

NOTES ON HYGROPHORUS—II

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(With 36 Text-figures and Plate 20)

Hygrophorus (Hygrocybe) marchii Bres. and four closely related species are described, and a key to this group of species is given. One species is described as new, viz. *Hygrophorus phaeococcineus*.

Hygrophorus subsection *Coccinei* Bat. emend. Singer comprises brightly coloured species with broadly adnate gills and a dry, glabrous or somewhat fibrillose cap without squamules or a gelatinous pellicle (Singer, 1951: 152; Arnolds, 1974a: 169). This subsection includes some small-sized species with a cap less than 50 mm across, a stem less than 6 mm wide and, at least in young fruit-bodies, a red colour to the cap. These species are indicated below as the group of *Hygrophorus marchii* Bres. Among others *H. coccineus* (Schaeff. ex Fr.) Fr. is excluded from this group because of its larger size.

In recent years *H. marchii* has been described by many authors (see p. 244). As already observed by Singer (1969: 22) there are important discrepancies between several of these descriptions.

In order to assess the taxonomic significance of these differences I have studied a number of collections of this group from both Europe and the U.S.A. Besides *H. marchii* other European members of this group are *H. strangulatus* and *H. substrangulatus*, both described from Great Britain by Orton (1960: 267, 269). In addition a species already known to mycologists in the Netherlands for twenty years, is described here as *H. phaeococcineus* sp. nov. For the meaning of some terms and abbreviations used in this paper the reader is referred to my earlier note on *Hygrophorus* (Arnolds, 1974b).

I am very much indebted to Dr. C. Bas (Leiden), Dr. J. van Brummelen (Leiden), and to Mr. P. K. C. Austwick (London) for improving and correcting this paper. Thanks are also due to Mr. M. Bon (Lille), Drs. H. S. C. Huijsman (Beilen), Mr. P. D. Orton (Rannoch Station, Gr.-Br.), Dr. L. R. Hesler (Knoxville, U.S.A.), and Dr. R. Watling (Edinburgh) for sending me valuable collections and information.

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In the *H. marchii*-group the presence or absence of a constriction in the middle of the spores is frequently used as a key character. At the moment I find it difficult to decide on the taxonomic significance of this character, as I have not seen a single specimen of this group in which all the spores are constricted. On the other hand in only a few specimens constricted spores are completely lacking. This makes it necessary to determine the percentage of the spores in each preparation that are constricted. There are two complications. Firstly there are many spores with a shape intermediate between ellipsoid-oblong and constricted, and secondly the degree of constriction of a single spore depends on the side from which it is observed.

I have seen constrictions of spores more often in front-view than in side-view. The latter type seems to me more constant and of greater taxonomic importance, so that I have used this character in my key and descriptions. For the moment it is possible to distinguish two groups of taxa: one in which many spores are constricted (40–75% of the spores in side-view) and another in which only a few constricted spores occur (0–20% in side-view). Only in *H. substrangulatus*, otherwise characterized by large spores, do intermediate forms seem to occur regularly.

In certain other species of *Hygrophorus* the occurrence of constricted spores in part of the collections has not been used as a reason for distinguishing separate taxa, e.g. in *Hygrophorus ceraceus* (Wulf. ex Fr.) Fr. (Arnolds 1974a: 204, fig. 183; Orton 1960: 251) and *H. insipidus* (J. Lange) Lund. apud Lund. & Nannf. (Arnolds 1974a: 222, fig. 205; Orton 1960: 251).

Other problematic characters in the *H. marchii*-group are the degree of viscosity of the cap and the microscopical structure of the pileipellis. Both are influenced by climatological conditions and by the age of the carpophores. Moreover the thickness of the pileipellis is difficult to determine because a sharp border line between this tissue and the trama of the cap cannot be drawn, while measurements on dried specimens are strongly influenced by the quality of drying. In the following key and in the descriptions I have indicated as pileipellis the superficial layer of narrow hyphae (1.5–6 μm) as distinct from the broader hyphae underneath (5–15 μm), as seen in well-dried specimens.

In all specimens described here I have observed a more or less clearly differentiated layer between the pileipellis and the subparallel, radially disposed hyphae of the pileitrama. This tissue could be called a subcutis, using the terminology of Moser (1967). According to Bas (1969: 327) it is better to use the term '*subpellis*', analogous to 'pileipellis'. These are topographical terms free from etymological connections with descriptive terms like 'cutis'. The subpellis here consists of irregularly compacted interwoven hyphae with short, somewhat inflated cells, giving this tissue on radial section sometimes an almost cellular appearance as is the case in a hypodermal structure (e.g. Fig. 34).

In fresh specimens this layer contains the greatest concentration of vacuolar pigments. Of all authors describing *H. marchii*, only Bon (1974) pays attention to this special structure beneath the pileipellis. For the moment I cannot judge the taxonomic importance of this character for the delimitation of the *H. marchii*-group within

Hygrocybe. I observed a differentiated subpellis also in some collections of *H. miniatus* (Fr.) Fr. (Arnolds, 1974a: 184, 188).

In the field all species of the *H. marchii*-group can easily be confused with representatives of subsection *Squamulosi* Bat., especially with *H. miniatus* (Fr.) Fr. However, some fundamental microscopic differences exist, as is mentioned in the discussion on *H. strangulatus* below.

As a result of my investigations the following key has been prepared:

KEY TO THE SPECIES IN THE *Hygrophorus marchii*-GROUP IN EUROPE
(INCLUDING ONE NORTH AMERICAN SPECIES)

- 1a. Pileipellis composed of thin, gelatinized hyphae, 1.5–5 μ m broad (Figs. 10, 11, 15); cap slightly viscid at first. Spores 6.5–8.5(–10) \times 3.5–5 μ m 2
- b. Pileipellis composed of broader, non-gelatinized hyphae, (2.5–)3–7.5 μ m broad (Figs. 28, 34); cap dry. Spores often larger, 6.5–11.5(–12.5) \times 3.5–6.5(–7) μ m 3
- 2a. Spores in side-view not or rarely constricted (less than 20%; Figs. 3–6). Pileipellis rather compactly interwoven, 40–100(–120) μ m thick (Figs. 10, 11) *H. marchii*, p. 241
- b. Spores in side-view often constricted (more than 50%; Figs. 12, 13). Pileipellis loosely interwoven, 25–40 μ m thick, with stronger gelatinized hyphae (Fig. 15)
H. marchii sensu Hesler & Smith, p. 245
- 3a. Cap first scarlet, blood red or purplish red, discolouring orange-yellow with age, in well-dried fruit-bodies turning typically dark brown or dark orange-brown. Superficial hyphae of cap in fresh fruit-bodies with brown vacuolar pigment, in part also with greyish granulae and clots; brown pigment persistent in dried specimens and in KOH 5%. Spores (7–)7.5–11(–11.5) \times (3.5–)4–6.5(–7.5) μ m, not or only a small part (less than 20%) constricted in side-view (Figs. 21–24). Basidia relatively short: (26.5–)28.5–47.5(–49) \times (4.5–)5.5–9(–9.5) μ m (Fig. 26) *H. phaeococcineus*, p. 247
- b. Cap first vermilion or orange-red, discolouring orange-yellow with age, in well dried specimens turning ochre or pale orange-brown. Superficial hyphae of the cap colourless or with pale yellow, vacuolar pigment, colourless in KOH 5%. Spores 6.5–11.5(–12.5) \times 3.5–6.5(–7.5) μ m, mostly in greater part (40–70%) constricted in side-view. Basidia (34–)36–63.5(–65.5) \times (5.5–)6–10.5(–12.5) μ m. 4
- 4a. Spores 6.5–10(–11.5) \times 3.5–5(–5.5) μ m, averages 7.5–9.3 \times 3.7–4.7 μ m; many (40–70%) clearly constricted in side-view (Figs. 31, 32). Basidia (5.5–)6–8 μ m broad (Fig. 33)
H. strangulatus, p. 250
- b. Spores (8–)9–11.5(–12.5) \times 4.5–6.5(–7.5) μ m, averages 10.4–10.9 \times 6.0–6.3 μ m, in side-view rather frequently weakly constricted (Figs. 16, 17). Basidia (7.5–)8–10.5(–12) μ m broad (Fig. 18). *H. substrangulatus*, p. 253

