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ON TWO SPECIES OF FALSE MORELS (Gyromitra) IN UTAH

Kent H. McKnight

The "Giant Helvella," Gyromitra gigas (Krombh.) Quél., is well known to collectors of spring mushrooms at high elevations in the Rocky Mountains. Although there are conflicting claims regarding its edibility, it is often collected for food. Study of dried specimens in various herbaria throughout North America and some from Europe, as well as numerous fresh collections from the United States, reveal two different species that are commonly called Gyromitra gigas. The second species is here referred to as Gyromitra fastigiata (Krombh.) Rehm. Although the two may look alike macroscopically, they are readily distinguishable on spore characteristics, with G. fastigiata having broadly fusiform spores with well-developed apiculi. Gyromitra gigas has more elliptic spores with little or no apiculi. The two North American species fit quite well the descriptions given by Krombholz (1832) for his two species of Helvella. Since there appear to be no holotypes extant, final disposition of these two entities must await their more critical study in central Europe where the one which Krombholz called H. gigas appears to be uncommon. Detailed descriptions follow for the two species, based on study of fresh collections as well as specimens from herbaria listed below. Differences between G. gigas and G. fastigiata and other species with which they are confused will be explored. Loans or use of facilities by the following institutions are gratefully acknowledged: Botanical Department of the National Museum, Prague (PR); Brigham Young University (BRY); Colorado State University (CS); Cornell University (CUP); Forest Disease Laboratory, U.S. Forest Service, Laurel, Md. (BFDL); Harvard University (FH); Institut für Spezielle Botanik der Eidg. Technischen Hochschule, Zurich (ZT); Naturhistorische Museum, Vienna (W); New York Botanical Garden (NY); Oregon State University (OSC); Plant Research Institute, Canada Department of Agriculture, Ottawa (DAOM); San Francisco State College (SF); University of Michigan (MICH); University of Tennessee (TENN);
and the University of Toronto (trtc). Color names in small caps follow Kelly and Judd (1955).

_Gyromitra fastigiata_ (Krombh.) Rehm.

Fig. 1


Ascocarp stipitate, shape irregular but roughly globose to ellipsoid, 3.5-9.0 cm in diameter, receptacle everted, wrinkled to convoluted and lobed, outer surface adnate with the stipe and in places intergrown with it, 0.5-2.0 mm thick, hymenium DARK GRAYISH YELLOW (2.5Y 6/5) to STRONG YELLOWISH BROWN (10YR 5/6), STRONG BROWN (7.5YR 4/6), or MODERATE BROWN (7.5YR 4/3 to 6YR 3/4); excipulum white. Odor and taste not distinctive. Stipe thick and fleshy, hollow with several anastomosing channels, even or expanded downward, 1.5-5.0 x 2.5-8.0 cm, longitudinally ribbed with rounded ribs, surface white or nearly so, glabrous to minutely furfuraceous.

In section, hymenium 350-450 μ thick; subhymenium indistinct, 100-150 μ broad, consisting of textura intricata having protoplasm which stains dark in lactofuchsin and in cotton blue and including scattered oleiferous hyphae; medullary excipulum indistinctly 2-layered, the upper layer, 200-250 μ thick, of compact textura intricata, gradually becoming less compact outward, the lower, less compact layer 800-1200 μ thick, of very loose textura intricata; ectal excipulum 2-layered, the inner layer 170-200 μ thick, consisting of compact, much interwoven textura intricata, the outer layer, 75-95 μ thick, consisting of loose, radially oriented textura intricata tending to textura porrecta, hyphae 8-15 μ in diameter, terminal cells variable in shape, clavate to cylindrical or ventricose and sometimes capititate; conspicuous oleiferous hyphal segments scattered through subhymenium and medullary excipulum. Asci cylindric, contorted and tapered gradually at the base, 360-415 x 14-20 μ, J-, protoplasm of young asci STRONG ORANGE YELLOW (near 7.5YR 7/12) in Melzer’s solution. Ascosporos fusiform to narrowly elliptic, flattened in one view, hyaline, typically with one large central guttule and two smaller terminal guttules, apiculate, smooth at first but soon ornamented with a very faint to distinct, low, complete reticulum of narrow, closely spaced ridges, (21) 23.5-32.0 x 10-14 μ, apiculi truncate to broadly rounded, 1-3 μ long. Paraphyses tips cylindric to clavate, sometimes tending to be capititate, dull ochraceous brown in H₂O, fading rapidly to dull grayish yellow in KOH, darker (dull ochraceous brown) on dried specimens revived in KOH, BRIGHT YELLOW (2.5Y 8.5/6) when revived in Melzer’s solution, 7-12 μ across at apex, 4.0-5.5 μ in diameter below.

