# A RECONSIDERATION OF THE CLASSIFICATION OF THE HYGROPHORACEAE

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Much splitting of the Friesian genus Hygrophorus (1835) has taken place in the last two decades, particularly after anatomical characters were introduced into the taxonomy of the agarics. In the second edition of Singer's "Agaricales in Modern Taxonomy" (1962), this fragmentation climaxed with the recognition of no less than eight genera to cover this same group of agarics and its allies: the recent treatment by Moser (1967) of the European members follows Singer's arrangement very closely. However, this is certainly not the concept expressed in Hesler & Smith's account of the North American species of Hygrophorus (1963) for although the groupings are very much the same they are here found at only sectional level within a single genus. This approach parallels that of the New Check List of British Agarics and Boleti (1960) but in view of the preparation of a manual of the British agaries to be found in the British Isles it was considered necessary to review critically the evidence for and against the two extremes. It has long been realised that because the fungi are simply constructed organisms the characters available for use in their classification are few when compared with the number utilised in the classification of flowering plants. There is little doubt that because of this, and the fact that the fungi have not been critically examined for as long a period as flowering plants, extreme views often exist side by side.

#### DELIMITATION OF THE GENUS HYGROCYBE

Differences in the structure of the hymenophoral trama have been widely used in the more recent approaches to the classification of agaric genera. However, many authorities have questioned the validity of the use of this character to the degree carried out by Singer and his school unless it is positively correlated with several additional characters.

It has been shown by experimental studies in other groups (Watling, 1965 and Disbrey & Watling, 1967) that changes take place in the trama during maturation of the carpophore and Smith has found this also to be the case in Catathelasma (personal communication). The present authors therefore are prepared to accept that the bilateral arrangement of the hyphae in the hymenophoral trama is far more important taxonomically than the differences which exist between the so-called regular and irregular arrangements exhibited in other hygrophori, particularly when the bilateral nature is correlated with the frequent development of a veil and a very probable mycorrhizal habit. In fact, one could well believe that the regular and irregular trama types are extremes of a single morphological series which can be completely bridged by examination of a wide range of species at

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different stages in their development. Even in certain species where the hymenophoral trama does appear to be irregular when immature, this can take on a more regular aspect when the elements of the subhymenium begin to expand and orientate themselves, and, at the other extreme, disorganization sometimes takes place in the trama of a regular type as maturity approaches e.g. Hygrophorus marchii.

It appears that Donk (1962), although he does not state it in so many words, is also of the opinion that the Hygrophorus conicus and H. pratensis groups are more closely related than the H. eburneus group is to either H. conicus or H. pratensis. The opinion is expressed in his nomenclatural changes since he assigns the last two to the genus Hygrocybe and H. eburneus and its allies to the genus Hygrophorus sensu stricto. Hesler & Smith (1963) have also expressed similar ideas as to the close relationship of the H. conicus and H. pratensis groups. This approach will undoubtedly be unpopular for it does mean that some of our more common pasture-loving hygrophori will take on a generic name that is for a time less familiar, but we feel this solution is far more logical than previous schemes.

Our choice of names however is naturally 'very rigorously controlled and guided by the International Code of Botanical Nomenclature (1965) and by the nature of the species which we consider as type of the genus Hygrophorus. Although Earle (1909), Murrill (1916) and Imai (1938) have all indicated Hygrophorus chrysodon Batsch ex Fries as type and Clements & Shear (1931) suggested Hygrophorus minitatus Fr., we prefer to typify the genus Hygrophorus Fries, 1835, by Hygrophorus demureus Bull. ex Fr.; in so doing we follow Singer & Smith (1946), Donk (1949 and 1962), Dennis (1953) and Dennis, Orton & Hora (1960).

With this treatment, Hygrophorus hypothejus, H. chrysaspis, H. pustulatus, H. agathosmus and all their allies are retained in the genus Hygrophorus whereas H. pratensis and allies and the H. conicus, H. miniatus and H. coccineus groups are placed in Hygrocybe, the first name at generic level available for consideration. In agreement with Donk (1962) and Kühner & Romagnesi (1953), Hygrophorus camarophyllus, formerly included with H. pratensis in the subgenus Camarophyllus, is here considered to be closer to H. eburneus and is therefore retained in Hygrophorus. Although there is full agreement that Hygrocybe is a valid grouping, some disagreement exists or has existed amongst mycologists as to the species which must be selected as type. Like Singer (1962), regardless of his earlier convictions (1959), we follow Donk (1949) and select Hygrocybe conica (Fr.) Kummer as type species for Hygrocybe.