HYGROPHORUS MARCHII Bres.¹—Plate 20c; Figs. 1–11

Hygrophorus marchii Bres., Ic. Mycol. 7: 343. 1928. — *Hygrocybe marchii* (Bres.) Sing., in Lilloa 22: 153. '1949' [1951].

Misapplication.—*Hygrophorus marchii* sensu Hesler & Smith, North American species of *Hygrophorus*: 209. 1963.

COLOURED ILLUSTRATIONS.—Bresadola, l.c.; Reid, Col. Ic. rare interest. Fungi 3: pl. 18a. 1968.

¹ The description is based on the collections available from the Netherlands.



Figs. 1–11. *Hygrophorus marchii* Bres. — 1–2. Carpophores, $\times 1/2$. — 3–6. Spores, $\times 1000$. — 7–8. Basidia, $\times 1000$. — 9. Elements of trama of gills, $\times 250$. — 10. Radial section of pileipellis and subpellis, $\times 500$. — 11. Radial section of pileipellis, $\times 500$. (Figs. 1, 3, 7, 9 from *Arnolds* 3278; Figs. 2, 10 from *Arnolds* 3067; Fig. 4 from *Jensen*, 29 Oct. 1960 (*Hesler* 23.940); Figs. 5, 8 from *Huijsman* 67.450; Figs. 6, 11 from *Henderson* 4174).

Cap 15–40 mm wide, first broadly flattened conical, then expanded, sometimes slightly obtuse umbonate, often with slightly wavy, lobed, finally sometimes reflected margin, clearly hygrophanous, when young and moist scarlet, vermilion or orange-red (M. 8B8, 9B8, 10B8)² with extreme margin bright orange-yellowish, gradually discolouring to orange, orange-yellow or pale orange-ochre (M. 5A7, B5, 6A7, 7A7) when drying and by ageing; non-striate or striate at outmost margin only (max. 4 mm); surface especially of young caps greasy or slightly viscid when moist, drying to glabrous or at centre finely adpressedly hairy. Gills (L 17–25, l 1–5) broadly adnate or slightly decurrent, often slightly ventricose, up to 7 mm broad, thick and distant, brittle; colour varying from pale yellow to orange-yellow, orange, orange-red or rose-red, always with broad paler edge. Stem 26–54 × 3–6 mm (–8 mm when compressed), l/b 6–14.5, rather slender, stuffed or hollow, straight, slightly curved or somewhat flexuose, attenuated downwards, sometimes compressed, vermilion or orange-red with lighter orange or yellowish base, or entirely orange- or chrome yellow, shiny when moist but not viscid, smooth or slightly striate when dry. Flesh in cap thin, rather fragile, concolorous with surface of cap; in outer layer of stem also of the same colour, but in spongy centre yellowish. Smell and taste none or slightly sweetish. Well-dried specimens light orange, light orange-brown or ochre-brown (M. 4A4–5A4, 5A4, 5A6, 5B5, 5B6).

Spores [30/3/2] 7–8.5(–10) × 4–5 μ m, l/b 1.5–2.0, ellipsoid-oblong or ovoid-oblong, sometimes slightly curved, more rarely (<10%) slightly constricted in face-view, with moderately large oblique apiculus, colourless in water and alkaline solutions, yellowish in Melzer's (Fig. 3). Basidia [30/3/2] (39.5–)41–53(–56.5) × (6–)6.5–8.5(–9.5) μ m, l/b 5.2–7.1(–7.9), rather slender or slenderly clavate, 4-spored, sometimes a few 2- or 3-spored (then a minor part of the spores longer than 8.5 μ m; Fig. 7). Pleuro- and cheilocystidia not seen. Trama of gills subregular, composed of subparallel hyphae with long chains of moderately long, cylindrical or somewhat ventricose cells with obtuse ends, measuring [25/3/2] (45–)52–122(–143) × (4.5–)7.5–15(–16.5) μ m, l/b 4.2–10.9(–15.6) (Fig. 9). Pileipellis a cutis, 40–70 μ m thick, composed of mainly radially oriented, prostrate hyphae, just beneath surface loosely interwoven, colourless, slightly gelatinous and often with scattered upright ends; all hyphae slender with long cylindrical cells, 1.7–5(–7) μ m broad, not constricted at septa; more downward gradually passing into hyphae of trama (Fig. 10). Pileitrama almost regular, beneath pileipellis slightly interwoven with short cylindrical cells, 5–18(–22) μ m broad (a subpellis); in fresh specimens with brightly yellow vacuolar pigment; beneath the subpellis with more slender subparallel, cylindrical hyphae, 5–14.5 μ m broad, with pale yellow vacuolar pigment or colourless. Stipitepellis a thin dry cutis of non-gelatinous hyphae of 1.5–5.5 μ m broad. Clamps observed in most collections at base of basidia.

HABITAT.—In the Netherlands rare; only known from two dike-slopes grown with short mossy grassland extensively grazed by cows and not treated with fertilizers, on dry, rather rich, loamy soil. October–November.

COLLECTIONS EXAMINED.—THE NETHERLANDS: prov. Friesland, Island of Terschelling, dike near Midsland, 4 Nov. 1973, *Arnolds 3067* (L, WBS); prov. Gelderland, Wilp, dike along the river IJssel, 26 Oct. 1974, *J. Piepenbroek & G. Piepenbroek Grooters (Arnolds 3278; L, WBS)*.

² Colour codes are according to Kornerup & Wanscher, *Methuen Handbook of Colour*, 2nd Ed., 1967. London.

Studies on some dried collections from other European countries resulted in the following additional microscopic features:

Spores [120/12/12] (6-)6.5-8.5(-10) \times 3.5-5(-6) μ m, averages 6.9-8.4 \times 3.9-5.0 μ m, l/b 1.5-2.1(-2.2), ellipsoid-oblong or ovoid-oblong, in some collections frequently slightly curved (Fig. 4), not or weakly constricted in a small minority (at most 20%; Figs. 4-6). Basidia [52/9/9] (40-)41-58(-60.5) \times (5.5-)6-8.5(-9) μ m, l/b 5.5-9.0(-10.4), rather to very slenderly clavate, in all specimens mostly 4-spored, rarely some 2- or 3-spored (Fig. 8). Cheilo- and pleurocystidia none. Pileipellis a well-developed cutis or slightly gelatinized ixocutis 40-100(-120) μ m broad, hyphae 1.5-5(-6.5) μ m thick, in upper layers often slightly gelatinous (Fig. 11), otherwise as described from the Netherlands' collections above.