Habit, Habitat, and Distribution.—Solitary to gregarious; on soil in hardwood or mixed hardwood-conifer forests, in valleys or lowlands; Atlantic Seaboard to Utah, Oregon, Idaho, and Washington.
Fig. 1. *Gyromitra fastigiata*, apothecia and ascospores. a, b. apothecia, X ½. c. ascospores, X 1,000.

Observations.—A distinctive characteristic of the species is its broadly fusiform, 1- to 3-guttulate spores having well-developed apiculi which are truncate to broadly rounded at the apex (Fig. 1c).

*Gyromitra gigas* (Krombh.) Quél.

Fig. 2


Ascocarp stipitate, irregular in shape but roughly globose to ellipsoid, (1x5) 5-18 cm across, receptacle everted, strongly convolute with outer surface appressed against the stipe and sometimes interwoven with it, 1.5-2.5 mm thick; hymenium strong yellowish brown (near 7.5YR 5/6) to strong brown (7.5YR 4/6) or moderate brown (7.5YR 4/4); excipulum white or nearly so. Odor and taste not distinctive. Stipe thick and fleshy, hollow with several anastomosing channels, even or expanded toward the base, 2-14 x 3-15 cm, longitudinally ribbed with rounded ribs, surface white or nearly so.

In section, hymenium 380-450 μ thick; subhymenium indistinctly differentiated from medullary excipulum, 150-200 μ broad, consisting of compact texture intricata and containing numerous oleiferous hyphae; medullary excipulum 650-750 μ thick, of texture intricata which is progressively more compact toward the subhymenium and less compact toward the ectal excipulum, hyphae 7-13 μ in diameter; ectal excipulum poorly differentiated, 150-250 μ thick, consisting of an outer layer about 80-100 μ broad, of filamentous cells (textura por-
recta) and a more compact inner layer tending toward textura angul-laris about 100-150 μ broad, terminal cells clavate, 5.5-8.0 x 23-28 μ. The outer layer is visible only around the margin, as it soon becomes crushed and partially or wholly eroded away. Asci cylindric, contorted at the base, 350-400 x 18-24 μ, J-, young asci and immaturity spores strong orange yellow (near 7.5YR 7/12) in Melzer's solution. Ascospores hyaline, eliptic, typically flattened on one side,
1-3 guttulate, smooth or very faintly roughened with an incomplete reticulum, (21.4) 24.3-35.8 (37.5) x (9) 10.7-15.8 μ, apiculus very short and truncate or more often broadly rounded, or lacking, 0-1.1 μ long. Paraphyses 2-4 septate above the branches, terminal cell cylindric-capitate, contorted, 4-12 μ across, PALE YELLOW (5y 8.5/4) in Melzer's.

Habit, Habitat, and Distribution.—Solitary to gregarious, in early spring, on soil in conifer or mixed forests from the Rocky Mountains to the West Coast in North America, apparently rare in Europe, often found around melting snowbanks and sometimes developing to considerable size under the snow.


