

SPECIFIC AND GENERIC DELIMITATION
IN THE HELVELLACEAE*

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(With Plate 23)

A revised Latin and English diagnosis is given for the family Helvellaceae as emended by Berthet and Dissing. The delimitation of the genera and some species in the family is discussed. Some comments are given on a new tool: the scanning electron microscope (SEM).

The studies by Le Gal on spore morphology (1947) and especially the cytological studies by Berthet (1964) yielded important information that made it possible to give a more reliable classification of the composing elements of the family Helvellaceae and of the operculate discomycetes in general. All members of the family are devoid of carotinoid pigments, a conclusion also reached by Arpin's chemical studies (1970).

It would be very interesting to know the chemical composition of the pigments in the Helvellaceae, while the guttules of the spores might also be worth a study.

The Helvellaceae as discussed below is taken in the sense of Berthet (1964) and as emended by Dissing (1966). It includes the following taxa: tribus *Helvelleae* Diss., with *Underwoodia* Peck (not considered by Berthet, l.c.), *Helvella* L. ex St-Amans emend. Nannf., and *Wynella* Boud.; tribus *Gyromitreae* Diss., with *Gyromitra* Fr., including *Pseudorhizina* Jačevskij (= *Helvellella* Imai; not considered by Berthet); and tribus *Discineae* Diss., with *Neogyromitra* Imai, *Discina* (Fr.) Fr., *Rhizina* Fr. ex Pers.

This concept of the family was accepted by Dennis (1968; European genera only), Rifai (1968), and Kimbrough (1970), while Maas Geesteranus (1967) and Eckblad (1968) found reasons not to do so.

Maas Geesteranus recognized three families in the group: Helvellaceae, including *Helvella*, *Gyromitra*, and *Pustulina* (*Wynella* was not considered), while his Discinaceae and Rhizinaceae correspond to these families as conceived by Benedix (1961).

Eckblad (l.c.) restricted the Helvellaceae to the genera included in the tribus Helvelleae Diss.; he excluded the Rhizinaceae corresponding to Dissing's tribes Gyromitreae and Discineae. Characters of the excipulum motivated Eckblad to make this separation.

Since the Helvellaceae have been radically emended since the inception new descriptions are given below.

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H E L V E L L A C E A E Fr. emend.

Carposoma sessile vel stipitatum, cupulatum, ephippioides, auriforme, gyromitroides vel clavatum (raro pulvinatum). Stipes, si praesens, teres, compressus vel lacunosus. Hymenium planum vel convolutum, albidum, cinerascens, fuscescens vel nigrum. Superficies exterior glabra vel pubescens.

Excipulum omnino textura intricata vel medullare excipulum texture intricata ab excipulo exteriore textura globosa vel angulata insigni bene discretum.

Asci operculati, 8-spori, cylindrici, J-, non ex hymenio eminentes. Paraphyses plerumque rectae, septatae, apice paulum incrassatae, pigmentis carotenoidibus nullis. Sporae hyalinae, quadrinucleatae, 1-4nas guttulas sat magnas continentes, aut globulares vel anguste ellipticae laeves, interdum involucre perisporiali indutae, aut late ovaes vel ellipticae vel fusiformes, pustulis rotundatis vel reticulo cyanophilo ornatae.

Nulli status imperfecti in familia observati.

Terrestris vel ligno carioso arborum coniferarum connexa.

GENUS TYPIFICUM:—*Helvella* L. ex St-Amans emend. Nannf.

Fruitbody sessile or stipitate, cup-shaped, saddle-shaped, ear-shaped, gyromitroid, or clavate (rarely pulvinate). Stipe when present, terete, compressed, or lacunose. Hymenium even or convoluted, whitish, greyish, brownish or black. Outer surface glabrous or pubescent.

Excipulum of textura intricata throughout, or medullary excipulum of textura intricata and well distinct from the outer excipulum of textura globosa to textura angulata.

Asci operculate, 8-spored, cylindric, J-, not protruding beyond the hymenium. Paraphyses normally straight, septate, slightly enlarged above, without carotinoid pigments. Spores hyaline, tetranucleate, with 1-4 large guttules, globose or narrow elliptic, smooth, sometimes with a perisporial sheath, or broadly ovate, or elliptic to fusiform, with blunt pustules or a reticulate cyanophilous ornamentation.