COLLECTIONS EXAMINED.—FAEROES, Syderö, ved Lopra Hvalstation, 28 Aug. 1938, *F. H. Möller s.n.* (C).

DENMARK: Kejlsö, Tegnet, 12 Oct. 1941, *F. H. Möller s.n.* (C); Sjaelland, Dyrehave, Jaegersborg, 29 Oct. 1960, *J. P. Jensen (Hesler 23940; TENN)*; Jylland, 9 Oct. 1971, *M. Lange s.n.* (C); Jutland, Hvalpsund, 22 Oct. 1969, *J. Barkman 9121* (WBS).

FRANCE: Franche-Comté, Lougres près de Monthéliard, 1 Nov. 1967, *H. S. C. Huijsman 67.450* (L); St. Valéry la Garenne, 24 Oct. 1974, *M. Bon 72102402* (herb. Bon); Creuse?, 18 Oct. 1971, *P. Joly (M. Bon 71101804; herb. Bon)*.

GREAT BRITAIN: Tomich, 27 Aug. 1957, *R. Watling 114C* (E); Loch an Eilean, 7 Sept. 1958, *D. M. Henderson 4174* (E); Mull, Ben Mohr, 14 Sept. 1968, *D. M. Henderson 9107* (E); St. Kilda, Mollach Bi, 8 Sept. 1967, *R. Watling 5972* (E).

SWITZERLAND: Neuchâtel, Les Pontins, 10 Sept. 1959, *H. S. C. Huijsman s.n.* (L); Neuchâtel, Boudry, 17 Oct. 1965, *H. S. C. Huijsman s.n.* (L).

It is remarkable that so many authors have extensively described *H. marchii* in the last decades. Without trying to be complete I refer to Möller, 1945; Favre, 1955; Haller, 1956; Orton, 1960; Svrček, 1962; Hesler & Smith, 1963; Reid, 1968; Singer, 1969; Bon, 1974. Not all their descriptions are identical with the one given above.

Of the descriptions of species in the *H. marchii*-group given in this paper, the one above is the only one that fully agrees with the original diagnosis and plate by Bresadola (l.c.). Important characters in this respect are the vermilion or orange-red, first slightly viscid cap and the non-constricted spores (cf. spores pictured by Bresadola). It seems that there is no material left of *H. marchii* collected by Bresadola himself. Such collections are lacking in the herbaria of Stockholm (S) and Beltsville U.S.A. (BPI) according to the informations kindly given to me by the directors.

According to the accounts in recent literature *H. marchii* seems to be a widespread and locally common mushroom in Western and Central Europe. It is rather variable in some characters, e.g. spore size. The smallest spores observed by me are in the British collection *Henderson 4174*, viz. (6.2-)6.5-7.3(-7.5) \times 3.6-4.2 μ m; the largest in the collection *Barkman 9121* from Denmark, viz. 7.6-8.7(-10.0) \times 4.2-5.0(-5.2) μ m. Reid (1968: 5) has already mentioned the variations in the descriptions of this species. However, there is no reason to distinguish different taxa on this basis, as demonstrated in a scatter diagram (Fig. 36).

Some variability also exists in the thickness of the pileipellis and in the abundance

of hyphae projecting upwards with hair-like ends. In some collections the latter are completely lacking (Fig. 10), in others upstanding hyphae are rather frequent (Fig. 11) like those figured by Bon (1974, Fig. 1 J). Both types grade into each other. The presence of erect hyphae is correlated with the macroscopic appearance of the cap, which then is hairy when dry.

Singer (1969) distinguished three concepts of *H. marchii*: sensu Orton (1960), sensu Favre (1955) and Möller (1945), and sensu Hesler & Smith (1963) respectively. I agree with him in separating the latter (see p. 000), but in my opinion *H. marchii* sensu Orton is identical with *H. marchii* sensu Favre and Möller. According to Singer (l.c.) the main difference between both concepts would be that Orton's fungus should have the cap transparently striate over one half of the radius, and Favre's fungus should not have striations at all. Singer concluded this from the fact that Orton (l.c.) did not mention in his key any difference in striation between *H. marchii* and *H. strangulatus*, whereas *H. strangulatus* should have a striate cap. However, Orton states in his description of *H. strangulatus* (1960: 266): 'when moist striate at margin only', which is also obvious from his figure 77. Favre (1955: 35) and Bresadola (1928: 343) both describe and depict *H. marchii* with a non-striate cap. Fruit-bodies without and with a short striation often grow together in the same locality.

HYGROPHORUS MARCHII sensu Hesler & Smith—Figs. 12–15

Hygrophorus marchii sensu Hesler & Smith, North American Species of *Hygrophorus*: 209–210, fig. 60. 1963.

For a complete macroscopic description and a photograph the reader may be referred to Hesler & Smith (l.c.). A study of two collections, kindly sent to me by Dr. L. R. Hesler, revealed the following microscopical features:

Spores [22/2/2] (6–)6.5–8(–8.5) \times 3.5–4.5 μ m, averages 7.1–7.5 \times 4.1 μ m, l/b 1.7–2.0(–2.1), ellipsoid-oblong, but for the greater part (more than 60%) slightly to strongly constricted in side- as well as in face-view, with a small acute apiculus (Figs. 12, 13). Basidia [17/2/2] (30–)32–46.5 \times 5.5–7.5 μ m, l/b (5.0–)5.2–7.2(–7.4), rather slenderly clavate with 4 sterigmata (Fig. 14). Pleuro- and cheilocystidia none. Trama of gills composed of subparallel hyphae c. 6–16 μ m broad. Pileipellis a thin (25–40 μ m), clearly differentiated ixocutis of repent and ascending, narrow, gelatinous hyphae 1.5–5 μ m broad (Fig. 15). Trama of pileus consisting of radial subparallel hyphae 5.5–14 μ m broad, but beneath the pileipellis rather strongly interwoven (a subpellis). Stipitepellis a thin dry cutis; superficial hyphae 1.7–5 μ m broad. Clamps present at base of basidia.