Observations.—Spore shape distinguishes this species readily from G. fastigiata. Spores of G. fastigiata taper more toward the ends and have elongated, narrow apiculi giving them a distinctly fusiform shape (Fig. 1c), while those of G. gigas have shorter, more rounded apiculi or none at all, resulting in a wider ellipsoid to oval shape (Fig. 2c). In some cases there is no evidence of an apiculus in G. gigas, while in others the only suggestion of an apiculus is a slightly thickened wall at one or both ends of the spore. Rarely the apiculus is truncate and depressed as in Discina leucoxantha Bres.; but in all cases, when present, it is much broader than in G. fastigiata. The habit of fruiting under or near melting snowbanks may be significant in distinguishing the two species also.

Discussion

In a single publication (1832) Krombholz described five new species of Helvella that apparently belong in Gyromitra Fr. (sensu Harmaja, 1969). He distinguished between them largely on characters of gross morphology and color of the ascosporo so that it has been very difficult for later workers to apply his names accurately to the species they find. However, with G. gigas and probably also with G. fastigiata he did give sufficient microscopic details for correct
identification, but it appears that quite generally the names have been applied incorrectly.

Krombholz stated that both species were found in the vicinity of Prague in early springtime. His descriptions specify a distinct difference in spore shape, as he described the spores of *G. gigas* as “gross und vollkommen oval,” whereas spores of *G. fastigiata* are said to be “elliptisch-spindelformig.” He did not illustrate the microscopic characters of *G. fastigiata* and his drawings of *G. gigas*, by themselves, are ambiguous since fine details of spore structure are not shown and since he shows both 1- and 2-guttulate ascospores. Most of the spores are shown with broadly rounded apices, although some are more or less pointed. It should be noted, however, that at the magnification used details of surface patterns and apiculus might not be discernible unless the original drawings were more accurate than those of Krombholz apparently were. No mention is made of an apiculus on spores of either species. However, if apiculi were included in the description of spore shape, it would make the spores more nearly fusiform as Krombholz gives for the spore shape of *G. fastigiata*, rather than the oval shape he described for spores of *gigas*. The fact that he mentioned the 3-guttulate spores in *G. fastigiata* (and in this species only) clearly identifies it as a member of the *caroliniana-gigas* complex and refutes a possible identity with *G. esculenta* (Pers.) Fr. This, together with the brief descriptions of spore shape in the two species cited above, convinces me that the species with more definitely fusiform spores having longer apiculi should be called *fastigiata*, although it is commonly known as *gigas* both in Europe and in America. Just how the epithet *gigas* came to be associated with a species having fusiform spores with well-developed apiculus is not clear, but Krombholz’s mention of brownish ascus tips and a taste of fresh almonds for *G. fastigiata* may have discouraged use of this name for the common European species. Both his description and illustrations indicate a tricuspidate-lobed receptacle which may not be consistently apparent. His reference to Flora Danica Plate 116 (Oeder, et al., 1766-1883) and his suggestion of a close relationship to *Gyromitra infula* (Schaeff. ex Fr.) Quél. may have encouraged the idea that *G. fastigiata* was a synonym of *G. esculenta* in spite of his description of 3-guttulate spores for *G. fastigiata*. Fresh specimens referable to this species, which I have studied, have no taste and I have not seen brownish ascus tips in any of the collections studied; however, if there is a European species in this complex having these characters and a consistently fastigiate form, then perhaps the American species, which lacks them, should have a new name. Until this is confirmed, however, I prefer to use Krombholz’s species names as indicated above.