Whilst accepting the grouping above, we still consider that it would be very wrong not to recognies some differences between Hygrophorus pratensis and its allies and the H. conicus—H. coccineus group and reflect these differences in our scheme of classification; we have satisfied this feeling at sections level. It appears that Donk (1962) has already made the necessary erection of Cuphophyllus as a subgenus to fulfil this concept; new combinations where necessary are listed below, although Moser (1967) has made many of the recombinations in Hygrocybe which arise on accepting the genus. In order to complete this task for the British species and draw our procedure into line with the 'New Check List of British Agaries & Boleti' (1960) and the proposed agair Flora, the following nomenclatural changes are necessary:—

#### Hygrocybe section Hygrocybe

H. clivalis (Fr.) Orton & Watling, comb. nov.

Basionym: Hygrophorus fornicatus\* H. clivalis Fr., Monographia Hymenomycetum Sueciae II, 135 (1863).

H. conicoides (Orton) Orton & Watling, comb. nov.

Basionym: Hygrophorus conicoides Orton in Trans. Brit. Mycol. Soc. 43: 262 (1960).

H. lepidopus (Rea) Orton & Watling, comb. nov.

Basionym: Hygrophorus lepidopus Rea in Trans. Brit. Mycol. Soc. 12: 214 (1927).

H. sciophanoides (Rea) Orton & Watling, comb. nov.

Basionym: Hygrophorus sciophanoides Rea in British Basidiomycetae 303 (1922). (= H. sciophanus s. Cke., Cooke, Illust. no. 905, t. 937 fig. A).

H. substrangulata (Orton) Orton & Watling, comb. nov.

Basionym: Hygrophorus substrangulatus Orton in Trans. Brit. Mycol. Soc. 43: 269 (1960).

#### Hygrocybe section Cuphophyllus (Donk) Orton & Watling, comb. nov.

Basionym: Hygrocybe subgenus Cuphophyllus Donk in Nova Hedwigia Beihefte 5 (1962).

H. berkeleyi (Orton) Orton & Watling, comb. nov.

Basionym: Hygrophorus berkeleyi Orton in Trans. Brit. Mycol. Soc. 43: 259 (1960).

H. cinerea (Fr.) Orton & Watling, comb. nov.

Basionym: Hygrophorus cinereus Fr., Sverg. atl. Svamp. t. 30 (1861).

H. colemanniana (Blox. apud. Berk. & Br.) Orton & Watling, comb. nov. Basionym: Hygrophorus colemannianus Bloxam apud Berkeley & Broome in Ann. & Mag. Nat. Hist. 2 Ser. 13: 396 (1854).

H. lacma (Fr.) Orton & Watling, comb. nov.

Basionym: Hygrophorus subradiatus\* lacmus Schum. ex Fr., Epicrisis Systematis Mycologici 329 (1838).

H. nivea (Fr.) Orton & Watling, comb. nov.

Basionym: Hygrophorus niveus Scop. ex Fr., Epicrisis Systematis Mycologici 327 (1838).

H. russocoriacea (Berk. & Miller) Orton & Watling, comb. nov.

Basionym: Hygrophorus russocoriaceus Berk. & Miller in Berkeley, Outlines of British Fungology, 199 (1860).

H. subradiata (Secr.) Orton & Watling, comb. nov.

Basionym: Agaricus subradiatus Schum. ex Secr., Mycographie Suisse 783 (1833).

H. subviolacea (Peck) Orton & Watling, comb. nov.

Basionym: Hygrophorus subviolaceus Peck in N.Y. State Mus. Ann. Rept. 53: 842 (1901).

H. virginea (Fr.) Orton & Watling, comb. nov.

Basionym: Agaricus virgineus Wulf. ex Fr., Systema Mycologicum 100 (1821).