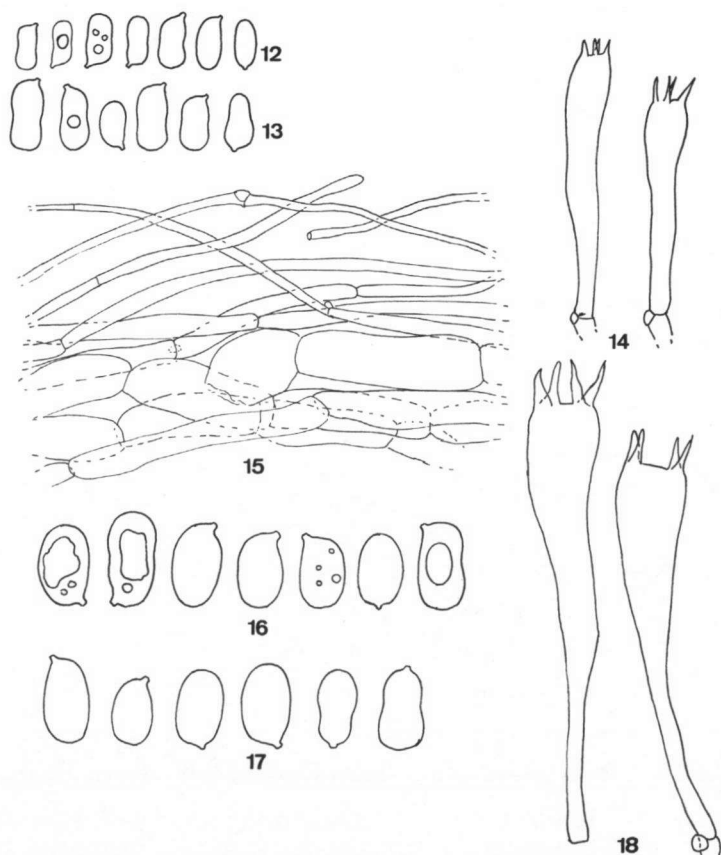
COLLECTIONS EXAMINED.—U.S.A.: California, Trinidad, 3 Dec. 1956, A. H. Smith 56213 (TENN); Cheboygan Co., Colonial Point, Douglas Gate, 4 July 1974, A. H. Smith 32421 (MICH).

I found the spores significantly smaller than the size range given by Hesler & Smith (l.c.: 209), viz. 7–10 \times 3.5–5 μ m. Singer (1969: 22) observed still larger spores: 8.8–10.2 \times 4.3–5 μ m. This difference is possibly due to rather great variation between

some collections. It is also remarkable that Hesler & Smith mention the spores being 'at times faintly' constricted, whereas Singer describes them as 'often (although by far not all) slightly constricted in the middle'. I found the majority of spores clearly constricted.

The abundance of constricted spores forms the main difference with *H. marchii* Bres., as described by various European authors. Moreover the pileipellis is thinner but at the same time more clearly gelatinous. The cap seems to flatten sooner and to be darker red (blood red) in young fruit-bodies (Hesler & Smith, l.c.).

The spores are much like those of the European *H. strangulatus* Orton (see p. 252), but *H. marchii* sensu Hesler & Smith is much more robust and has an ixocutis instead



Figs. 12–15. *Hygrophorus marchii* sensu Hesler & Smith. — 12–13. Spores, $\times 1000$. — 14. Basidia, $\times 1000$. — 15. Radial section of pileipellis and subpellis, $\times 700$. (Figs. 12, 14, 15 from Smith 56213; Fig. 13 from Smith 32421)

Figs. 16–18. *Hygrophorus substrangulatus*. — 16–17. Spores, $\times 1000$. — 18. Basidia, $\times 1000$. (Figs. 16, 18 from Orton 2365; Fig. 17 from Orton 477)

of a thin dry cutis. So it seems that *H. marchii* sensu Hesler & Smith has to be re-described under a new name.

Hesler & Smith (l.c.) think that their concept of *H. marchii* is very close to that of *H. flavescens* (Kauffm.) Smith & Hesl. I do not agree with this point of view. The trama of the gills of the latter species has quite another structure. It consists of strictly parallel hyphae with very long and broad, tapering cells $450-1300 \times 9.5-30 \mu\text{m}$ (Arnolds 1974a: 146, Figs. 110, 111). Besides the basidia are much broader, and the outermost hyphae on the stem of *H. flavescens* are very slender and gelatinous. In my opinion *H. flavescens* belongs to another section of *Hygrophorus*, viz. sect. *Hygrocybe* (Holotype: *Hygrophorus conicus* (Scop. ex Fr.) Fr.). (See Arnolds, 1974a: 144.)

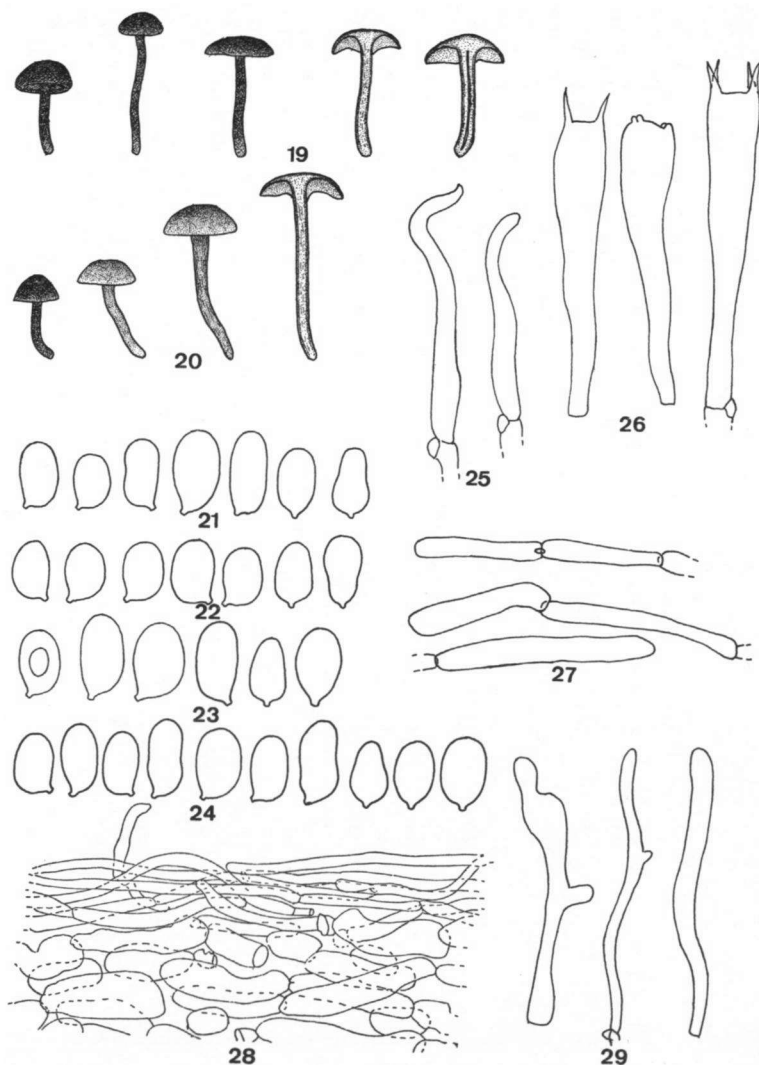
***Hygrophorus phaeococcineus* Arnolds, spec. nov**