Quélet (1873) transferred *Helvella gigas* Krombh. to the genus *Gyromitra* Fr., giving no illustrations and such an incomplete description, based on macroscopic characters, that no one can be certain what species he had in mind. However, in his very brief synopsis of the genus he states, “Spore ovale, bi-oellée.” Later (1886) he listed *G. curtipes* Fr. as a synonym of *G. gigas*. Although, at the
time he transferred *H. fastigiata* Krombh. to *Gyromitra*. He recognized both species, Rehm (1896) illustrated the spores of *G. gigas* with narrow, pointed apices and described them as “breit spindelförmig,” which is very nearly identical with Krombholz’s description of the spores of *H. fastigiata*. Thus it seems that the species concepts of Krombholz were not clearly understood from the time the two species were first included in *Gyromitra*. Since my objective here is to elucidate species concepts, the broader argument of generic limits will not be entered, except to say that *Gyromitra* appears to be the best genus for these two species. After they were transferred to *Gyromitra* Fr., later workers have quite consistently given *G. fastigiata* as a synonym of *G. gigas*.

The confusion between these and related species is very complex, as indicated by the following resume of only a few of the many reports concerning them. Cooke (1879) illustrated the spores of *G. gigas* as broadly fusiform with distinctly pointed ends quite different from those published with Krombholz’s original description and quite like those Krombholz described for *G. fastigiata*, but which he did not illustrate. According to Phillips (1893), Cooke’s figure was drawn from a specimen in the Berkeley herbarium at Kew. Velenovsky (1920-1922) described and illustrated both species, but he depicted the *G. fastigiata* kind of spores for *G. gigas*, and for *G. fastigiata* he showed spores of the type found in *G. esculenta*. Lohwag (1966) recognized that material which he collected had the fusiform spores of *G. fastigiata*, as he reproduced Krombholz’s original description and illustrations of that fungus; but he was apparently persuaded by Maas Geesteranus that it was identical with *G. caroliniana* (Bosc ex Fr.) Fr. [= Neogyromitra caroliniana (Bosc ex Fr.) Imai], a species which actually has quite different spores. Boudier (1905) did not report *G. fastigiata*; but he described and illustrated, separately, *G. gigas* and *G. curtipes* Fr. and showed spores of the *G. fastigiata* type for both of them, while stating that *G. curtipes* may be just a young stage of *G. gigas*. Seaver (1928) likewise failed to mention *G. fastigiata* and regarded both *G. gigas* and *G. curtipes* as synonyms of *Helvella caroliniana*. Later (1942) he stated his dissatisfaction with Imai’s (1938) separation of *G. gigas* and *G. caroliniana* and recommended that more field work was necessary to resolve the problem. In the latter I strongly concur. His illustrations of spores (Seaver, 1942) are not representative of either *G. gigas* or *G. fastigiata* but appear to be *G. caroliniana* or *G. costata* Schw. ex Cke. In detailing the effects of KOH on species of *Helvella*, Kanouse (1948) did not mention its distorting effect on ascospores (McKnight, 1968). She described the ascospores of *H. gigas* as smooth and indicated as preference for the illustration of Bresadola (1932) over that of Boudier (1905-1910) in interpreting the species. Both authors show strongly apiculate spores, as found in *G. fastigiata*, but Bresadola shows them without surface ornamentation.

Benedix (1969) writes of the typical *gigas apiculus* (“die durchweg typische gigas-anhängsel”) with reference to the strongly apiculate-spored species which I call *fastigiata* and treats *H. fastigi-
ata Krombh. as a synonym of the American species, Neogyromitra caroliniana (Bosc ex Fr.) Imai. The latter appears to be a rare species in America, not clearly differentiated at this time from Gyromitra costata Schw. ex. Cke. and quite widely confused with a much more common species, Gyromitra brunnea Underwood [= Helvella underwoodii (Underw.) Seaver]. Although inadequate details are given, Smith (1963) is the only recent author, to my knowledge, who has correctly distinguished G. brunnea and G. caroliniana. The spores of these two American species are very much alike and quite different from those of Krombholz’s two species being considered here. Nannfeldt (1932) considered G. fastigiata, G. curtipes Fr., and G. labyrinthica Fr. all as synonyms of Neogyromitra gigas (Krombh.) Imai. His description of the ascospores of N. gigas is more like Krombholz’s H. fastigiata than H. gigas, and the specimens at BP1 and PR in the Lundell and Nannfeldt exsiccati confirm this. Fries’s original descriptions of G. curtipes (1866) and G. labyrinthica (1871) give neither illustrations nor written details of the ascospores needed to determine their possible affinity with G. gigas and G. fastigiata. On the basis of gross morphology Fries (1871) indicated a close similarity of G. labyrinthica with G. esculenta and G. caroliniana. He placed labyrinthica and caroliniana in a separate subgenus, Lacunaria. His illustrations of G. curtipes show a fungus very different in color from the other Gyromitra species and very much like a variety of Discina olympiana Kan. reported recently from Wyoming (McKnight, 1969) and possibly also comparable to Pilat’s (1953) pallid variety of Gyromitra infusa.

