



UNIVERSIDAD DE GUADALAJARA

Centro Universitario de Ciencias Biológicas y Agropecuarias

**Filogenia del género *Helvella*
(Ascomycota)**

**Tesis
que para obtener el grado de
Doctor en Ciencias en Biosistemática,
Ecología y Manejo de Recursos Naturales y
Agrícolas**

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Por

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Doctor en Ciencias en Biosistemática, Ecología y Manejo de Recursos Naturales y Agrícolas

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RESUMEN

El género *Helvella* (Fungi, Ascomycetes, Pezizales) se caracteriza por presentar apotecios en forma de copa o lobados. El estípite es liso, costillado o lagunoso, superficie glabra, subpubescente o pubescente. El excípulo está diferenciado en medular de textura intrincada y ectal de textura angular. Sus ascosporas son unigutuladas (normalmente), lisas, ligeramente verrugosas o verrugosas. Existen tres propuestas de clasificación infragenérica basadas en características macromorfológicas y sólo en una de ellas utilizan además el tipo de asca. Para tener un mejor concepto y establecer los límites de las especies descritas de *Helvella*, se estudiaron 26 especímenes tipo. Como resultado, fue posible completar las descripciones originales. Se concluyó que *H. costifera* es sinónimo de *H. hyperborea*. También fue posible reconocer a *H. griseoalba* de *H. costifera*, *H. subglabra* de *H. atra*, *H. stevensii* de *H. latispora*, y *H. sulcata* de *H. lacunosa*. Se designaron los lectotipos de *H. albella*, *H. elastica*, *H. ephippium* y *H. sulcata*. Se corrigió la tipificación de *H. fusca*. Por separado, la evaluación de las propuestas de clasificación que se han establecido para el género fue mediante un análisis filogenético, usando datos morfológicos y secuencias de ADN de la región 28S del DNA ribosomal. Se usaron 44 especímenes de 24 especies de *Helvella* y *Wynella silvicola* como grupo externo para el análisis filogenético. La matriz combinando datos moleculares y morfológicos generó árboles con mejores soportes, en comparación con la matriz sólo con datos moleculares. Sólo las secciones *Elasticae*, *Helvella*, *Lacunosa* y *Leucomelaenae* se recobraron de los análisis con soporte estadístico y/o probabilístico. Los resultados de este trabajo apoyan la división del género en *Helvella* subgénero *Helvella* y *Helvella* subgénero *Leucomelaenae*. Las características morfológicas que lo apoyan son el tipo de asca, pleurorricosa para el primero y aporrincosa para el segundo. Por último, se hizo una revisión del género en México y se reconoce la presencia de 18 especies para el país.

Capítulo I. Introducción

INTRODUCCIÓN

El presente trabajo es un estudio taxonómico y filogenético del género *Helvella* L. con base en datos morfológicos y secuencias de ADN. Se discuten las relaciones filogenéticas entre las especies y se comparan con las propuestas infragenéricas que han sido postuladas para el género. Se incluyen los resultados de los estudios macro y micromorfológicos de las especies estudiadas, siendo en la mayoría de los casos de ejemplares tipo. Además se aportan nuevas características microscópicas y reacciones microquímicas que deben de ser consideradas cuando se hacen estudios taxonómicos sobre *Helvella*.

El trabajo consta de seis capítulos. El primer capítulo es una introducción general al estudio de *Helvella*. Por su parte, el capítulo II (Landeros et al. 2012) es la revisión de 16 especímenes tipo, y material adicional de 15 especies de *Helvella*. En él se argumenta que *H. subglabra* N.S. Weber es diferente de *H. atra* J. König, así como *H. griseoalba* N.S. Weber de *H. costifera* Nannf., mientras que *H. hyperborea* Harmaja debe de ser considerada un sinónimo de *H. costifera*. Se apoya que *H. queletii* Bres. es un sinónimo de *H. solitaria* P. Karst. de acuerdo con Hamaja (1977). Además, se hace una revisión de ciertos conceptos (apotecio, costillado, hemiamiloide, lagunoso, píleo, pubescente, pruinoso, sulcado, veloso) que generan ambigüedad en su uso, y de los que debe haber una estandarización en su aplicación. Se incluye una clave sinóptica para la determinación de las especies estudiadas.

El capítulo III fue publicado por Landeros y Korf (2012). Se argumenta que Abbott y Currah (1997) propusieron incorrectamente un neotipo (el cual sólo puede ser seleccionado cuando no existe material original) para *H. fusca* Gillet. En la obra original donde se describió esta especie, Gillet (1879) publicó una figura, la cual automáticamente debe ser considerada el lectotipo. En el artículo se citan los artículos del Código de Nomenclatura Botánica de Viena que apoyan la designación del lectotipo para *H. fusca*, y además se hace la designación de un epitipo (material que sirve como ayuda para interpretar cuando el material tipo designado para el taxon genera ambigüedad).