Plate 20b; Figs. 19-29

Pileus (6.5-)10-40(-56) mm latus, semiglobatus vel convexus, dein leviter convexus vel expansus, hygrophanus, coccineus vel sanguineus vulgo margine aurantius vel flavus, posterior totus aurantio-luteus, in exsiccata vulgo brunnescens, glaber vel leviter tomentosus. Lamellae (L 14-32, l 1-3(-5)) late adnatae vulgo dente decurrentes, subdistantes, fragiles, primo pallide miniatæ vel flavæ, dein salmonicolores, ceraceæ vel pallide aurantio-luteæ. Stipes (12-)20-60 \times 1.5-4(-5) mm, deorsum aequalis vel attenuates, vulgo leviter flexuosus, fragilis, primo totus vel ad apicem coccineus vel aurantio-miniatus, dein aurantius vel ceraceus, siccus, glaber, basis albo tomentosus. Caro fragilissima, sub cuticulæ pilei et stipitis concolor, intus flava vel pallide aurantia. Odor et sapor nulli. Sporae (7-)7.5-11(-11.5) \times (3.5-)4-6.5 (-7.5) μm , l/b (1.4-)1.6-2.1(-2.3), ellipsoideo-oblongae vel ovoideo-oblongae, raro pro parte minoris leviter strangulatae. Basidia (26.5-)28.5-47.5(-49.0) \times (4.5-)5.5-9(-9.5) μm , vulgo 4 sporigera, raro pro parte minoris 3 vel 2 sporigera. Lamellarum acies fertilis interdum paucis cystidiis cylindricis, (18-)25-35(-49) \times 1.5-2.5(-3) μm . Lamellarum trama subregularis, cellulis 46.5-180(-230) \times (4.5-)6.5-15.5(-20) μm . Pileipellis cutiformis, 15-35(-45) μm latus, hyphis 3.5-6.5 μm latis, cylindricis, interdum pro parte erectis. Pileitrama sub pileipellis irregularis, cellulis, inflatis, 5-9 μm latis. Inter musci et graminos ad terram in locis humidis et acidis. Holotypus: 'Vlieland, Kroon's Polders, 31 Oct. 1976, Arnolds 3710' (in herb. Biol. Stat. Dr. W. Beyerinck, Wijster=WBS; isotypus L).

ETYMOLOGY: phaeus, dark; coccineus, bright red or scarlet.

Cap (6.5-)10-45(-56) mm wide, first semiglobate or strongly convex, then slightly convex, rarely flattened, rather hygrophanous; bright scarlet or dark blood red at first (M. 9B8, 9C8, 10C8, 10D8, 11C8), often with narrow orange or yellow margin, drying pinkish red; gradually discolouring orange-red, orange or orange-yellow (M. 6A7, 6B8, 7B8, 8A8-B8), finally mostly light orange-brown or ochre-brown (M. 5C8, 6C8, 7C7); when moist slightly greasy, often appearing waxy, as covered by a thin, greyish coating, drying smooth or very faintly golden-yellow to orange adpressedly velvety-hairy; margin not striate or rarely short-striate when moist. Gills [L 14-32, l 1-3(-5)] broadly adnate, mostly with decurrent tooth, thick, subdistant, very brittle, when young at most pale rose-red (M. 7B6, 8A6, 8B6, 10A7) with narrow pinkish yellow or sulphur yellow edge, entirely passing into light salmon pink, pinkish wax yellow or light yellow-orange (M. 5A3, 5A6, 6A4-A6, 7A5). Stem (12-)20-60 \times 1.5-4(-5) mm, l/b (3-)6-18, slender, stuffed or slightly hollow, mostly somewhat curved, generally tapering downwards, very fragile, scarlet or orange-red



Figs. 19–29. *Hygrophorus phaeococcineus*. — 19–20. Carpophores, $\times 1/2$. — 21–24. Spores, $\times 1000$. — 25. Basidioles, $\times 1000$. — 26. Basidia, $\times 1000$. — 27. Elements of trama of gills, $\times 250$. — 28. Radial section of pileipellis and subpellis, $\times 500$. — 29. Cheilocystidia, $\times 1000$. (Figs. 19, 22, 28 from Kalf, 20 Aug. 1961; Figs. 20, 24 from Arnolds 644; Figs. 21, 26, 29 from Arnolds 3650 (Holotype); Figs. 23, 25 from van de Bergh, 7 Oct. 1969)

(M. 8A8, 9B8, 10B8) at first, at least at apex, gradually discolouring orange, orange-yellow or wax yellow (M. 4A5, 5A5–A8, 6A8) from base upward; extreme base white tomentose; surface glabrous or finely striate, dry on the touch. Flesh very brittle, beneath the surface of the cap concolorous, otherwise egg or lemon yellow; outer tissue of the stem coloured like surface; in the centre fibrous, pale orange or pale yellow. Smell and taste absent. Well-dried specimens remarkably dark brown or purplish brown (M. 5E6, 5E7, 6E6, 7E6), also dull orange- or ochre brown (M. 5C7, 5D6, 5D7, 6D7) after some years.

Spores [150/13/11] $(7-7.5-11(-11.5) \times (3.5-4-6.5(-7.5) \mu\text{m}$, averages $8.0-10.3 \times 4.4-5.6 \mu\text{m}$, l/b $(1.4-1.6-2.1(-2.3)$, in side-view ellipsoid-oblong, ovoid-oblong or subcylindrical, often slightly curved, rarely (at most 20%) slightly constricted in the middle; in front-view mostly broader ovoid, sometimes pyriform or constricted (Figs. 21–24). Basidia [90/12/12] $(26.5)28.5-47.5(-49) \times (4.5-5.5-9(-9.5) \mu\text{m}$, l/b $(3.6-4-6.7(-8.7)$, moderately to rather slenderly clavate, 4-spored, sometimes a few 3- or 2-spored (Fig. 26); basidioles sometimes frequent, approximately cylindrical (Fig. 25). Cheilocystidia present in some collections but not constant in all specimens, scattered, hair-like to cylindrical or shaped like basidioles, rather frequently forked, about $(18-25-35(-49) \times 1.5-2.5(-3.5) \mu\text{m}$ (Fig. 29). Pleurocystidia absent. Trama of gills subregular, composed of slightly interwoven hyphae with cylindrical or somewhat inflated cells with rounded ends, about $46-180(-230) \times (4-6-15(-20) \mu\text{m}$ (Fig. 27). Pileipellis a thin dry cutis, $15-45 \mu\text{m}$ thick, consisting of a few layers of narrow repent hyphae with a few scattered erect hair-like ends, $3.5-6.5(-8) \mu\text{m}$ wide, with brownish vacuolar pigment and often with grey-brown intracellular granulae and clots, often agglutinated in older fruit-bodies and then with very obscure structure (Fig. 28). Pileitrama beneath the pileipellis forming a subpellis consisting of compact, irregularly interwoven hyphae with inflated cells $4-13 \mu\text{m}$ broad, in fresh specimens with red to orange-yellow vacuolar pigment; beneath this layer subparallel radial hyphae with cylindrical or slightly inflated cells $(6-9-20(-25) \mu\text{m}$ broad, with pale yellowish vacuolar pigment. Stipitepellis hardly differentiated, with parallel longitudinal narrow hyphae, $3-5 \mu\text{m}$ broad. Stipitetrama subregular, consisting of hyphae with cylindrical cells with rounded ends, $4.5-12 \mu\text{m}$ broad. Clamps sometimes not found but in most specimens present at base of basidia; also seen at hyphae of pileipellis and trama of gills.