The collections reported here fall into two distinct categories as far as spore shape is concerned. These correlate very well with the descriptions given originally by Krombholz for Helvella gigas and H. fastigiata and permit easy separation of the two species (Figs. 1c, 2c). The fact that the two species have been regarded as one by most observers since their original descriptions by Krombholz tends to obscure the differences which actually exist between them. This is especially true with regard to gross morphology, since many collections have changed on drying so much that the dried specimens give little information about their original form. Having recognized spore differences as a practical criterion for separation of the two species, one can begin to make meaningful observations on other characters such as size, shape, color, and ecology.

These two species appear to have different ecological requirements, as indicated by their distribution in North America (Fig. 3). On the basis of the collections cited here, Gyromitra gigas appears to be restricted to the mountains of the West, while G. fastigiata appears to be primarily an eastern species, although a few collections of it were taken in Utah, Oregon, Idaho, and Washington. It remains to be seen just how far north and south G. gigas extends in the western mountains and how common G. fastigiata is in the West and particularly in the Northwest. Snyder (1938) reports H. caroliniana from Tacoma, Wash., although his description is not sufficiently detailed to distinguish it from G. fastigiata. In an unpublished thesis, Brough
Gyromitra fastigiata + Gyromitra gigas

Fig. 3. Distribution of two species of *Gyromitra* in North America based on collections studied for this report.

(1958) refers the Tacoma collection and two other Washington collections to *Neogyromitra gigas* (Krombh.) Imai. His drawings of the spores of one of them, presumably from near Lake Keechelus, show the long apiculus of *G. fastigiata*. The specimens could not be obtained for study. The number of European collections examined in this study is too small to reach any conclusion except the tentative suggestion that *G. fastigiata* appears to be much more common than *G. gigas*.

There may be a significant difference in the conditions which stimulate fruiting for these two species. Krombholz described *H. gigas* as fruiting in March and April and *H. fastigiata* as appearing in April. Nannfeldt (1932) stated that *G. gigas* emerges slower than *G. esculenta*, and Falck (1923) gives the fruiting for *G. esculenta* as March to May and for *G. gigas* as April to May. From their illustrations and descriptions as well as the Lundell and Nannfeldt exsiccatai specimen cited above it is clear that Nannfeldt and Falck both were dealing with *G. fastigiata* as the species is used here, not *G. gigas*. This difference in time of fruiting may not be significant in itself, since all three are clearly early spring-fruiting species; but the frequent association of *G. gigas* with melting snowbanks may be important. In those areas where both *G. fastigiata* and *G. gigas* occur observations should be made on this and on details of morphology to see if other differences can be found.
Much has been written about spore ornamentation in the G. gigas-G. caroliniana complex. There is some confusion resulting from faulty taxonomy of the species but also some due to differences in spore ornamentation in different populations of G. gigas and in maturity of spores of G. fastigiata. Although Krombholz illustrated the spores of H. gigas as smooth, I admit into the species those with slightly roughened spores having spore characteristics otherwise appropriate for G. gigas. Actually there is much variation within the species with regard to this character and to spore size, shape, and apiculus. Since, when present, spore ornamentation seems to develop late in maturation of the spores of all the Discineae, this character must be used with caution in characterizing the species. However, spores of some specimens of G. gigas collected on a coverslip from maturing ascocarps have smooth spores while those of other specimens are faintly roughened (Fig. 2). In G. fastigiata the reticulum is more distinct and more consistently present on mature spores. In both G. fastigiata and G. gigas, in contrast to G. caroliniana and G. brunnea, the reticulum is much finer and lower and is not drawn up into spicules toward the spore apices. These differences were accurately shown by Maas Geesteranus (1965, Figs. 3 and 4) and parallel the differences in ornamentation shown by me (McKnight, 1969) for Discina macrospora Bub. and Discina warnei (Pkt.) Sacc.