Since the publication of the New Check List, Watling (1965) has redescribed Hygrophorus Isporinus Fr. from British material. It must also be drawn to mycologists' notice that Hygrophorus fuscescens Bres. appears to exist in the British Isles\*. Material agreeing in all respects with Bresadola's plate and description has been collected in a rough pasture at Tomich, Inverness-shire, 30 viii 1957. Unfortunately material was not preserved. Nevertheless, the following combinations are proposed:

Hygrocybe leporina (Fr.) Orton & Watling, comb. nov.

Basionym: Hygrophorus leporinus Fr., Epicrisis Systematis Mycologici 326 (1838).

H. fuscescens (Bres.) Orton & Watling, comb. nov.

Basionym: Hygrophorus fuscescens Bres. in Iconographia Mycologica 7: 330 (1928).

## Anomalous candidates for Hygrocybe

Some problems are experienced when trying to place certain British hygrophori in infrageneric categories; foremost in our minds are Hygrophorus metapodius and the H. hymenocephalus group. The former has amyloid basidiospores and because of this is anomalous in the genus but nevertheless we prefer to retain it in Hygrocybe for it has affinities with the H. ovina–H. nitrata complex, a group which we regard as fairly closely related to the typical, but more brightly coloured Hygrocybe spp.—unlike Herink who has rected (1959) the new genus Neohygrocybe with Hygrophorus ovinus as type. However, we do feel it valuable to recognise some distinction between the Hygrocybe conica–H. coccinea group and the dull coloured, strong smelling, red- or brown-staining H. ovina complex; we have therefore taken up Herink's name at sectional level, as indicated in the conspectus below.

Amyloidity also occurs in a second part of Hygrophorus, as the genus is outlined by Hesler & Smith (1963), for H. anglesianus Smith & Hesler (1942) which is placed in subgenus Pseudohygrophorus is said to be closely related

to the Hygrophorus pratensis group and has amyloid spores.

Superficially in the field Hygrophorus metapodius resembles in many ways Tricholoma atroviolaceum of North West America which has been collected by one of us (RW); Hesler & Smith (1963) have already erected a suitable subgenus for this fungus and we have accepted this after slight modifications so that it might fit into our proposed scheme. We find it acceptable to have amyloid and non-amyloid spored species within a single genus as already done in Mycena and Dermoloma, and more recently by Bas (1965) in

\* Since the above was written, several populations of a fungus also referable to this taxon were seen during September 1968 in Mull, Argyllshire. Material is deposited at E and BM.

Squamanita, although we would be very unhappy to place an agaric which lacked amyloid ornamentation on the spores in the Russulaceae. However, careful work is still required, for a second species, Hygrophorus translucens (Murr.) Murr. as described by Hesler & Smith (1963) may have affinities with Hygrophorus metapodus or may even be a species of Mycena. Smith (pers. comm. 1963) has frequently drawn attention to the affinities of certain hygrophori with the Tricholomataceae particularly certain species of Momphalina and Mycena and this can be seen in the field e.g. Omphalina luteolilacina and O. luteovitellina; Mycena lilacifolia and Hygrophorus xanthochrous; both pairs have been collected in the field by one of us (RW). The last two species form a very close species pair following Smith's general concept, although Omphalina luteolilacina also approaches them both in general facies.

Hygrophorus hymenocephalus, atropunctus, foetens, micaceus and schulzeri have a "cellular cap cuticle" and so are anomalous in a group of fungi which is characterised by a filamentous cap cuticle structure. Because these five species are anomalous in the Hygrophoraceae it was at first felt that they would be better placed elsewhere in the Agaricales, for thick gills and pale spores are not confined to the Hygrophoraceae but also occur in the Tricholomataceae (e.g. Dermoloma, Laccaria and Omphalina). Furthermore, since one of the generic characters of Dermoloma is a "cellular cap cuticle" and the other characters of gill and over-all dull colour seem to be in agreement, this appeared to be a genus whose limits should be explored; if found suitable there would then be no need to make a fresh genus. This appeared even more of a suitable disposition, for the recently described D. josserandii is even more bygrophoroid in general appearance than either D. cuneifollum or D. attocinereum.