HABITAT.—Known from several mossy and grassy valleys in the coastal dunes, on moist, acid, sandy soil poor in lime (pH 4.5–5), rich in humus, and from a few mossy and grassy spots on moist acid peat or peaty sand in the inland (cf. Arnolds, 1974: 92, map 20). August–October.

COLLECTIONS EXAMINED.—THE NETHERLANDS: prov. Friesland, Island of Vlieland, Kroon's Polders, 31 Oct. 1976, *E. Arnolds 3710* (holotype herb. Biol. Stat. Dr. W. Beyerinck, Wijster: WBS; isotype L); Island of Terschelling, Midland, 9 Sept. 1954, *Jansen-v. d. Plaats s.n.* (L); prov. Gelderland, Overasselt, Hatertse Broek, 26 Sept. 1954, *Exc. Ned. Mycol. Ver.* (L); 20 Aug. 1961, *J. Kalf s.n.* (L); Winterswijk, Korenburgerveen, 29 Sept. 1973, *C. Bas 6174* (L); prov. Noord-Holland, Petten, Derde Korfwater, 7 Oct. 1969, *F. v. d. Bergh s.n.* (L); Bergen, Verbrande Pan, 5 Oct. 1969, *E. Arnolds 347* (L); Island of Texel, De Geul, Calamagrostis-valley, 30 Oct. 1970, *E. Arnolds 579* (L); 30 Oct. 1971, *E. Arnolds 644* (L); Island of Texel, De Geul, path in the dunes, 9 Oct. 1969, *E. Arnolds 380* (L); Island of Texel, De Geul, grassland in the dunes, 9 Oct. 1969, *E. Arnolds 385* (L); prov. Noord-Brabant, Deurne, Helenaveen, 15 Oct. 1958, *C. Bas 1583* (L); Eindhoven, Liessel, 9 Oct. 1965, *E. Kits van Waveren s.n.* (L).

This fungus has been known to mycologists in the Netherlands for many years but was at first usually mistaken for small specimens of *H. coccineus*. Dr. C. Bas (Rijks-herbarium, Leiden) recognized already in 1954 the great difference in size and stature between *H. phaeococcineus* and the latter, and found some peculiarities, e.g. the browning of dried specimens. On account of these features he already noted a provisional name, *H. phaeococcineus*, on the wrappers.

Probably this species is most related to *H. marchii*. Macroscopic differences with the latter are the dark red colour of the cap and the more slender stem. Besides, *H. phaeococcineus* is the most fragile of all species treated here, and the only one turning brown after drying (especially adult specimens). Microscopic differences with *H. marchii* are the thinner, dry pileipellis and in general also the occurrence of larger spores and shorter basidia. Although some overlap exists between both species in size of spores (Fig. 36), basidia, and fruit-bodies, the total complex of characters certainly justifies the distinction of two taxa. In the Netherlands an ecological difference also exists: whereas *H. phaeococcineus* has been always found on moist, peaty, acid soils, *H. marchii* grows in grasslands on dry, loamy, subneutral soils. Perhaps the records of *H. marchii* for Great Britain refer in part to *H. phaeococcineus*. From the published descriptions of *H. marchii* the one by Orton (1960: 252) comes closest to the species described above. However, I could not find proof for this supposition in the few British collections of *H. marchii* I was enabled to examine. Orton studied one collection of *H. phaeococcineus* many years ago, and concluded in a letter to Bas (16 Apr. 1961): 'I agree this species is not in my key'. Also Hesler studied some dried specimens in preparing the book on *Hygrophorus* in North America, and stated in a letter (7 Feb. 1961) that he did not know the species.

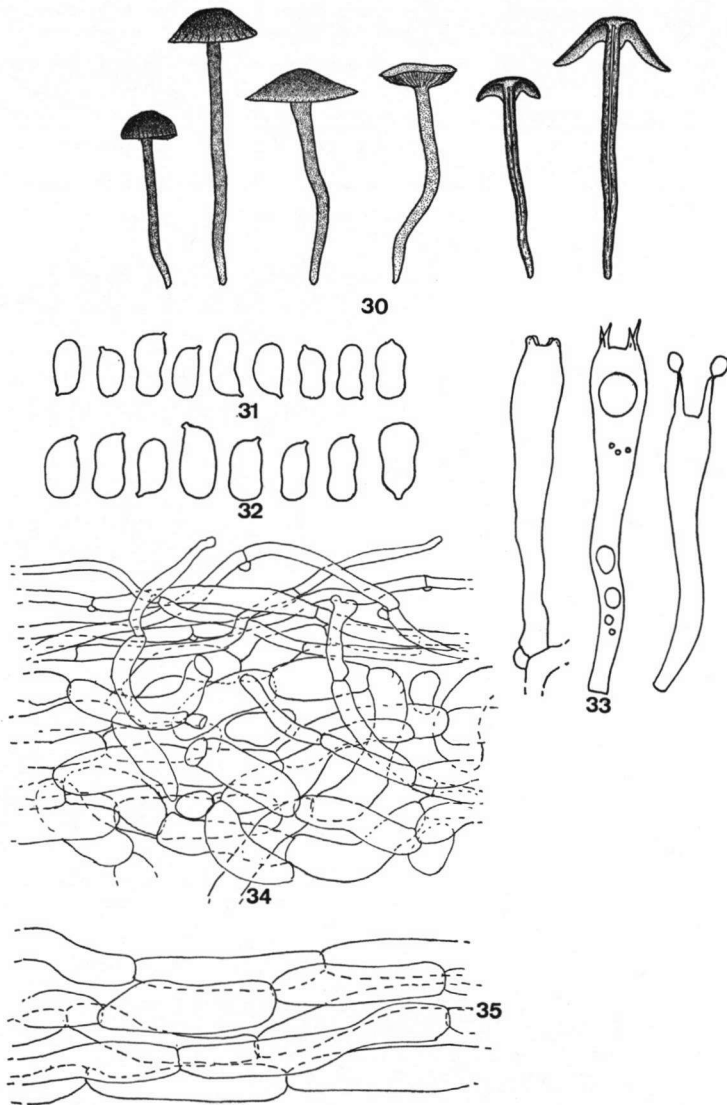
It could be useful to study the relationship between *H. phaeococcineus* and *Hygrocybe mexicana* Sing. (Singer 1958: 225; Hesler & Smith 1963: 181). The latter seems to be related, also by presence of remarkably short basidia. However, on account of some minor discrepancies in the short description of *H. mexicana* (e.g. the cap is strongly striate) and a different distributional pattern, it seems improbable that these two taxa are conspecific.

HYGROPHORUS STRANGULATUS P. D. Orton—Plate 20a; Figs. 30–35

Hygrophorus strangulatus P. D. Orton in Trans. Br. mycol. Soc. **43**: 266. 1960. — *Hygrocybe strangulata* (P. D. Orton) Švrček in Česká Mykol. **16**: 167. 1962.

MISAPPLICATION.—*Hygrophorus strangulatus* sensu Reid in Nova Hedw. **15** (Suppl.; Col. ic. rare interest. fungi **3**): 6, pl. 18 b, fig. 5. 1968 (= *H. miniatus* (Fr.) Fr.).

