

# A revision of the *Helvella acetabulum* group (Pezizales) in Fennoscandia

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What has been regarded as *Helvella acetabulum* (St-Am.) Quél. in Fennoscandia is shown to be a diverse assemblage of species. This is due partly to a collective species concept, partly to true misidentifications. Two new species are described: *Helvella arctoalpina* Harmaja and *H. dryadophila* Harmaja. The diagnostic characters, phenology and distribution of *H. acetabulum* s.str. and the two new species are presented; the concept of the first taxon is restricted to a large, rather pale, early southern species, while the other two are small, dark, late arctic-alpine species. Differences in anatomy, including some 'new' features, were observed between the species, and the usefulness of such characters at specific level in the genus *Helvella* St-Am. is emphasized.

Four quantitative characters of *H. acetabulum*, *H. arctoalpina* and *H. dryadophila* were analysed statistically. The material for *H. dryadophila* was insufficient for comparison, but highly to fairly significant differences could be shown between the two other species.

*H. pocillum* Harmaja, described earlier, is reported as new to Norway, this being the second known collection of the species. *H. palustris* Peck, which does not belong to the *acetabulum* group, is a valid species occurring in northern Finland and new to this country.

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## Introduction

The genus *Helvella* St-Am. (Pezizales) was recently monographed by the Danish mycologist Dr. Henry Dissing (1966), who made a most valuable contribution to the clarification of old epithets and the examination of a great many type and other collections from different parts of the world. Unfortunately, however, this study contains certain discrepancies between the key, the species descriptions, the lists of specimens examined (especially their published label notes), and the distribution maps. There are also errors in printing, spelling of names, and nomenclatorial matters, and, for some reason, the Finnish *Helvella* material was not included (except for a very few specimens). The species concept is too collective in the work. Careful comparison of the macroscopic and anatomical characters, and the distribution and phenology of different collections would have revealed more specific hiatuses in the

material of the monograph. As regards the microscopic characters, exact illustrations are given of the individual excipular cells, but the descriptions and illustrations of the anatomy of the excipulum are somewhat too simplified and generalized.

Dissing's descriptions are undoubtedly more accurate than any published earlier, but my own studies have revealed more specific differences in the excipular details, including some features which have not been used previously in the taxonomy of *Helvella* or the Pezizales in general (cf. also Harmaja 1977). The monograph also contains obvious misidentifications, which often appear to be due to failure to examine the specimens microscopically. The type specimen of *H. pocillum* Harmaja (Harmaja 1976) was determined and published by Dissing as *H. acetabulum* (St-Am.) Quél., a species which, according to Dissing himself, has spores 16—19  $\mu\text{m}$  long, whereas the spores of the specimen are surprisingly large for a *Helvella*, measuring 25—28

$\mu\text{m}$ . The material also contained mixed collections. E.g. a specimen named and published as *H. acetabulum* (Norway, Oppland, Lom, Høyrokampen, *Dryas* association, 29.VIII.1957 Eckblad, O), consisting of 83 apothecia, did not contain *H. acetabulum* s.str., but no less than four other species of *Helvella* instead: *H. arctoalpina* n. sp. (31 apoth.), *H. dryadophila* n. sp. (10 apoth.), *H. pocillum* n. sp. (40 apoth.; already described on the basis of another specimen in Harmaja 1976), and *H. solitaria* Karst. (2 apoth.; syn. *H. queletii* Bres.: see Harmaja 1977).

The fact that *H. acetabulum* appeared to have too wide a phenological amplitude in the monograph made me begin some revisory work in the genus *Helvella*. Some taxonomically apparently uniform species of this genus do in fact seem to possess long fruiting periods (and wide distributions), but certain things made me suppose that *H. acetabulum* is properly a spring to early summer species in Europe. According to the label notes of the specimens given in Dissing (1966), the fruiting period in Sweden and Norway lasts from mid-May to late September (there is, however, some discordance between this information and the fruiting period he gives at the end of the species description). I have examined 13 of the 15 collections (partly mixed ones; see e.g. above) reported by him from these two countries as collected after July 22 and found that they represent six different *Helvella* species, but not *H. acetabulum* s. str., and one species of *Otidea* (Pers.) Bon.: *H. arctoalpina* n. sp. (9 exx.), *H. dryadophila* n. sp. (2), *H. pocillum* n. sp. (2), *H. solitaria* (2 in mixed collections; one was mentioned above, the other: Norway, Oppland, Lom, Blåhø, 30.VIII.1957 Eckblad, O), *H. costifera* Nannf. coll. (1; Norway, Buskerud, Hol, *Dryas* association, 4.IX.1960 Sivertsen, O), *H. sp.* (1; Sweden, Uppland, Danderyd, 12.IX.1948 Berggren, S; a species with large spores,  $18-24 \times 11.5-14 \mu\text{m}$ , unknown to me), and *Otidea propinquata* (Karst.) Harmaja (syn. *O. indivisa* Vel.; *O. abietina* auct.) (1; Sweden, Södermanland, Halla, 23.IX.1962 Julin, UPS).

Kallio & Kankainen (1964) reported a late find of *H. acetabulum* from Utsjoki, Inari Lapland, Finland (17.VIII.1964 Kallio, TUR). My examination showed that it does not belong to *H. acetabulum* either; it represents the variable species *H. costifera*.

If the three fruiting diagrams in Fig. 14 were united into one histogram, the graph would possess a long 'tail' on the right. Such asymmetry and deviation from normal distribution (which would be

even more pronounced if the data of all the specimens published under *H. acetabulum* in Dissing 1966 were included) would indeed have suggested that the material is heterogeneous and in need of revision.

Besides the phenological features, the distribution of *H. acetabulum* sensu Dissing attracted by attention. A more or less clear division into southern and northern or alpine subareas in a species distribution should always suggest that the material concerned may require revision (though species do exist, in *Helvella* also, which occur over wide regions from beech woods to alpine and arctic areas).

It can be added that a specimen deposited in S under *H. acetabulum*, which for some reason was not included in Dissing's monograph and lacks any annotation of his, proved to belong to *H. silvicola* (Beck) Harmaja (*Otidea auricula* auct., *Wynnella silvicola* (Beck) Nannf.). The label notes may be summarized as follows: '*Acetabula sulcata* (Pers.) Fuck., (Sweden,) Uppland, Lovö, Prästvik, 6.V. 1945 Santesson, det. F. Petrak 1951'. On the other hand, one of the specimens published as *H. costifera* in Dissing (1966) proved to belong to *H. acetabulum* s. str.: Sweden, Västmanland, Sala, Gröna gången, Måns-Ols, 2.VII.1945 Morander 60, UPS.

Thus, the Fennoscandian material determined previously as *H. acetabulum* comprises (1) true *H. acetabulum*, (2) three new species: *H. arctoalpina*, *H. dryadophila* and *H. pocillum*, and (3) some obvious misidentifications. The two first new species will be described here, and *H. pocillum* has already been published (Harmaja 1976). *H. pocillum* was earlier known only from the type collection from Swedish Lapland. It is not treated in detail in the present paper but some notes on it are given. A mixed collection, mentioned above, contained the second known specimen of *H. pocillum*, which was also the first from Norway. Its dry apothecia are shown in Fig. 6, and the stars in Fig. 15 indicate its known distribution.