Basidial length is one of the characters used to differentiate the Hygro-phoraceae, its members having relatively long, thin basidia, often up to 60 or 70µ long or even longer and 5-7 times as long as broad. Examination of basidia of H. hymenocephalus, atropunctus, foetens, micaceus and schulzeri shows that although only in the first do the basidia approach the length commonly found in the Hygrophoraceae, the length/breadth ratios of the basidia, and length of basidium/length of spore ratios of the four other agarics are typical for the same family whilst the basidial length of the British species of Dermoloma are typical of the Tricholomataceae. The cap cuticle in Dermoloma consists of a fairly compact and continuous hymeniform layer as opposed to an irregular loosely arranged layer of short, swollen and erect end-cells as in the H. hymenocephalus group and therefore it was finally concluded that the fungi under discussion are in fact members of the Hygrophoraceae; this is in agreement with the designation made by Singer (1662) and Moser (1667).

Hygrophorus schulzeri is intermediate between the H. hymenocephalus group and H. nitratus; because of this the whole H. hymenocephalus is better treated as a section of Hygrocybe and not as the separate genus Hygrotrama as suggested by Singer (1959), or in the allegedly synonymous genus Aerusimospora as recently emended by Singer (1962).

Because the spores of *Hygrophorus schulzeri* show some rugulosity when mounted in Melzer's reagent and in alkali, a feature also noted by Jacqueline Perreau (1967), and the cap cuticle is very loosely arranged with only a small

proportion of cells orientated as if in a hymeniform epicutis it was considered better to place this species in a separate section of *Hygrocybe*; the section proposed is based on a genus originally suggested by Herink (1959)

for the same fungus, as indicated below in the conspectus.

The reasons for accepting Hygrotrama and not Aeruginospora are: 1, it is felt more field work is required on the type species Aeruginospora singularis, a tropical fungus considered congeneric with Hygrophorus hymenocephalus and H. schulzeri by Singer; 2, certain anomalies exist in the original description of the genus and type species; 3, the species on which Hygrotrama is based, H. dennisianum Singer, is well documented as are the three other species, two of which, although uncommon, appear to be widespread in Europe.

We follow Hesler & Smith in the adoption of *Hygrotrama* at sectional level, not however in *Hygrophorus* but in *Hygrocybe*. The necessary combinations are made herewith.

Hygrocybe section Hygrotrama (Singer) Orton & Watling, comb. nov. Basionym: Hygrotrama Singer in Sydowia 12: 221 (1959).

H. atropuncta (Fr.) Orton & Watling, comb. nov.

Basionym: Agaricus (Clitopilus) atropunctus Pers. ex Fr. in Systema Mycologicum 195 (1821).

H. foetens (Phillips apud Berk. & Br.) Orton & Watling, comb. nov. Basionym: Hygrophorus foetens Phillips apud Berkeley & Broome in Ann. & Mag. Nat. Hist. 5, Ser. 3: 202 (1879).

H. hymenocephala (Smith & Hesler) Orton & Watling, comb. nov.Basionym: Hygrophorus hymenocephalus Smith & Hesler in Elisha Mitchell Sci. Soc. Journ. 56: 311 (1940).

H. micacea (Berk. & Br.) Orton & Watling, comb. nov.Basionym: Hygrophorus micaceus Berk. & Br. in Ann. & Mag. Nat. Hist.5, Ser. 3; 202 (1879)

### Material examined (E):

Hygrocybe atropuncta (as Eccilia): Henbury, 9 x 1879 (ex Herb. C. E. Broome); Swaledale near Richmond, Yorkshire, 1 x 1956, Orton 815; Skellingthorpe, Lincolnshire, 5 x 1957, Orton 1186; Ingleton, Yorkshire, 28 vii 1958, Henderson 4128.

H. Joetens: On lawn, Shrewsbury, W. Phillips (Herb. M. C. Cooke, Fungi Brit. Exsicacti No. 612-type?); Juniper Hill, Mickleham, Surrey, 2 viii 1954, Orton 230; Park Wood, Nork, Banstead, Surrey, 13 x 1958, Orton 1547. H. hymenocephala: Badger Falls, Glen Affric, Inverness-shire, 18 xii 1958, Orton 1544.

H. micacea: Skellingthorpe Wood, Lincolnshire, 5 ix 1957, Orton 1188.

H. metapodia: In rough pasture, in huge troop, Tomich, Inverness-shire, 28 viii 1957 (2 collections: Orton 1201; Watling 77C); in limestone pasture, Tornapress, Kishorn, Ross & Cromarty, 13 ix 1963, Watling 743C; fixed dune system near old burial ground, Kilmory, Isle of Rhum, 26 viii 1964, Watling 827C.