Cap 8–32 mm broad, first convex or broadly flattened conical, gradually less convex or expanded, rarely flattened or slightly depressed, strongly hygrophanous, when moist in young fruit-bodies scarlet, vermilion or orange-red (M. 8B8, 9B8) with narrow orange or orange-yellow margin, gradually discolouring orange, orange-yellow (M. 5A8, 6A8), finally dull light brownish orange when old (M. 5B6); drying pale orange (M. 5A3, A4) or even light yellow (M. 4A4) from the centre outwards; when moist the margin shortly translucently striate (up to 1/4 R of cap);



Figs. 30–35. *Hygrophorus strangulatus*. — 30. Carpophores, $\times 1/2$. — 31–32. Spores, $\times 1000$. — 33. Basidia, $\times 1000$. — 34. Radial section of pileipellis and subpellis, $\times 500$. — 35. Radial section of pileitrama, $\times 500$. (Fig. 30 from *Arnolds* 544; Figs. 31, 33, 34, 35 from *Arnolds* 3486; Fig. 32 from *Kits van Waveren*, 6 Oct. 1961).

surface glabrous or slightly greasy when moist, not viscid; when dry dull and especially at centre often covered with very fine hairy fibrils, giving a velvety impression, sometimes very fine golden scurfy but never distinctly squamulose or scaly. Gills (L 17–23; l 1–3(–5)) broadly adnate, often with tooth, or short decurrent, not or slightly ventricose, up to 5 mm broad, rather thick, distant, first pale yellowish, then pale orange (M. 5A4) with broad yellowish edge, finally mostly darker pinkish orange (M 6A6) or orange-red with narrower sulphur yellow or orange-yellow edge. Stem (14–)23–60(–72) × 1.5–4 mm, l/b (4.0–)9.3–18.0, slender, often somewhat curved, attenuated downwards or equal, stuffed, first orange-red or orange, with base more yellow-orange, later often becoming entirely orange- or chrome yellow (M. 3A7, 5A7) from base upwards, sometimes whitish or whitish tomentose at base; surface smooth or slightly striate, dry or slightly greasy, not viscid when moist. Flesh in cap thin (up to 2.5 mm thick), in cap and stem rather firm and concolorous with surface; in centre of stem fibrous, pale yellowish. Smell and taste not distinct. Well-dried specimens dull ochre-orange or brownish ochre.

Spores [70/7/7] 6.5–10(–11.5) × 3.5–5(–5.5) μ m, averages 7.5–9.3 × 3.7–4.7 μ m, l/b 1.6–2.2(–2.4), ellipsoid-oblong, obovoid-oblong or cylindrical, sometimes pyriform but many (40–70%) clearly constricted in side-view and often in front-view too, with prominent rather large oblique apiculus (Figs. 31, 32). Basidia [40/6/6] (34–) 36–58 × (5.5–)6–8 μ m, l/b (4.6–)5.0–8.6, slenderly clavate, mostly 4-spored but in some collections a few 2- or 3-spored; sometimes mixed 2-, 3-, and 4-spored (then spores in part longer than 9 μ m; Fig. 33). Pleuro- and cheilocystidia not seen. Trama of gills subregular, composed of subparallel to slightly interwoven hyphae with rather short cylindrical or somewhat inflated cells with obtuse ends, measuring [20/3/3] (32–)41–88 × (6–)8–18 μ m, l/b (3.0–)3.4–10.7. Pileipellis a thin cutis, 20–40(–60) μ m thick, composed of a few layers of colourless, mostly radially arranged, repent hyphae, sometimes very slightly gelatinized, with long cylindrical cells 2.5–6 μ m broad; locally with scattered, narrow, ascending or erect ends sometimes constituting small fascicles (Fig. 34), downwards gradually passing in pileitrama. Hyphae close beneath pileipellis rather strongly interwoven, with short cylindrical or inflated cells 6–11 μ m broad, in fresh fruit-bodies with bright yellow vacuolar pigment (a subpellis); pileitrama under this layer consisting of more regularly, radially disposed hyphae with rather short cylindrical cells 6–15 μ m broad, with pale yellowish vacuolar pigment when fresh (Fig. 35). Stipitepellis a poorly differentiated dry cutis with long cylindrical cells 2.5–5 μ m broad. Stipitetrama consisting of longitudinal subparallel hyphae 4–11.5 μ m broad. Vascular hyphae not seen in trama. Clamps observed at base of basidia and at hyphae of pileipellis.

HABITAT.—In the Netherlands not common, mostly met with in moss-rich, unmanured grasslands on weakly acid, mesotrophic, sandy soil; also once in oak-scrub on sand. October–November.

COLLECTIONS EXAMINED.—THE NETHERLANDS: prov. Gelderland, Warnsveld, De Kop, 20 Oct. 1961, *E. Kits van Waveren s.n.* (L); prov. Noord-Holland, Aerdenhout, dunes of Amsterdam Water Supply, 6 Oct. 1961, *E. Kits van Waveren s.n.* (L); Island of Texel, De Koog, 29 Oct. 1971, *E. Arnolds 637* (L); prov. Zuid-Holland, Oostvoorne, Weevers' Duin, 6 Nov. 1970, *E. Arnolds 598* (L); prov. Noord-Brabant, Drunen, dike along Drongelens Kanaal, 22 Oct. 1970, *E. Arnolds 544* (L); 26 Oct. 1975, *E. Arnolds 3486* (WBS).

The preceding description is based on collections from the Netherlands. It agrees well with the diagnosis and the illustrations given by Orton (l.c.). I investigated also two of his collections (Orton 1220 and 2987, E), and found the same features, e.g.

spores $6.5-9.5 \times 3.5-5 \mu\text{m}$, many (40–50%) constricted in the middle. In literature this species has also been reported from Czechoslovakia (Svrček, 1962) and Chile (Singer, 1969). When studying collections from Central Europe, provisionally determined as *Hygrocybe marchii*, I came across a collection from Switzerland (Col de Julier, Sept. 1968, *M. Bon 80939*) which in my opinion is identical with *H. strangulatus*. The most important microscopical details are: Spores [10/1/1] $6.5-8 \times 3.5-4 \mu\text{m}$, l/b 1.6–2.0, ellipsoid-oblong but often clearly constricted in side-view (50–70%). Pileipellis a thin dry cutis c. $30 \mu\text{m}$ thick, with slender hyphae $1.5-4 \mu\text{m}$ wide.

In my opinion *H. strangulatus* is closely related to *H. marchii*, but in most cases it can be distinguished already in the field on account of the more slender habit, the less fragile flesh and the more hygrophanous cap (cf. Orton, 1960: 252). Microscopically it differs not only in having constricted spores but also in a thinner and drier pileipellis.

Some problems seem to exist about separating *H. strangulatus* from *H. miniatus* (Fr.) Fr. In my opinion the description and plate of *H. strangulatus* by Reid (1958) relate to *H. miniatus*. Orton communicated to me in a letter (27 Feb. 1976) that Dr. Watling and he '... feel that the spores given by Reid for *strangulatus* are not those of that species and that the plate much more likely represents *H. miniatus*'.