Some other revisions of *Helvella* will be done by me later and one of them is published together with the present contribution (Harmaja 1977). I wish to report already here that, after examining the type specimen macroscopically and microscopically, I consider *H. palustris* Peck a valid species. This agrees with the opinion of Weber (1972), but Dissing (1966) treated the species as synonymous with *H. lacunosa* Fr. *H. palustris* has been found in some localities on moist calcareous ground in northern Finland, and is new to this country.

## Materials and methods

The dried Fennoscandian material deposited as *H. acetabulum* has been examined in most of the important Fennoscandian herbaria (H, HFR, O, S, TUR, UPS), and the 20 specimens listed below have been investigated in detail. Some other material has also been studied. *H. acetabulum* s. str. was examined when fresh as well. The list below comprises all the specimens, nine and two respectively, of the two new species *H. arctoalpina* and *H. dryadophila*, and nine specimens of *H. acetabulum* s. str. examined for comparison. The material of *H. acetabulum* was chosen deliberately from different geographic areas (even outside Fennoscandia) within its distribution, and it includes the northernmost specimens of Fennoscandia; Fennoscandian specimens collected late in the fruiting period have also been included. These 20 specimens were all examined macroscopically and under the microscope, free-hand sections being taken from the apothecium ca. 2–4 mm below the cup margin and mounted in Melzer's reagent. Some sections of each species were also mounted in 5 % KOH and heated cotton blue.

Statistical analyses were made of the variation in spore length, spore width, paraphysis apex diameter and the diameter of the excipular end cells in each of the three species, as represented by the 20 specimens. Twenty measurements (cf. p. 54) were made per specimen for each of these four characters, on sections of one mature dried apothecium mounted in Melzer's reagent. The measurements, made with an ocular micrometer at a magnification of  $\times 600$ , are exact to 0.5  $\mu\text{m}$ . The arithmetical mean, standard deviation, and standard error were calculated for the variation of each of the four characters, for each specimen and, from the specimen means, for the whole material of each of the three species. The confidence limits at the 95 % level were also calculated for all the 80 means of the specimens and the eight specific means of *H. acetabulum* and *H. arctoalpina* (confidence limits for specific means were not calculated for the limited material of *H. dryadophila*).

Student's test (t test) was used to examine whether the four characters, as represented by the nine mean values of the specimens, differ significantly between *H. acetabulum* and *H. arctoalpina*, the two species with sufficient material. All the statistical calculations were made with a Hewlett-Packard 9100B calculator, using the appropriate programmes.

The data presented in Table 1 are based on all the material seen. Besides the nine specimens examined in detail, several other collections of *H. acetabulum* s. str., including all the northern and late ones, were studied microscopically. Free-hand sections of dried apothecia were mounted in Melzer's reagent and studied at a magnification of  $\times 600$ , but the matter in which the paraphysis tips are embedded was observed in heated cotton blue, and the wall thicknesses of the *textura prismatica* cells were measured at a magnification of  $\times 1500$ . The zonal distributions of the species are described in the terms of Ahti et al. (1968).

## Specimens examined in detail

### *H. acetabulum*

1. Finland, Varsinais-Suomi, Lohja rural district, Virkkala, 30.V.1967 Harmaja (H).
2. Finland, Uusimaa, Sipoo, Östersundom, 6.VI.1937 Häyrén (H).
3. Sweden, Västmanland, Sala, the town, 22.VII.1956 Morander (UPS).
4. Sweden, Jämtland, Östersund, Odensala, 22.VII.1950 Holm (UPS).
5. Norway, Akershus, Baerum, Kalvøya, 21.VI.1953 Eckblad (O).
6. Norway, Nordland, Vega, Vega, 3.VII.1962 Vasshaug (O).
7. Denmark, Sjaelland, Boserup, 6.VI.1950 M. Lange, Bille-Hansen & Eckblad (O).
8. Austria, Niederösterreich, Velm, coll. in May, G. de Beck (Krypt. exs. (Vindob.) no. 139, H).
9. Canada, Ontario, L. Opinicon, Queen's Biol. Sta., 9.VI.1963 Kendrick (H).

### *H. arctoalpina*

1. Sweden, Jämtland, Åre, Storlien, fjeld Rekdalshöjden, top of the fjeld, on bare soil among fjeld plants, VIII. 1943 Romell (UPS).
2. Sweden, Torne Lappmark, Jukkasjärvi, fjeld Låktatjåkko, on talus on slopes above Kopparåsen railway station, 5.VIII.1943 Sandberg (UPS).
3. Norway, Oppland, Lom, eastern end of lake Bøvertvatn, alt. ca. 950 m, 22.VII.1967 Løkken (O).
4. Norway, Oppland, Lom, Bøverdalen, fjeld Høyrokampen, alt. 1250–1300 m, 10.VIII.1952 Nordhagen (O).
5. Norway, Oppland, Lom, fjeld Høyrokampen, alt. 1400–1440 m, *Dryas octopetala* assoc., 29.VIII.1957 Eckblad, p.p. (O).
6. Norway, Oppland, Lom, western part of fjeld Blåhø, *Dryas* heath, 30.VIII.1957 Eckblad, p.p. (O).
7. Norway, Hordaland, Eidfjord, fjeld Dyranut, *Dryas* heath, 1.VIII.1959 Eckblad (type; O).
8. Norway, Hordaland, Eidfjord, fjeld Dyranut, *Dryas* assoc., 12.VIII.1960 Eckblad (O).
9. Norway, Finnmark, Nordkapp, Magerøya, fjeld Duksfjordfjell, together with *Braya purpurascens*, 30.VII.1965 Ryvarden (O).

### *H. dryadophila*

1. Sweden, Torne Lappmark, Jukkasjärvi, fjeld Nuolja, on very top of the fjeld, 7.VIII.1903 Vestergren (S).
2. Norway, Oppland, Lom, fjeld Høyrokampen, alt. 1400–1440 m, *Dryas* assoc., 29.VIII.1957 Eckblad, p.p. (type; O).

Table 1. The most important characters differentiating *Helvella acetabulum*, *H. arctoalpina* and *H. dryadophila*. For explanations, see 'Materials and methods' and 'Statistical analysis ...'.