H. schulzeri: the Cleeves, Membury, Devon, 29 x 1957, Orton 1212, 2 xi 1957, Orton 1223; Great Down, Membury, Devon, 3 xi 1957, Orton 1214; in pastures, Clapham Wood, Yorkshire, 27 viii 1958, (2 collections: Henderson 4108 and Watling 118C); in base flushed pasture, Comrie Farm, Coshieville, Perthshire, 2 x 1961, Henderson 6855.

CLITOCYBE ASTEROSPORA AND THE GENUS HYGROASTER SINGER (1959)

The opportunity is here taken to discuss another so-called hygrophoroid agaric i.e. Clitocybe or Omphalia asterospora, more recently placed in Rhodocybe by M. Lange & Skifte (1967). Probably because of its ornamented basidiospores, Singer transferred this species to Hygroaster, a genus based on the tropical Hygrophorus nodulisporus Dennis; it, however, unlike H. nodulisporus possesses gills of normal shape and thickness which are not at all waxv

Hesler & Smith (1963) treat Hygroaster as a subgenus of Hygrophorus but we feel that neither of these treatments is necessary for Clitocybe asterospora (Lange) Moser, particularly after seeing herbarium material of the type species and the accompanying coloured illustrations made by R. W. G. Dennis

We have critically examined the basidia of material assigned to Omphalia asterospora as originally described by J. Lange (1938) and found them to be typically tricholomoid being 25-35 (-40) x 5-10μ (sterigmata 2.5-4 (-8)μ) with basidiospores 6-8 x 5-7 \u03c4. Because of what has already been said concerning the delimitation of the Hygrophoraceae we feel these facts coupled with the gill type are very significant in excluding this species and its close allies from the Hygrophoraceae. It is pertinent to note here that Singer (1962) has suggested connections between the two families, Hygrophoraceae and Tricholomataceae; it may be later found that one such connection is through the Clitocybe asterospora group, Jakob Lange's fungus was transferred by Moser (1953) to Clitocybe which it approaches in colour, stature and anatomy but not basidiospore morphology, although some typical members of the genus Clitocybe, e.g. C. flaccida, have punctate basidiospores. This is in contrast to its placing in Omphalina where it is more anomalous, although there is some feeling in some quarters to consider Clitocybe and Omphalina purely one large morphological series.

There is evidence of at least one other agaric, if not two, in this complex present in the British Flora; one is much darker than Clitocybe asterospora and grows amongst Empetrum and on wet Rhacomitrium heaths, and the other is included by Kühner & Romagnesi (1953) under the name Clitocybe obolus Fries in the sense of Quelet; the former is Rhodocybe borealis M. Lange & Skifte (1967)\* and has tricholomoid basidia, but specimens have been met with rarely and further collections will be worthy of very careful study. Although we do not agree with M. Lange & Skifte's disposition primarily because we do not think the colour of spore deposit and coloration of fruit-body fit neatly into Rhodocybe, we feel that what is worthy of further analysis is the distribution of pseudocystidia in our British Clitocybe spp.

Clitocybe borealis (M. Lange & Skifte) Orton & Watling, comb. nov.
 Basionym: Rhodocybe borealis M. Lange & Skifte in Acta Borealia A. Scientia No. 23-45 (1967).

Material in Edinburgh (E) has been redetermined as follows:-

Clitocybe asterospora (Lange) Moser.

- I Loch Craiglush, Dunkeld, Perthshire 6 x 1956, Orton 767.
- 2 In moss under Fagus, Balerno, Midlothian 17 x 1958, Henderson 4331.

3 Black Wood of Rannoch, 1 x 1961, Orton 2332.

- 4 In moss amongst Vaccinium myrtillus and Alchemilla alpina, Beinn Bahn, Kishorn, Ross-shire, 13 ix 1963, Henderson & Watling, Henderson 7143.
- 5 In bog amongst Sphagnum, Minishal, Isle of Rhum, 29 vii 1964, Watling 873C.

6 Camghouran, Perthshire, 4 x 1964, Orton 2648.

7 Black Wood of Rannoch, Perthshire, 31 x 1965, Orton 2704.

Clitocybe borealis (M. Lange & Skifte) Orton & Watling.