Although I have seen few fresh specimens of G. fastigiata, my notes on these and on numerous collections of G. gigas indicate that there may be a very subtle but significant difference in color of the fresh hymenium of the two species, G. fastigiata being more yellow than G. gigas. In both species there is considerable color variation on a single specimen and even more between specimens and between collections. However, the various hymenium colors of both are in the large blocks of color designated "strong yellowish brown," "strong brown," and "moderate brown" by Kelly and Judd (1955). Some specimens of G. fastigiata were also recorded as "dark grayish yellow," and the "strong yellowish brown" is more yellow than that of G. gigas, as indicated by the Munsell notations reported above. Such small color differences really may not be significant at the species level, but they do seem to be confirmed by a subtle difference in hymenium color in the two species as seen in well-dried herbarium specimens. Observations on color range of the two species fruiting in the same area could be important in establishing the significance of this character in species differentiation. Collectors in Washington, Idaho, Oregon, and Utah should watch for such an opportunity.

The significance of gross morphology and ascocarp size in distinguishing these two species cannot be assessed without more field observations, particularly on G. fastigiata. While admitting to having seen two few fresh collections of G. fastigiata for a final judgment, I get the impression that differences in size and macroscopic form between it and G. gigas are not enough to permit distinction of fresh specimens of the two in the field without examining their spores. The "fastigiate" form described originally and illustrated by Krombholz (1832) appears to be uncommon in either species, but this con-
clusion may be premature for *G. fastigiata*. Both species are exceedingly variable in gross form and size. The receptacle is very much convolute in some specimens with numerous small folds extending in all directions, whereas in others it is almost smooth. This character does not necessarily change with age. Although the stipe varies greatly also, it can always be characterized as thick, longitudinally ribbed or lobed, and containing multiple channels inside throughout part or all of its length, contrasting with the typically solid stipe developed on some specimens of *Discina*. The receptacle is usually folded back against the stipe and is often intergrown with it. The entire asccarp may be wider than it is tall, and the stipe may be almost completely hidden by the recurved receptacle. In all specimens of some populations the stipe may be very long, calling to mind Krombholz’s (1832) illustration of *Helvella tremellosa* Krombh. It may be basically cylindrical or expanded downward. The very short stipitate forms of *G. gigas* bear a close resemblance to specimens of *Discina apiculatula* McKn. which have an especially well-developed stipe, and short stipitate forms of *G. fastigiata* look superficially like *D. perlata* or *D. macrospora* Bubák. They are readily recognizable in the field, however, in spite of the fact that they sometimes grow in mixed populations as do different species of *Discina* (McKnight, 1969) and other combinations of *Gyromitra* and *Discina*. Last summer in the Uinta Mountains I found one specimen of *G. gigas* with a specimen of *Discina perlata* (Fr.) Fr. actually touching its stipe. Fruiting in such close proximity suggests that the mycelia grow intermixed in the soil. One small, solitary specimen of *G. fastigiata* collected in Maryland (McKnight 11739, BPI) had an entirely discinoid receptacle and multilacunate stipe. Further observations are needed on species in both genera to circumscribe the species accurately, after which the thorny problem of generic concepts may be resolved.

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