Character	<i>H. acetabulum</i>	<i>H. arctoalpina</i>	<i>H. dryadophila</i>
Apothecium size (height × diameter)	2—8(—12) × 2—8 cm	1—2 × 1—3(—6) cm	0.5—1.5 × 1—2 cm
Apothecium height in relation to diameter	usually higher than broad, at times both dimensions about equal (rather rarely distinctly broader than high)	almost always broader than high, more pronouncedly so in age	relation variable; in age mostly broader than high
Stipe	mostly very well differentiated, prominent	weakly to moderately well differentiated, less prominent	weakly to moderately well differentiated, less prominent
Ribs of apothecium	± sharp, mostly double-edged, branching upwards, usually reaching slightly more than half-way along cup (at times almost to the margin or less than halfway)	± sharp, mostly indistinctly double-edged, branching upwards, mostly reaching about halfway along cup, at times restricted to lower part of cup	± blunt, pronouncedly double, not branching, only reaching lower part of cup
Nature of external surface towards cup margin	very delicately roughened to finely pubescent (mostly appearing glabrous to bare eye)	slightly more coarsely pubescent to villose	finely pubescent
Colour of hymenium	pale to medium brown when fresh; medium to dark brown (rarely black-brown) when dry	dark brown when fresh; black (rarely black-brown)	most probably dark brown when fresh; black when dry
Colour of external surface in upper part of cup	medium brown (rarely dark brown)	dark brown, at times black-brown (rarely medium brown)	dark brown
Colour of external surface in lower half of dry apothecium, towards base	orange-tinged brown to yellow-brown, yellow towards base	orange-tinged brown to yellow-brown, usually with a yellowish tint at least lowest down between ribs	dark brown to pale brown, paling downwards (without any orange or yellowish tinges)
Spore size: ranges of length and width	(14.5—) 16.0—18.0(—21.0) × 10.0—12.5(—13.5) μm	(16.0—) 17.0—20.0(—23.5) × 10.5—13.0(—15.0) μm	17.0—21.0(—25.0) × 11.0—13.5(—16.0) μm
Spore size: means of length and width	17.09 × 11.37 μm	18.06 × 11.90 μm	18.73 × 12.23 μm
Shape and contents of submature spores	almost all ellipsoid and uniguttulate	almost all ellipsoid and uniguttulate	a proportion subfusiform and three-guttulate
Length of terminal cell of paraphyses	55—100 μm	25—70 μm	35—70 μm
Contents of paraphyses	subhyaline to pale brown, ± homogeneous	pale brown to medium brown, ± homogeneous	medium brown to fairly dark brown, ± granular
Mucilaginous matter on and between paraphysis apices	scanty or lacking, very weakly cyanophilic (practically cyanophobic)	fairly abundant, weakly to moderately cyanophilic	in moderate amount, very weakly cyanophilic (practically cyanophobic)
Colour of hyphal wall in ental excipulum ( <i>textura intricata</i> )	(very) slightly brownish to pale brown	(very) slightly brownish to pale brown	hyaline

## Comparison of *H. acetabulum*, *H. arctoalpina* and *H. dryadophila*

Table 1 shows the most important characters differentiating the three species (*H. pocillum*, which grows in habitats similar to those of the two new species and has apparently a similar type of distribution, differs from all three in its very large spores, which measure ca.  $25\text{--}28 \times 13\text{--}16.5 \mu\text{m}$ ; Harmaja 1976). Tables 2—5 and Figs. 1—7 and 14 and 15 may also be consulted for a comparison of different characters. Some additional notes are presented here and the results of the statistical analyses are discussed in the following section.

The apothecia of *H. dryadophila* tend to broaden gradually from the base towards the cup, especially when young (cf. Fig. 5); this tendency is not so evident in the other species.

The border between the *textura intricata* and *t. angularis* layers in the excipuli of *H. acetabulum* and *H. arctoalpina* is sharp, and the intercellular spaces in the latter tissue contain strongly cyanophilic matter. As a layer of *t. prismatica* is also present, composing the outermost part of the excipulum and the external 'warts', the structure of the excipulum of these two species is very similar to that of, e.g., *Otidea* (Harmaja 1974). Dissing (1966) did not distinguish between the *t. angularis* and *t. prismatica* layers in *H. acetabulum* coll. or in the greater part of *Helvella*.

Due to the more or less dark brown intracellular and encrusted pigments (discernible in Melzer's reagent as well as in 5 % KOH) of the *t. prismatica* of *H. arctoalpina* (at times also in the lower part of *t. angularis*) and *H. dryadophila*, this layer is seen as the distinctly darkest part of the context in microscopic mounts, and even with the bare eye. In *H. acetabulum*, the rather pale red-brown *t. angularis* is usually the darkest part of the context, and never very pronouncedly so; occasionally, the *t. angularis* and *t. prismatica* together form the darkest part, or the excipulum is of about the same colour intensity throughout (cf. Table 1). In *H. dryadophila*, the border between the ental and ectal excipulum is very conspicuous, owing to the contrast between the *t. intricata*, with its hyaline thin-walled hyphae, and the directly adjacent *t. prismatica*, with its large inflated darkly coloured cells with thickened walls. It is probable that the darker colour in four different parts of the apothecium in the two arctic-alpine species (contents of *t. prismatica* cells, encrustation on walls of these cells, and contents and encrustation of paraphyses) is due to a single chemical compound, a single kind of pigment, at least within each of the two species. The paler *H. acetabulum* may contain the same pigment in lesser quantity or its apothecia may lack this dark compound and contain only some paler pigment.

The paraphysis contents, especially in the terminal cell, appear to display another interspecific differ-

<i>Textura angularis</i> layer	distinct, typical, 45—85 (—120) $\mu\text{m}$ thick, pale red-brown	distinct, typical, (50—) 70—110 $\mu\text{m}$ thick, pale brownish like <i>t. intricata</i>	lacking or narrow and indistinct
<i>Textura prismatica</i> : colour of contents of normal cells	almost hyaline to pale brown, at times fulvous	distinctly brown	distinctly brown
<i>T. prismatica</i> : approximate thickness of cell wall	0.6—1.0 $\mu\text{m}$	0.8—1.3 $\mu\text{m}$	0.9—2.0 $\mu\text{m}$
<i>T. prismatica</i> : colour of cell wall in normal cells	hyaline (without coloured encrustation)	medium to dark brown due to encrusted layer	dark brown due to encrusted layer
<i>T. prismatica</i> : diameter of end cell of tufts, or warts: total range and mean	6.0—13.0 $\mu\text{m}$ ; $\bar{x} = 8.54 \mu\text{m}$	7.0—20.0 $\mu\text{m}$ ; $\bar{x} = 10.87 \mu\text{m}$	7.5—20.0 $\mu\text{m}$ ; $\bar{x} = 12.02 \mu\text{m}$
Fruiting period in Fennoscandia	from early May to late July	from late July to end of August	August
Zonal distribution in Fennoscandia	temperate to northern boreal, very uncommon north of hemiboreal zone	lower oroarctic (low alpine), most probably also in the adjacent zones	lower and middle oroarctic (low and middle alpine), most probably also in oro-hemiarctic zone





Fig. 1. *Helvella acetabulum* fresh *in situ*, in about natural size (Finland, Etelä-Savo, Lappeenranta, Ihalainen, 2.VII.1976 Korhonen, H). Photo: Mauri Korhonen. — For other photographs of typical fresh *H. acetabulum*, see Dissing (1966, Fig. 14a) and Weber (1972, Figs. 19–21).

ence besides that in colour intensity. In *H. acetabulum* and *H. arctoalpina*, the contents are homogeneous to very slightly granular, but in *H. dryadophila* they are rather granular. This character, though not distinct in this case, may possess significance in the group, since in *H. pocillum* the paraphysis contents are very markedly granular (Harmaja 1976).

The terminal cell of the paraphyses is pronouncedly longer in *H. acetabulum* than in the two other species. This difference would no doubt have proved highly significant if analysed statistically. The usefulness of this character in infrageneric taxonomy of the Pezizales has been almost completely ignored (but see Maas Geesteranus 1967 as concerns *Peziza* St-Am.).