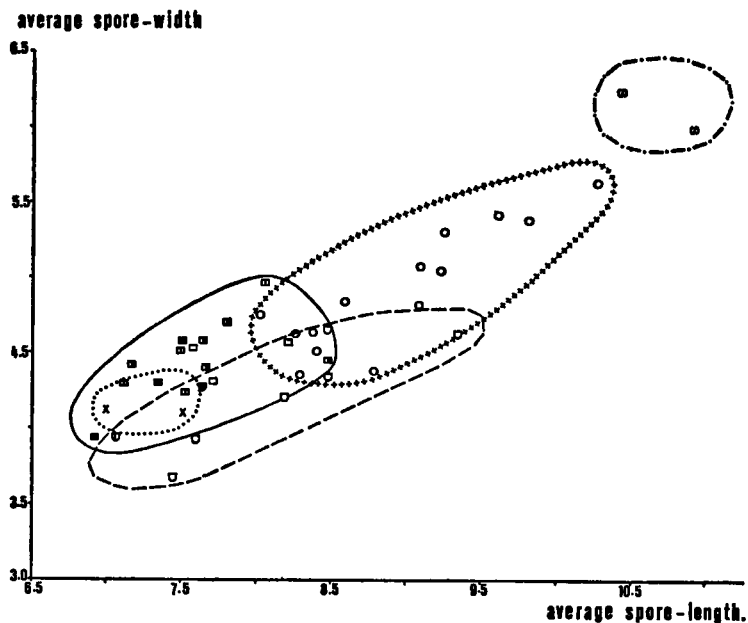
Two facts might have contributed to this misinterpretation: (i) Orton (l.c.) has described the cap of *H. strangulatus* being 'sometimes reflexed scurfy scaly round centre'; (ii) the spores of typical *H. miniatus* are often constricted in some views, but this feature has been rarely stated in descriptions, e.g. neither by Orton (l.c.) nor by Hesler & Smith (1963). In fact the cap of *H. strangulatus* is never really scaly but often covered with fine adpressed hairs. At most these constitute small irregularities, which give the cap a minutely roughened appearance under a hand-lens. Orton expressed the same opinion in the letter mentioned above. Close microscopical examinations indicate fundamental differences between the pileipellis in *H. strangulatus* and *H. miniatus*. In the latter the outermost tissue of the cap consists of hyphae with short, rather broad cells ($5-15 \mu\text{m}$), constricted near the septa, forming local fascicles of erect hyphae with broadly rounded clavate end cells (cf. Arnolds, 1974a: figs. 158, 159, 161; Hesler & Smith, 1963: fig. 8e).

Spores in *H. miniatus* are also different in shape: in side-view they are ellipsoid or ovoid and only rarely slightly constricted, but in front-view their shape is often constricted and typically widened towards the apiculus. This is shown in the drawing by Reid (l.c.: fig. 5) and also by Arnolds (1974a: fig. 152).

HYGROPHORUS SUBSTRANGULATUS P. D. Orton—Figs. 16–18

Hygrophorus substrangulatus P. D. Orton in Trans. Br. mycol. Soc. **43**: 269. 1960. — *Hygrocybe substrangulata* (P. D. Orton) P. D. Orton & R. Watling in Notes R. bot. Gdn Edinb. **29**: 131. 1969.

I have seen no fresh fruit-bodies of this species. Also no proof has been given till now of its occurrence in the Netherlands. So I refer to Orton (l.c.) for a macroscopic



- | | | |
|---|---|-----------------------------|
| □ | <i>Hygrophorus marchii</i> | from the Netherlands |
| ▤ | <i>Hygrophorus marchii</i> | from France and Switzerland |
| ▥ | <i>Hygrophorus marchii</i> | from Denmark |
| ■ | <i>Hygrophorus marchii</i> | from Great Britain |
| X | <i>Hygrophorus marchii</i> sensu Hesler & Smith | from the U.S.A. |
| ○ | <i>Hygrophorus phaeococcineus</i> | from the Netherlands |
| ◻ | <i>Hygrophorus strangulatus</i> | from the Netherlands |
| ◷ | <i>Hygrophorus strangulatus</i> | from Switzerland |
| ● | <i>Hygrophorus strangulatus</i> | from Great Britain |
| ⊙ | <i>Hygrophorus substrangulatus</i> | from Great Britain |

Fig. 36. Scatter diagram of average length and width of basidiospores of specimens examined of the *Hygrophorus marchii*-group.

description. Some microscopical details based on my investigation of two British collections are given below:

Spores [20/2/2] (8-)9-11.5(-12.5) \times 4.5-6.5(-7.5) μ m, averages 10.4-10.9 \times 6.0-6.3 μ m, l/b (1.5-)1.6-2.0, in side-view ellipsoid-oblong and rather frequently slightly constricted, in front-view often clearly constricted (Figs. 16-17). Basidia [20/2/2] (44-)47.5-63.5(-65.5) \times (7.5-)8-10.5(-12) μ m, l/b 5.3-7.1(-7.5), rather slenderly clavate, 4-spored (Fig. 18). Pleuro- and cheilocystidia not seen. Trama of gills subregular, consisting of subparallel hyphae with short cylindrical or inflated cells with rounded ends, c. 20-90(-140) \times (6.5-)8.5-14 μ m, l/b (2.3-)2.6-10.7. Pileipellis difficult to study in detail, probably a thin dry cutis consisting of thin, repent, colourless hyphae with a few erect ends, 2.5-6(-7.5) μ m wide. Pileitrama close beneath the pileipellis rather interwoven, consisting of weakly coloured hyphae 5-12 μ m wide (a subpellis); downwards more regular with radial hyphae 7-17(-24) μ m wide. Vascular hyphae present or not, irregularly flexuous, 3-6 μ m wide. Well-dried specimens orange-ochre or dull-orange-brown (M. 5C6, D6).

COLLECTIONS EXAMINED.—GREAT BRITAIN: Studland, Dorset, 27 Oct. 1955, P. Orton 477 (E; from type-locality); Loch an Eilean, Inverness-shire, 21 Aug. 1961, P. Orton 2365 (WBS dupl.).

It is probably impossible to distinguish *H. substrangulatus* from *H. strangulatus* on macroscopic characters only. However, the spores of the first are significantly larger and more rarely and weaker constricted (Fig. 17). I only observed constriction in the face-view of a few spores in collection Orton 477. Spores are also significantly larger than those of *H. marchii* and *H. phaeococcineus*, as demonstrated in the scatter diagram of Figure 36.

Like *H. strangulatus*, *H. substrangulatus* can be easily mistaken for *H. miniatus* (Fr.) Fr. However, it seems to differ fundamentally in the structure of the pileipellis, which in the latter species is a trichoderm without narrow repent hyphae. The report by Barkman (1964: 22) of *H. cf. substrangulatus* in the Netherlands relates in fact to *H. miniatus*.

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EXPLANATION OF PLATE 20

Fig. a. *Hygrophorus strangulatus* ($\times 1$, from Arnolds 3486). — Fig. b. *Hygrophorus phaeococcineus* ($\times 1$, from Arnolds 3710). — Fig. c. *Hygrophorus marchii* ($\times 1$, from Arnolds 3278). — Fig. d. *Hygrophorus helobius* ($\times 1$, from Arnolds 511; see Persoonia **8**: 99. 1974). — All Figs. del. E. Arnolds.