No imperfect stages known in the family.

Terrestrial, or connected with decaying wood of coniferous trees.

TYPE GENUS:—*Helvella* L. ex St-Amans emend. Nannf.

S U R V E Y O F T H E G E N E R A

H E L V E L L A L. ex St-Amans emend. Nannf.

Generic delimitation in accordance with Nannfeldt (1932, 1937), who worked out Quélet's ideas (1886). Dissing (1966: 12-14) gave a brief historic review of the genus.

Maas Geesteranus (1967), Eckblad (1968), Rifai (1968), Kempton & Wells (1970), Kimbrough (1970), Nothnagel (1971) accepted Nannfeldt's generic delimitation and Dissing's species concept, although some authors intimated that the number of species recognized (26) was rather low. Dennis (1968) still found reasons to keep the genera *Paxina*, *Cyathipodia*, and *Leptopodia* apart in addition to *Helvella* sensu stricto.

Svrček & Moravec (1968) added *Helvella branzeiana* to the list of European species. In 1967 Dr. A. Raitviir, Estonia found a *Helvella* in Asia which is considered to be identical with *Acetabula aestivalis* Heim & Remy. This will be published as *Helvella aestivalis* (Dissing & Raitviir, 1973) in a joint paper.

Thus the number of species now recognized is 28.

There can be no doubt that serious studies of the North American flora will increase this number. A study of a rather rich material from India (carefully collected by Drs. R. A. Maas Geesteranus and C. Bas, The Netherlands, and at present in the author's possession) will probably further increase the number of species.

Until now distinctive characters on the species level are: type of fruitbody, colour, glabrous or pubescent outer surface. With the exception of *H. macrospus* the spores are of minor diagnostic value.

Keys to the European species (except *H. branzeiana*) were given by Dissing (1966; in English). A German translation was given by Nothnagel (1971). Maas Geesteranus (1967) gave a key to the species known from The Netherlands (in Dutch).

WYNELLA Boud.

Only one species: *W. silvicola* (Beck apud Sacc.) Nannf. Nannfeldt (1967) discussed its delimitation, nomenclature and distribution.

I agree with Nannfeldt in all points but one: viz. that *Wynella* (as represented by *W. silvicola*) should be placed in a tribe of its own. Surely it differs from the other genera of the family because of its ear-shaped apothecia but due to characters of the spores and the excipulum I regard it closely allied to *Helvella* and continue to believe that it has to be placed in the same tribus (cf. *Helvelleae* Diss., 1966).

The reddish brown colours found in *W. silvicola* seem (i.e. without a chemical analysis) to correspond to those found in *Helvella aestivalis* (see Dissing & Raitviir, 1973). One might therefore be tempted to claim that the only difference between the two genera is that *Wynella* has ear-shaped apothecia. However, I agree with Nannfeldt (l.c.) that the 'horny consistency' of the dried fruitbodies is a character of importance. At present it is difficult to evaluate this character. When describing the excipulum of *Wynella* one has to use the same terms as when describing for instance *Helvella lacunosa*. It is true that there are quantitative but no qualitative differences, although it might be necessary to examine the content of the cells in the excipulum to find a sound explanation for the difference in the consistence.

UNDERWOODIA Peck

The distribution of the species of this genus is remarkable, with one species in each of the following continents: North America (*U. columnaris* Peck), South America (*U. fuegiana* (Speg.) Gamundi), Australia (*U. beatonii* Rifai).

Gamundi (1957), who did not circumscribe the Helvellaceae, considered *Underwoodia* a true member of that family. Dissing (1966) found the characters of the excipulum and of the spores very similar to those of some species of *Helvella* and he included *Underwoodia* as a member of the tribus *Helvelleae*.

It has never been shown that the spores in any *Underwoodia* species actually possess four nuclei.

Eckblad (1968), who stresses anatomical characters, included the species of *Underwoodia* in *Helvella*, because it "does not differ in any other character than form".

Although this might be correct, it seems that the form is so deviating from any known fruitbody type in *Helvella* that it cannot possibly be included in that genus.

A key to the known species of *Underwoodia* is given by Rifai (1968).

GYROMITRA Fr.