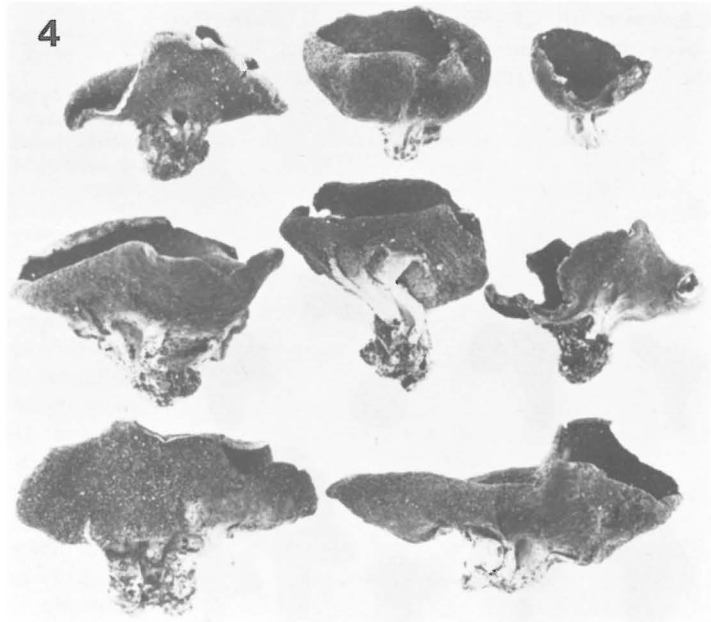
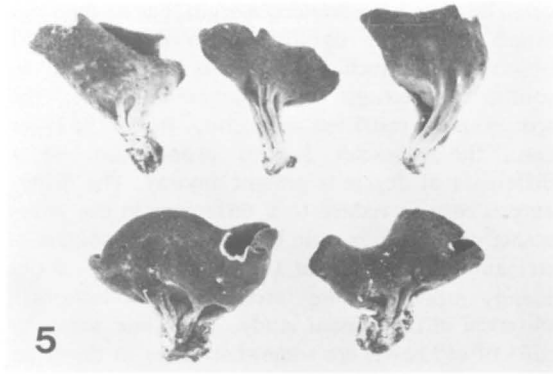
A proportion of the submature spores of *H. dryadophila* are subfusiform and three-guttulate, but such spores are only rarely observed in the other two species (cf. Harmaja 1977). *H. acetabulum* is the only one of the three species in which a minor proportion of the fully mature released spores are not infrequently subfusiform.

The hyphae of the *t. intricata* are, on the average, slightly thinner in *H. dryadophila* (ca. 2.0–7.5  $\mu\text{m}$  in diam.) than in *H. arctoalpina* (ca. 2.5–10.0  $\mu\text{m}$ ) and *H. acetabulum* (ca. 2.0–8.0 (–10.0)  $\mu\text{m}$ ).

A few characters common to all three species also deserve mention. According to my studies, the ascus development is pleurorhynchous in all three (and *H. pocillum*) (cf. Weber 1972). The dried apothecia display about the same responses to ultra-violet light (UV254): the hymenium retains its original colour with, however, faint violet and chlorine tinges; the external surface behaves in about the same way, but the originally  $\pm$  yellow or whitish colour of the base of the apothecium and the areas between the ribs becomes more pronounced. The habitats of the species appear very similar, judged from the information available: they all grow on  $\pm$  bare, distinctly calcareous, and almost always well-drained, soil. The two arctic-alpine species prefer *Dryas octopetala* vegetation, an interesting feature shared by surprisingly many species of macrofungi, both exclusively (oro)arctic species and those  $\pm$  wide-spread ones which reach (oro)arctic zones.

Some discussion has been devoted to the presence versus absence of a 'white margin' in the cup of the *Helvella* apothecium and the taxonomic significance of this character (cf. e.g. Dissing 1964 and 1966). It appears that the nature of this feature has been partly misunderstood. Dissing (1966) states that the arctic-alpine collections of *H. acetabulum* (coll.)

Figs. 2—6. Dried apothecia of four species of the *Helvella acetabulum* group,  $\times 1.5$ .—2: *H. acetabulum* (part of specimen no. 2 in the list of specimens examined in detail). — 3: *H. arctoalpina* (part of type, specimen no. 7). — 4: *H. arctoalpina* (part of specimen no. 5) — 5: *H. dryadophila* (part of type, specimen no. 2). — 6: *H. pocillum* (part of the apothecia separated from the mixed specimen mentioned on p. 46). — Photo: Mauri Korhonen.



often have such a white cup margin, but he does not attach taxonomic significance to this feature. I observed that such a margin is often found in southern collections of *H. acetabulum* (i.e., the species in the restricted sense), too. But in the latter cases the character is less pronounced, so a difference of degree is present anyway. The difference is easy to reduce to a difference in the pubescence of the cup margin between *H. acetabulum* s. str. and *H. arctoalpina* (which Dissing no doubt mainly meant by the 'arctic-alpine collections'), observed in the present study. The white warts, or tufts of cell rows, are somewhat larger in the latter species, and thus more conspicuous than in *H. acetabulum* s. str. (cf. Figs. 2, 3 and 4), where they have escaped the attention of mycologists. What are these 'white marginal warts'? Dissing (1964 and

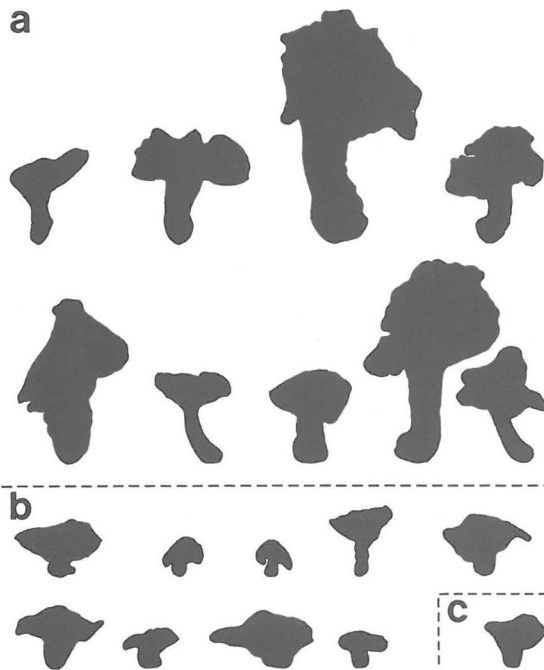


Fig. 7. Silhouettes of dried apothecia of *Helvella acetabulum* (a), *H. arctoalpina* (b) and *H. dryadophila* (c). One apothecium of each of 19 of the 20 specimens listed here is presented,  $\times 0.5$ . The specimen numbering proceeds from the upper left corner to the lower right corner in the figure. The silhouette for specimen no. 6 of *H. arctoalpina* has been partly reconstructed, having been spoilt in pressing. Specimen no. 1 of *H. dryadophila* contained such badly fragmented apothecia that it had to be excluded. Note the large apothecium, fairly high in relation to breadth, of *H. acetabulum*.

