W.-Y. & Wang Z. 1998. — Discomycetes of tropical China. I. Collections from Hainan Island. *Mycotaxon*, 67: 21-31.

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