“The genera in the tribus Gyromitreae have a habit much like the highest developed species in the genus *Helvella* (considered to be the species in the sections *Lacunosae* and *Elasticae*), but can be separated well on characters of the spores and on anatomy. The spores are narrow elliptical with two small guttulae, or sphaerical with one guttula. In the genera *Gyromitra* and *Helvellula* it is not possible to distinguish clearly an outer excipulum and a medullary excipulum. . . . Mutually the genera *Gyromitra* and *Helvellula* are mainly separated on characters of the spores, but I am not at all sure these characters can separate the genera if examined in detail.” (Dissing, 1966: 28).

Harmaja (1969b) included *Pseudorhizina* (*Helvellula*) *sphaerospora* in *Gyromitra*. I can accept this, whereas I disagree in including *Discina* and *Neogyromitra* in *Gyromitra* as well (see below). At present the following species can be referred with certainty to *Gyromitra*: *G. esculenta* (Pers. ex Fr.) Fr., the type species, *G. infula* (Schaeff. ex Fr.) Quél., *G. ambigua* (Karst.) Harmaja, *G. californica* (Phill.) Raitv., *G. tasmanica* Cooke, and *G. sphaerospora* (Peck) Sacc. Raitviir (1965) described *G. infula* var. *apiculatispora*, with “apiculate” perisporium, Harmaja (1969b) found this taxon identical with *G. ambigua*. He further evaluated in a promising way the character of the perisporium. However, I find that the presence of a perisporium in some species of *Gyromitra* cannot justify the merging of *Gyromitra*, *Discina*, and *Neogyromitra*.

Hitherto only one species (*G. tasmanica*) has been described from the Southern hemisphere (New Zealand), but material from South America may increase the number of species by two (Gamundi, personal information). A critical study of the whole genus is highly needed.

A key to the species is not known to me.

DISCINA (Fr.) Fr.

Fruitbodies sessile or short stipitate, cup-shaped or expanded. Eckblad (1966) included *Neogyromitra* in *Discina* because “. . . . *Neogyromitra* actually does not differ from *Discina perlata* in any other character than a slight difference in form: pileate apothecia in *Neogyromitra* versus stipitate, cupulate to convex apothecia with folded hymenium in *Discina*”.

I feel much attracted by Eckblad's ideas, which might well prove to be correct. I hesitate however to follow him until details of the ornamentation of the spores have been studied in both genera (see Appendix p. 429).

Harmaja (1969a) combined the genera *Gyromitra*, *Discina*, and *Neogyromitra*. At a first glance his illustration (l.c., fig. 1) looks very fascinating. Still it is not proved (as far as I know) that the perisporial sheath is homologous with the appendages

found on the spores in *Discina* and *Neogyromitra*. According to Harmaja it is the periplasma which stains in spores of *Gyromitra*, while it is the ornamentation that is taking stain in *Discina* and *Neogyromitra*. Further the fruitbodies do not reflect the same beautiful line (of "evolution") expressed in Harmaja's figure.

McKnight (1969) made a critical study of the North American species of *Discina*; European species were also considered. He gave a key to the six species recognized by him.

Paradiscina Benedix (1969) is considered to be superfluous.

NEOGYROMITRA Imai

Fruitbodies stipitate, gyromitroid. Closely allied to species of *Discina*. Fruitbodies varying much in size, shape, and colour. A greater number of 'species' have been described (formerly as species of *Gyromitra*; see Nannfeldt, 1932), but modern authors have reduced the number of species to two: *N. gigas* (Krombh.) Imai and *N. caroliniana* (Bosc ex Fr.) Imai (see Maas Geesteranus, 1965). The two species are separated by characters of the spores (Maas Geesteranus, l.c., figs. 2-4).

Fastigiella Benedix (1969) is considered to be superfluous.

RHIZINA Fr. ex Pers.

Only one species, *Rhizina undulata* Fr. ex Fr., which is unique in the Helvellaceae for three reasons: the brown, non septate setae in the hymenium (originating from the medullary excipulum), the numerous root-like structures from the underside of the fruitbody, and the parasitic habit, on young, planted coniferous trees. *Rhizina undulata* grows mostly on burnt areas (see Hagner, 1962; Petersen, 1970).