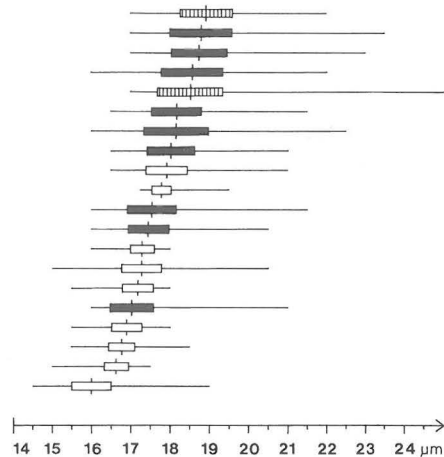


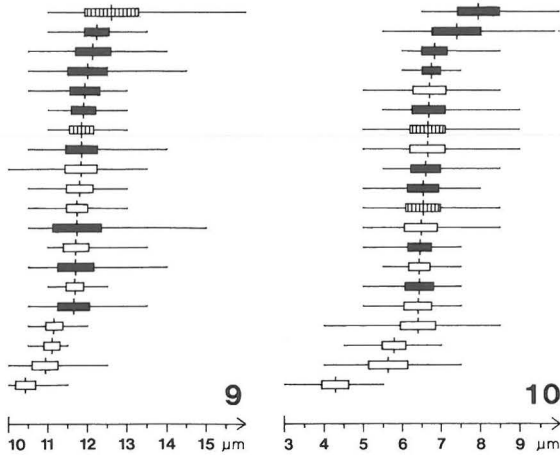
Fig. 8. Variability of spore length in specimens of *Helvella acetabulum* (graphs with open quadrangles), *H. arctoalpina* (solid quadrangles) and *H. dryadophila* (hatched quadrangles). The horizontal lines in the graphs show the range of variation of spore length. The quadrangle shows the confidence interval of the mean at the 95 % level. The vertical bars in the middle of the quadrangle show the arithmetical mean. The ranges and means are presented in numerical form in Table 2.

1966) finds (in *H. corium* (Weberb.) Massee s. lato) that they are composed of deviating hyaline, often collapsed, cells in the tufts (warts, hairs), which are most abundant in the apical parts of the tufts. I can confirm Dissing's observations as concerns *H. acetabulum*, *H. arctoalpina* and *H. dryadophila*, and can supplement this explanation with a further observation. I have noted that these marginal hairs, in particular, are often covered with abundant small white crystals. As all the species concerned grow on substrates rich in calcium, it seems probable that the crystals are lime ( $\text{CaCO}_3$ ), which is precipitated on the cell walls when water flowing upwards in the apothecium is evaporated. These crystals apparently partly account for the white margin of the cup, but to what extent is uncertain.

*H. acetabulum* occurs in Fennoscandia from sea level up to altitudes of ca. 700 m (Härjedalen, central Sweden). *H. arctoalpina* is known from altitudes of a few hundred metres (Finnmark, northern Norway) to ca. 1400 m (Oppland, southern Norway). *H. dryadophila* has so far been collected only at heights of 1200 m (Torne Lapland, northern Sweden) and ca. 1400 m (Oppland, southern Norway).

Dissing (1966) reports that the 'arctic-alpine form of *H. acetabulum*' occurs in Greenland, Switzerland, Iceland, Spitzbergen and the Scandinavian mountain range in Sweden and Norway. Without seeing all the specimens I cannot tell to which species these





Figs. 9—10. *Helvella acetabulum*, *H. arctoalpina* and *H. dryadophila*. — 9: Variability of spore width. — 10: Variability of diameter of paraphysis apices. See also Tables 3 and 4, and legend of Fig. 8.

records actually refer, and so the total distribution of *H. arctoalpina* and *H. dryadophila* (and *H. pocillum*) cannot yet be presented. However, some such specimens from beyond Fennoscandia have been seen and examined by me in addition to the great majority of the Fennoscandian specimens considered in detail in the present study (see also Addendum). The specimen from Iceland (M. Lange 659, C) turned out to be *H. costifera* coll., while both the Greenlandic specimens (M. Lange 193 and 292, C) unexpectedly proved to be typical *H. acetabulum* s. str. It is not known in which vegetation zone the specimens from Greenland have been collected, but in any case these two specimens represent the northern/upper limit of the distribution and the latest fruiting records (August 2 and 15) of *H. acetabulum* s. str. so far known. The four species may not be completely allopatric as might have been expected.

Despite the superficial similarities between *H. arctoalpina* and *H. dryadophila* (small dark apothecia, kind of *t. prismatica*, late fruiting, arctic occurrence) I consider the former species taxonomically a very close relative to *H. acetabulum*. The close relationship is shown in particular by the presence of the rather bright orange-brown to yellow-brown colour (usually with a yellow tint lowest down) in the apothecia, especially in the dried condition, and also by the kind of external ribs and the construction of the excipulum. *H. dryadophila* does not appear to be very close to either *H. arctoalpina* or *H. acetabulum*, being nearer to *H. pocillum*.

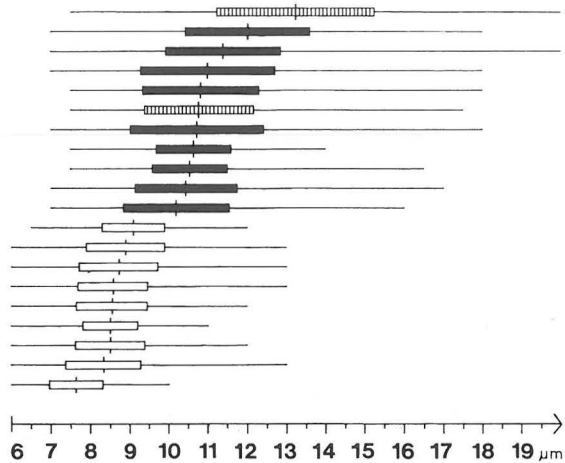


Fig. 11. Variability of diameter of excipular end cells in *Helvella acetabulum*, *H. arctoalpina* and *H. dryadophila*. See also Table 5 and legend of Fig. 8. — The confidence intervals and, in particular, mean values, of the specimens have obviously a higher discriminative power than the total distributions, or ranges, of the measures.

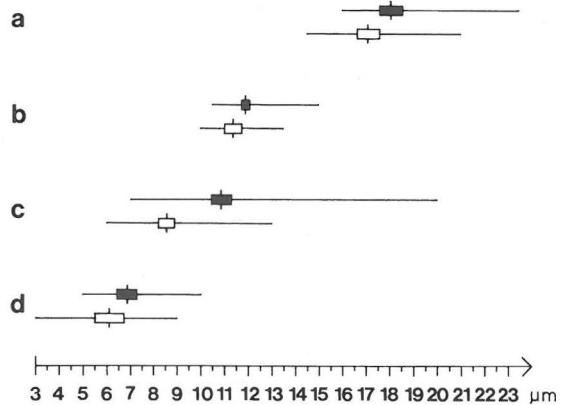


Fig. 12. Specific variability of the four quantitative characters in *Helvella acetabulum* and *H. arctoalpina*: a) spore length, b) spore width, c) diameter of excipular end cells, d) diameter of paraphysis apices. See also Tables 2—5 and legend of Fig. 8.

For the time being, all the three new species discovered in the neighbourhood of *H. acetabulum*, i.e. *H. arctoalpina*, *H. dryadophila* and *H. pocillum*, are best included in the section *Acetabulum* Diss.

In summary, as a result of the present study, *H. acetabulum* will, generally speaking, be restricted to comprise a large, rather pale, early and predominantly southern species, while *H. arctoalpina*, *H. dryadophila* (and *H. pocillum*) are small, dark, late, arctic-alpine species.