- Amongst Rhacomitrium, 2,800 ft. North slopes of Beinn Ghlas, Perthshire,
   5 viii 1958, Henderson 4087.
   In dwarf shrub community, Empetrum, 2,500 ft. Ghlas Maol. Glenshee,
- Perthshire, 28 ix 1962, ex D. M. Henderson.
- 3 Amongst Rhacomitrium 3,200 ft. Ben Wyvis, Ross-shire, Henderson & Watling, 8 ix 1963, Henderson 7096.

SUMMARY OF ARRANGEMENT FOR BRITISH MEMBERS OF THE HYGROPHORACEAE

Hygrophorus Fries in Fl. Scan. 339, (1835). Type species: H. eburneus

(Bulliard ex Fries) Fries.

Syn.: Limacium (Fr. ex Fr.) Kummer in Führ. Pilzk. 25, 118 (1871).

Hygrocybe (Fr.) Kummer in Führ. Pilzk. 26, 111 (1871). Type species: H. conica (Scopoli ex Fries) Kummer.

Syn.: Camarophyllus (Fr.) Kummer in Führ. Pilzk. 26, 117 (1871).
(=Hygrophorus sect. Camarophyllopsis Hesler & Smith, 1963). Type species Camarophyllus pratensis (Pers. ex Fr.) Kummer.

Camarophyllopsis Herink in Acta Mus. Bohem. Septentr. Liberecensis 1: 61 (1959). Type species: Camarophyllopsis schulzeri (Bres.) Herink (

≤ Hygrophorus sect. Camarophyllopsis Hesler & Smith).

Gliophorus Herink in Acta Mus. Bohem. Septentr. Liberecensis 1: 80 (1959). Type species: Gliophorus psittacinus (Schaeff ex Fr.) Herink. Godfrinia Maire in Bull. Soc. mycol. Fr. 18 (suppl.) 116 (1902). Type species: Godfrinia conica (Scop. ex Fr.) Maire (selected).

Hodophilus Heim in Rev. Mycol. 30: 231 (1966). Type species: Hodophilus foetens (Phillips) Heim.

Hygrotrama Singer in Sydowia 12: 22 (1959) (= Aeruginospora Höhnel sens. Singer, 1962 and Hygrophorus sect. Hygrotrama (Singer) Hesler & Smith (1963). Type species: Hygrotrama dennisianum Singer.

Neohygrocybe Herink in Acta Mus. Bohem. Septentr. Liberecensis 1: 70 (1959). Type species: Neohygrocybe ovina (Bull. ex Fr.) Herink.

Sect. 1. Hygrocybe. Type as above: H. conica (Scop. ex Fr.) Kummer.

Sect. 2. Amylohygrocybe (Hesler & Smith) Orton & Watling, comb. nov. Basionym: Hygrophorus sect. Amylohygrocybe Hesler & Smith in North American species of Hygrophorus, 246 (1963). Type species: Hygrocybe metapodia (Fr. ex Fr.) Moser.

Sect. 3. Camarophyllopsis (Herink) Orton & Watling, comb. nov.

Basionym: Camarophyllopsis Herink in Acta. Mus. Bohem. Septentr. Liberecensis 1: 61 (1959). Type species: Hygrocybe schulzeri (Bres.) Joss.

Sect. 4. Cuphophyllus (Donk) Orton & Watling, comb. nov.

Basionym: Hygrocybe subgenus Cuphophyllus Donk in Beihefte zur Nova Hedwigia 5: 45 (1962). Type species: Hygrocybe pratensis (Pers. ex Fr.) Donk.

Sect. 5. Hygrotrama (Singer) Orton & Watling, comb. nov.

Basionym: Hygrotrama Singer in Sydowia 12: 221 (1959). Type: Hygrotrama demnisianum Singer in Sydowia 12: 221, '1958' (1959) = Hygrocybe dennisiana (Singer) Orton & Watling, comb. nov. cf. Hodophilus Heim, Champ. Europ. 2 196, 219, 1957: nomen nudum: later validated in Rev. Mycol. 3o: 231, 1966.

Sect. 6. Neohygrocybe (Herink) Orton & Watling, comb. nov.

Basionym: Neohygrocybe Herink in Acta. Mus. Bohem. Septentr. Liberecensis 1: 70 (1959). Type species: Hygrocybe ovina (Bull. ex Fr.) Kühn.

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