Some authors prefer to place this species in a family of its own (Benedix, 1961; Maas Geesteranus, 1967).

APPENDIX

In Plate 23 some spores are shown photographed in the scanning electron microscope (SEM). The opportunity is used to show spores from non-helvellaceous discomycetes as well, because I wish to demonstrate that the SEM technique might prove to be a valuable tool in future work in the group. I do not, of course, expect that the use of the SEM in general will make revolutionary alterations in the classification of operculate discomycetes. Because the characters of the spores are so important in this group it is believed that in many cases use of SEM techniques will give more reliable, and better reproduceable results than drawings. This is in no way meant as slighting the very painstaking and skillful illustrators in discomycetology such as Le Gal, Rifai, Maas Geesteranus, and van Brummelen. It goes without saying that the much higher resolving power of the SEM makes it possible also to realize details which cannot be seen in the light microscope. Some examples are shown in Plate 23. It shows that in *Rhizina undulata* (Figs. f, i) the ornamentation does not cover the ends of the spores (arrow in Fig. f) while in *Neogyromitra* the whole

spore is covered by ornamentation. I believe it will be valuable to have the spores of all species of *Rhizina*, *Discina* and *Neogyromitra* illustrated in a similar manner.

It is also interesting that *Pustulina ochraceus* and *Peziza fimeti* are not "smooth-spored" as described in literature. In *Helvella acetabulum* the spores are completely smooth. The wart in the middle of the meshes in spores of *Aleuria aurantia* (Fig. g) can also be seen in light microscope provided the spores are stained in cotton blue. This has never been mentioned in previous descriptions.

Material and methods.

All collections photographed in Plate 23 are deposited in the Botanical Museum, Copenhagen (C). *Neogyromitra gigas* is illustrated from Swedish material and *Saccobolus versicolor* was growing on horse dung sent from Greenland. All other collections are from Denmark.

Preparation of the spores for study in the scanning electron microscope was very simple. The spores in Figs. c, d (in culture), e, f, h, i, j, k, n were all from fresh fruitbodies which were allowed to puff the spores on the metal stub. Because the fruitbodies are so tiny fresh material of *Peziza fimeti* and *Saccobolus versicolor* was placed in a drop of water on the stub, thus allowing the spores to be shot off in the water. After shooting had ceased the stub with water and spores was freeze-dried.

The specimens of *Neogyromitra gigas* and *Aleuria aurantia* (Figs. a, b, g) had been dried, but with spores deposited on the hymenium. A fragment of the hymenium was placed in a drop of 70 % alcohol on the stub. The spores then loosened from the hymenium; after this the alcohol was substituted by water, and the stub finally freeze-dried.

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REFERENCES

- ARPIN, N. (1968). Les caroténoïdes des Discomycètes: essai chimiotaxinomique. Thèse, Univ. Lyon (& in Bull. mens. Soc. linn. Lyon 38 (Suppl.): 169 pp. 1969).
- BENEDIX, E. H. (1961). Zur polyphyletischen Herkunft der Helvellaceen. In Z. Pilzkunde 27: 93-102.
- (1969). Art- und Gattungsgrenzen bei höheren Discomyceten. 3. In Kulturpflanze 17: 253-284.
- BERTHET, P. (1964). Essai biotaxinomique sur les Discomycètes. Thèse, Univ. Lyon.
- DENNIS, R. W. G. (1968). British Ascomycetes. Lehre.