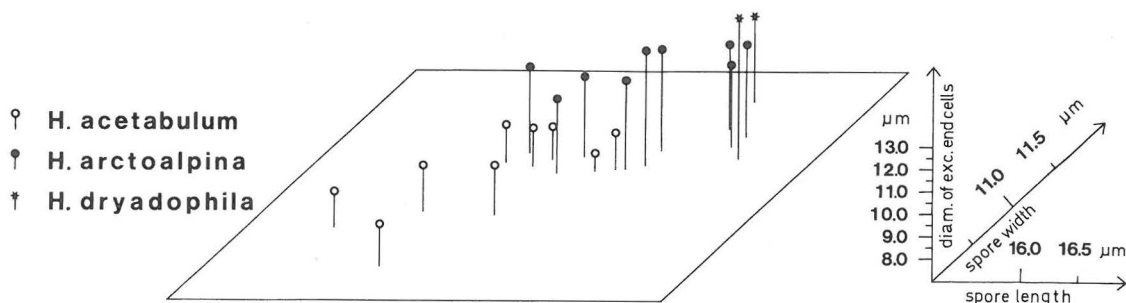


Fig. 13. Three-dimensional scatter diagram showing the variability of three quantitative characters in the 20 specimens of the three *Helvella* species. — Note the clustering of the short open-headed 'pins' towards bottom left, of the long solid-headed ones towards right and top, and of the long star-headed ones towards top right.

### Statistical analysis of four quantitative characters of *H. acetabulum*, *H. arctoalpina* and *H. dryadophila*

The results of the statistical analyses of the spore length, the spore width, the diameter of the paraphysis apices, and the diameter of the excipular end cells are shown numerically in Tables 2–5 and graphically in Figs. 8–13. The figures 8–12 also show the confidence intervals of the means at the 95 % level.

The confidence limits of a mean value can be considered analogous to the error of measurement of a single character. Raitviir (1972) considered the range of variation of spore measures within a single apothecium, and calculated the number of measurements of spore length and width required to give a confidence interval for the mean of the same order as the error of measurements made with an ocular micrometer at a magnification of  $\times 700$ . He found that in the majority of the Discomycetes (incl. *Helvella*) the required number was 20–30 for spore length and  $\leq 10$  for spore width. I made 20 measurements not only of spore length but also of the three smaller dimensions, partly because I used a magnification lower than Raitviir, partly because the diameters of paraphysis apices and excipular end cells generally have a wide range of variation in a single apothecium.

The present comparison of the measures of the four characters in *H. acetabulum* and *H. arctoalpina* could also have been performed with statistical tests other than the *t* test. Some type of variance analysis is also no doubt useful in treatments of material of this kind, even when a character is compared between only two species; if more than two species are compared, Student's *t* test cannot be used and the analysis of variance is apparently the most suitable of the various tests.

In comparisons of this kind, the objects measured must naturally be homologous entities at the same stage of development. Some difficulties are encountered in the measurement of spore lengths and widths in *Helvella*. In sections in the usual Melzer mounts, the measures of submature spores have unexpectedly proved to be greater than those of fully mature ones released from the asci. To ensure that only mature spores are obtained, care must be taken not to squash the section; pressure on the cover glass releases many submature and even quite young spores. Besides their free occurrence on the hymenial (and often also excipular) surface, the mature spores can also be recognized by their hyaline appearance; the contents of the submature ones, excluding the oil drop(s), appear slightly coloured, faintly yellowish. The difference is not conspicuous, but with some experience most spores can be classified as fully mature or not. I have noted (unpublished) the same phenomenon in the genus *Otidea*, where the mature spores of almost every species are easily distinguished from those at younger stages of

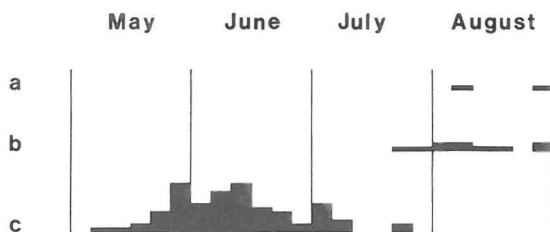


Fig. 14. Phenological diagram showing the fruiting periods of *Helvella acetabulum* (c), *H. arctoalpina* (b) and *H. dryadophila* (a) in Fennoscandia. The diagram is based on the dates, when exact, on the labels of all the Fennoscandian specimens actually seen by the author, except for three records of *H. acetabulum* (see legend of Fig. 15). Each month is divided into six periods of five days. The shading of the columns shows the number of specimens collected in a period.

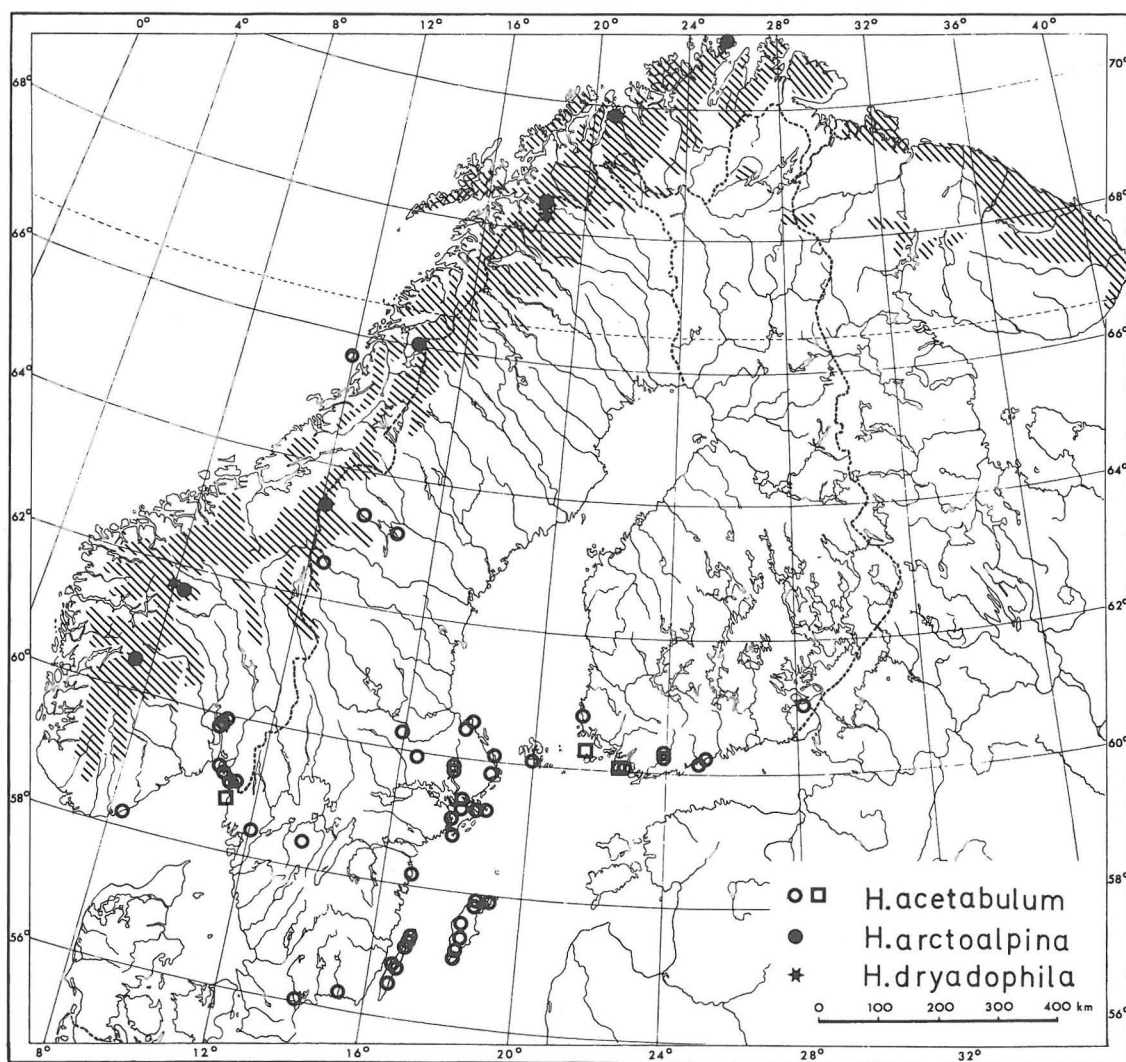


Fig. 15. Map of distributions of the three *Helvella* species in Fennoscandia. Based on all the specimens actually seen by the author, except for three records from the literature: the open squares represent obvious *H. acetabulum* s. str. (Mäkinen 1963; Jacobsson 1976). The oroarctic (alpine) area, according to Ahti et al. (1968), has been hatched. — Stars also show the two known localities of *H. pocillum*.

development by the conspicuous de Bary gas bubble they each contain. This phenomenon, that submature spores are larger than released fully mature ones, may be fairly common in the Pezizales and should be carefully considered in taxonomic work.

Another thing to be noted concerning the spores of *Helvella* has already been pointed out by Dissing & Nannfeldt (1966); in many of the species, occasional spores are often unusually large, even at the fully mature stage ('macrospores'). The asci bearing them are nevertheless eight-spored, but some or all

of the remaining spores are probably slightly smaller than usual.

These two phenomena contribute to widen the ranges of the spore dimensions, especially length, reported in the literature for single specimens and species of *Helvella*. When only fully mature spores are considered and the influence of the macrospores is kept under control, the ranges and mean values of the spore measurements can be somewhat diminished, and more quantitative differences between species will no doubt become apparent.

Table 2 and Fig. 8 reveal that the spores of *H. acetabulum* are shorter than those of the other two species. The difference between *H. acetabulum* and *H. arctoalpina* proved significant at the 99 % level ( $p < 0.01$ ). It is very probable that larger material would have shown this difference to be highly significant. It is also obvious that the deviation in individual specimens is greater in *H. arctoalpina* and *H. dryadophila* than in *H. acetabulum*, no doubt significantly so. This largely results from the occurrence of occasional macrospores in the two former species. I believe, however, that even if such spores were eliminated from measurements, differences in spore length would exist between the species. Moreover, the occurrence of macrospores is probably genetically controlled, and these spores could justifiably be included in comparisons concerning genetic diversity.

Table 2. Variability of spore length in  $\mu\text{m}$  in *Helvella acetabulum*, *H. arctoalpina* and *H. dryadophila*. S.D. = standard deviation of the mean, S.E. = standard error of the mean. Student's test was used in the comparison of the mean values of the specimens of *H. acetabulum* and *H. arctoalpina*, and the value of  $t$  ( $df = 16$ ) is shown. For further explanations, e.g. concerning numbering of specimens, consult 'Materials and methods'.

Specimen no.	Range	Mean	S.D.	S.E.
<i>H. acetabulum</i>				
1	15.5–18.5	16.78	0.70	0.16
2	15.0–20.5	17.28	1.09	0.24
3	16.0–18.0	17.30	0.64	0.14
4	17.5–19.5	17.78	0.50	0.11
5	15.0–17.5	16.63	0.67	0.15
6	15.5–18.0	16.90	0.79	0.18
7	15.5–18.5	17.18	0.80	0.18
8	16.5–21.0	17.93	1.13	0.25
9	14.5–19.0	16.00	1.08	0.24
all specimens	14.5–21.0	17.09	0.59	0.20

3.43\*\*

<i>H. arctoalpina</i>				
1	16.5–21.0	18.03	1.26	0.28
2	17.0–23.5	18.80	1.63	0.37
3	16.0–20.5	17.45	1.09	0.24
4	16.0–21.5	17.55	1.29	0.29
5	16.5–21.5	18.18	1.35	0.30
6	17.0–23.0	18.75	1.52	0.34
7	16.0–22.5	18.18	1.69	0.38
8	16.0–22.0	18.58	1.67	0.37
9	16.0–21.0	17.03	1.14	0.26
all specimens	16.0–23.5	18.06	0.61	0.20

<i>H. dryadophila</i>				
1	17.0–22.0	18.93	1.41	0.31
2	17.0–25.0	18.53	1.74	0.39
all specimens	17.0–25.0	18.73	0.28	0.20

Table 3 and Fig. 9 show that spore width is likewise greater in the two arctic-alpine species; the difference between *H. acetabulum* and *H. arctoalpina* is significant at the 99 % level ( $p < 0.01$ ). Larger material would presumably prove this difference highly significant.

The paraphysis tips are on the average wider in *H. arctoalpina* and *H. dryadophila* than in *H. acetabulum* (Table 4 and Fig. 10). However, the difference between *H. acetabulum* and *H. arctoalpina* was only fairly significant, i.e. at the 95 % level ( $p < 0.05$ ). In all three species the range of the measures within an apothecium is usually wide and the shape of the apex often varies (from practically filiform through clavate to subcapitate).

A marked difference was found between *H. acetabulum* and the two arctic-alpine species in the diameter of the end cells in the tufts ('warts', 'hairs') of the *t. primatica* in the external surface of the cup: the end cells are wider in the two arctic-alpine species (Table 5 and Fig. 11). The difference

Table 3. Variability of spore width in *Helvella acetabulum*, *H. arctoalpina* and *H. dryadophila*. For explanations, see legend of Table 2.

Specimen no.	Range	Mean	S.D.	S.E.
<i>H. acetabulum</i>				
1	10.0–11.5	10.43	0.52	0.12
2	10.0–13.5	11.83	0.85	0.19
3	10.5–11.5	11.10	0.38	0.09
4	11.0–12.5	11.68	0.44	0.10
5	10.5–12.0	11.15	0.46	0.10
6	10.5–13.0	11.80	0.73	0.16
7	10.5–13.0	11.73	0.60	0.13
8	11.0–13.5	11.70	0.68	0.15
9	10.0–12.5	10.93	0.65	0.15
all specimens	10.0–13.5	11.37	0.49	0.16

3.01\*\*

<i>H. arctoalpina</i>				
1	10.5–14.0	11.70	0.94	0.21
2	10.5–14.0	12.13	0.94	0.21
3	10.5–13.5	11.65	0.83	0.19
4	10.5–14.0	11.85	0.86	0.19
5	10.5–13.0	11.93	0.77	0.17
6	10.5–14.5	12.00	1.08	0.24
7	10.5–15.0	11.73	1.29	0.29
8	11.0–13.5	12.23	0.64	0.14
9	11.0–13.0	11.90	0.64	0.14
all specimens	10.5–15.0	11.90	0.20	0.07

<i>H. dryadophila</i>				
1	11.0–13.0	11.85	0.67	0.15
2	11.0–16.0	12.60	1.42	0.32
all specimens	11.0–16.0	12.23	0.53	0.37

between *H. acetabulum* and *H. arctoalpina* was highly significant, at the 99.9 % level (i.e.,  $p < 0.001$ ).