- DISSING, H. (1966). The genus *Helvella* in Europe, with special emphasis on the species found in Norden. *In Dansk bot. Ark.* 25 (1) 172 pp.
- DISSING, H. & A. RAITVIIR (1973). Discomycetes of Middle Asia. X. *In Eesti NSV Tead. Akad. Toim.* (In press).
- ECKBLAD, F.-E. (1968). The genera of the operculate Discomycetes. A re-evaluation of their taxonomy, phylogeny and nomenclature. *In Nytt Mag. Bot.* 15: 191 pp.
- GAMUNDI, I. J. (1957). Sobre la identidad de *Geomorium* Spegazzini con *Underwoodia* Peck ("Discomycetes"). *In Darwiniana* 11: 418-422.
- HAGNER, M. (1962). Några faktorer av betydelse för rotmurklans skadegörelse. *In Norrlands Skogsv. Förb. Tidskr.* 9: 245-270.
- HARMAJA, H. (1969a). A wider and more natural concept of the genus *Gyromitra* Fr. *In Karstenia* 9: 9-12.
- (1969b). A neglected species, *Gyromitra ambigua* (Karst.) Harmaja, n. comb., and *G. infula* s. str. in Fennoscandia. *In Karstenia* 9: 13-19.
- KEMPTON, P. E. & V. L. WELLS (1970). Studies on the fleshy fungi of Alaska. 4. A preliminary account of the genus *Helvella*. *In Mycologia* 62: 940-959.
- KIMBROUGH, J. W. (1970). Current trends in the classification of Discomycetes. *In Bot. Rev.* 36: 91-161.
- LE GAL, M. (1947). Recherches sur les ornements sporales des Discomycètes operculés. *In Anns Sci. nat. (Bot.)* XI 8: 73-297.
- MAAS GEESTERANUS, R. A. (1965). Einiges über *Neogyromitra caroliniana*. *In Proc. K. Ned. Akad. Wet. (C.)* 68: 128-134.
- (1967). De fungi van Nederland. 2a Pezizales - deel 1. *In Wet. Meded. K. Ned. natuurh. Ver.* 69: 72 pp.
- McKNIGHT, K. H. (1969). A note on *Discina*. *In Mycologia* 61: 614-630.
- NANNFELDT, J. A. (1932). Bleka Stenmurklan, *Gyromitra gigas* (Krombh.) Cke. *In Friesia* 1: 34-45.
- (1937). Contributions to the mycoflora of Sweden. 4. On some species of *Helvella* together with a discussion of the natural affinities within Helvellaceae and Pezizaceae trib. Acetabulae. *In Svensk bot. Tidskr.* 31: 47-66.
- (1966). On *Otidea caligata*, *O. indivisa* and *O. platyspora* (Discomycetes Operculatae). *In Anns. bot. fenn.* 3: 309-318.
- NOTHNAGEL, P. (1971). Die *Helvella*-Monographie von Dissing. *In Mykol. Mitteil Bl., Halle* 15: 8-25.
- PETERSEN, P. M. (1970). Danish fireplace fungi, an ecological investigation on fungi on burns. *In Dansk bot. Ark.* 27: 97 pp.
- QUÉLET, L. (1886). Enchiridion Fungorum in Europa media, et praesertim in Gallia vigentium. Lutetiae.
- RAITVIIR, A. (1965). Taxonomical notes on the genus *Gyromitra*. *In Eesti NSV Tead. Akad. Toim. (Biol. Seeria)* 3: 320-323.
- RIFAI, M. A. (1968). The Australasian Pezizales in the Herbarium of the Royal Botanic Gardens Kew. *In Verh. K. Ned. Akad. Wet., Afd. Natuurk.* II 57 (3): 295 pp.
- SVRČEK, M. & J. MORAVEC (1968). *Helvella (Leptopodia) branzeiana* sp. nov., eine neue Spezies aus Böhmen. *In Česká Mykol.* 22: 87-89.

EXPLANATION OF PLATE 23

Scanning micrographs. Spores. — a, b, *Neogyromitra gigas*, Lundell & Nannf. exs.

No. 1353, a, $\times 1,625$, b, $\times 2,880$. — c, *Peziza echinospora*, H.D. 71.23, $\times 3,120$. — d, *Ascobolus crenulatus*, H.D. 71.14, $\times 5,225$. — e, h, *Pustulina ochraceus*, H.D. 71.24, e, $\times 2,652$, h, $\times 5,250$. — f, i, *Rhizina undulata*, H.D. 71.42, f, $\times 1,195$, i, $\times 5,320$. — g, *Aleuria aurantia*, H.D. 64.236, $\times 2,625$. — j, *Peziza micheli*, H.D. 71.102, $\times 2,800$. — k, *Peziza praetervisa*, H.D. 71.31, $\times 2,780$. — l, *Peziza fimeti*, H.D. 71.12, $\times 2,150$. — m, *Saccobolus versicolor*, H.D. 71.06, $\times 900$. — n, *Helvella acetabulum*, H.D. 71.37, $\times 1,550$.