These terminal cells varied widely within a single apothecium in all three species, but the infraspecific variation was not great in the two with sufficient material (see Table 5). The variation within apothecium partly depends on the size of the tufts: in larger distinct tufts, the cells, including the terminal ones, are smaller than in lower indistinct tufts. The standard deviation is of about the same magnitude within *H. acetabulum* and *H. arctoalpina*, so the distributions of the measurements and means of this character can well be compared and tested statistically. The other cells of the *t. prismatica* are also wider in *H. arctoalpina* and *H. dryadophila*, and the difference in diameter is most probably even greater if the inner cells of the *t. prismatica* are compared.

The microscopic characters differentiating *H. acetabulum* most clearly from *H. arctoalpina* and *H. dryadophila* are those of the *t. prismatica*, and the less conspicuous feature of the length of the

paraphysis end cells. In the two new species the cells of the *t. prismatica* are large and have dark brown encrusted pigment and the terminal cells of the paraphyses are short, while in *H. acetabulum* the first-named cells are smaller, especially narrower, and lack brown wall encrustation (it occurs very rarely in some cells, and is then restricted to areas near the septa) and the paraphysis end cells are longer.

The three-dimensional scatter diagram in Fig. 13 shows as combined the variation of the mean values for spore length, spore width and the diameter of the excipular end cells among the 20 specimens of the three species. A very distinct positive correlation exists between the measures of these three characters, especially when the species are compared.

The variation in the four quantitative characters of the species does not show any clinal tendency when the values for specimens from different localities are compared. The four characters even vary widely between specimens from the same fields or the same areas.

Table 4. Variability of diameter of paraphysis apices in *Helvella acetabulum*, *H. arctoalpina* and *H. dryadophila*. For explanations, see legend of Table 2.

Specimen no.	Range	Mean	S.D.	S.E.
<i>H. acetabulum</i>				
1	4.0—8.5	6.40	0.98	0.22
2	3.0—5.5	4.28	0.70	0.16
3	5.0—8.5	6.48	0.88	0.20
4	5.0—8.5	6.70	0.91	0.20
5	4.5—7.0	5.78	0.64	0.14
6	5.0—9.0	6.65	0.99	0.22
7	4.0—7.5	5.63	1.06	0.24
8	5.0—7.5	6.40	0.75	0.17
9	5.5—7.5	6.43	0.57	0.13
all specimens	3.0—9.0	6.08	0.77	0.26

2.49\*

<i>H. arctoalpina</i>				
1	6.5—10.0	7.95	1.10	0.25
2	5.0—7.5	6.45	0.69	0.15
3	5.5—10.0	7.40	1.34	0.30
4	5.5—9.0	6.68	0.91	0.20
5	5.5—8.5	6.60	0.80	0.18
6	6.0—8.5	6.83	0.69	0.16
7	6.0—7.5	6.75	0.50	0.11
8	5.0—7.5	6.43	0.75	0.17
9	5.0—8.0	6.53	0.87	0.19
all specimens	5.0—10.0	6.85	0.51	0.17

<i>H. dryadophila</i>				
1	5.0—8.5	6.53	0.92	0.21
2	5.0—9.0	6.65	0.99	0.22
all specimens	5.0—9.0	6.59	0.08	0.06

Table 5. Variability of diameter of excipular end cells in *Helvella acetabulum*, *H. arctoalpina* and *H. dryadophila*. For explanations, see legend of Table 2.

Specimen no.	Range	Mean	S.D.	S.E.
<i>H. acetabulum</i>				
1	6.0—13.0	8.73	2.14	0.48
2	6.0—13.0	8.33	2.00	0.45
3	6.5—12.0	9.10	1.71	0.38
4	6.0—10.0	7.63	1.44	0.32
5	6.0—13.0	8.90	2.13	0.48
6	6.0—12.0	8.55	1.93	0.43
7	6.0—13.0	8.58	1.87	0.42
8	6.0—11.0	8.50	1.42	0.33
9	6.0—12.0	8.50	1.86	0.42
all specimens	6.0—13.0	8.54	0.41	0.14

10.17\*\*\*

<i>H. arctoalpina</i>				
1	7.5—18.0	10.83	3.19	0.71
2	7.0—18.0	11.00	3.61	0.81
3	7.0—16.0	10.20	2.91	0.65
4	7.0—17.0	10.45	2.76	0.62
5	7.0—20.0	11.40	3.09	0.69
6	7.5—16.5	10.55	2.02	0.45
7	7.0—18.0	12.03	3.35	0.75
8	7.5—14.0	10.65	2.01	0.45
9	7.0—18.0	10.73	3.61	0.81
all specimens	7.0—20.0	10.87	0.55	0.18

<i>H. dryadophila</i>				
1	7.5—20.0	13.25	4.27	0.96
2	7.5—17.5	10.78	2.97	0.66
all specimens	7.5—20.0	12.02	1.75	1.23

## Latin descriptions of *H. arctoalpina* and *H. dryadophila*

***Helvella arctoalpina*** Harmaja n. sp. — *Helvellae acetabuli similis*. Ab ea differt praecipue statura minore, stipite brevior et coloribus obscurioribus apothecii, cellulis distalibus texturae prismaticae crassioribus brunneoincrustatis, fructificatione seriore et distributione arctoalpina. — *Typus*: Norway, prov. Hordaland, par. Eidfjord, fjeld Dyranut, *Dryas octopetala* heath, 1.VIII.1959 F.—E. Eckblad (O).

***Helvella dryadophila*** Harmaja n. sp. — *Helvellae arctoalpinae valde similis sed ab ea plurimum differt: costae apothecii obtusae; apothecia sicca sine coloribus aurantiobrunneis, flavobrunneis vel flavis; hyphae texturae intricatae excipuli hyalinotunicatae; excipulum sine textura angulari*. — *Typus*: Norway, prov. Oppland, par. Lom, fjeld Høyrokampen, alt. 1400—1440 m, *Dryas octopetala* assoc., 29.VIII.1957 F.—E. Eckblad, p.p. (O).

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## Addendum

I am obliged to Mr. Ola Skifte, Tromsø Museum, Norway, for the loan the specimens of *H. acetabulum* coll. from that herbarium (TROM), too. However, they reached me so late that the 3 specimens of *H. arctoalpina* and one of *H. dryadophila*, detected by me among the borrowed specimens, are only listed below in this addendum. They were not examined statistically, but otherwise their information could be considered in the study and be incorporated in Table 1 and Figs. 14 and 15 (but not in Fig. 7).

Both the specimens from Spitzbergen originate from the middle arctic zone, which is present at and near the sea level there (Eurola 1968).

### *H. arctoalpina*

**Norway.** Nordland: Hemnes, W of Okstindan, between Bjuråga and Jordåga, in *Dryas octopetala* heath on limestone, 17.VIII.1968 Sivertsen; Troms: Skjervøy, Langneset, Gjøvarden, on limestone above forest limit, 6.VIII.1963 Skifte 2580 & Trefall. — **Spitzbergen.** West Spitzbergen: Woodfjorden, bottom of Bockfjorden, on mossy ground, 7.VIII.1960 Skifte 949.

### *H. dryadophila*

**Spitzbergen.** West Spitzbergen: Woodfjorden, bottom of Bockfjorden, in somewhat moist *Dryas octopetala* vegetation, 7.VIII.1960 Skifte 967.

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