El capítulo IV es un análisis filogenético y taxonómico de *Helvella*. En este capítulo se incluye la filogenia del género *Helvella*, con base en datos morfológicos y secuencias de ADN. También el estudio de ejemplares tipo que no se incluyeron en los capítulos II y III (*Acetabula calyx* Sacc., *H. chinensis* (Velen.) Nannf. & L. Holm, *H. compressa* (Snyder) N.S. Weber, *H. confusa* Harmaja, *H. connivens* Dissing & M. Lange, *H. cupuliformis* Dissing & Nannf., *H. melaleuca* Rifai, *H. pallidula* N.S. Weber, *Peziza debeauxii* Roum. y *P. Subclavipes* W. Phillips & Ellis). Se analizan los caracteres macro y micromorfológicos que son importantes para el estudio taxonómico del género, se presenta una clave para 34 especies, se describen los taxones estudiados, y finalmente se hace la propuesta de dividir al género en *Helvella* subgénero *Helvella* y *Helvella* subgénero *Leucomelaenae*. A su vez, *Helvella* subg. *Hevella* puede dividirse en *Helvella* sección *Helvella*, *Helvella* sección *Elasticae* Dissing sensu Weber y *Helvella* sección *Lacunosae* Dissing. Mientras que *Helvella* subg. *Leucomelaenae* sólo tiene una sección, *Helvella* sección *Leucomelaenae* Dissing sensu Weber.

El capítulo V es una revisión del género *Helvella* (Ascomycota: Fungi) en México. Se hizo una selección de 107 especímenes de los herbarios ENCB, FCME, IBUG, y XAL. Se hizo énfasis en los ejemplares referidos en las publicaciones. Después de estudiar el material, revisar los artículos originales, comparar con el material tipo, y consultar las descripciones originales, se reconoce la presencia de 18 especies de *Helvella* que en México: *H. acetabulum* (L.) Quél., *H. albella* Quél., *H. atra*, *H. compressa*, *H. costifera*, *H. crispa* (Scop.) Fr., *H. cupuliformis*, *H. elastica* Bull., *H. ephippium* Lév., *H. fibrosa* (Wallr.) Korf, *H. lactea* Boud., *H. lacunosa* Afzel., *H. leucomelaena* (Pers.) Nannf., *H. macropus* (Pers.) P. Karst., *H. pezizoides* Afzel., *H. solitaria*, *H. stevensii* Peck y *H. sulcata* Afzel., de

las cuales *Helvella compressa* es un nuevo registro para el país. Además *H. adhaerens* Peck, *H. corium* (O. Weberb.) Masee, *H. kichneri* Manzi, *H. latispora* Boud., *H. leucopus* Pers., *H. leucopus* var. *populina* I. Arroyo & Calonge, *H. pityophila* Boud., *H. queletiana* Sacc. & Traverso, *H. salvatierrae* Manzi, *H. sogarii* Manzi y *H. subglabra* no tienen el ejemplar de referencia o estaba incorrectamente determinado, en consecuencia, su presencia en México no puede ser confirmada. Se incluyen comentarios taxonómicos de las especies que crecen en México y observaciones de las que no están presentes. Se presenta una clave dicotómica para su determinación.

En el capítulo VI se presenta una discusión general y conclusiones. Se discute la importancia del estudio de los ejemplares tipo en los estudios taxonómicos. Al mismo tiempo, se enfatiza la importancia del uso de caracteres morfológicos en los análisis filogenéticos con secuencias de ADN. También se incluyen perspectivas sobre el estudio del género, haciendo énfasis en la revisión de los especímenes tipo que no fue posible estudiar, y de ejemplares de más regiones del mundo.

Género *Helvella* L.

La historia del nombre del género es confusa. Linnaeus (1737, 1745, 1753) escribió al género como *Elvela*. Posteriormente, en la segunda edición de la Flora Suecica, Linnaeus (1755), usó el nombre de *Elvella*, sin explicar el cambio. Finalmente, Linnaeus (1763) escribió el nombre del género como *Helvella*, sin volver a ofrecer explicación. Afzelius (1783), Persoon (1801) y Fries (1823), utilizaron el mismo nombre. La excepción fue Seaver (1942), quien intentó regresar al uso del nombre *Elvella*, pero no prosperó.

El significado del nombre es igualmente confuso. Phillips (1887) comentó que es una palabra en latín que usaba Cicerón para referirse a algún tipo de hongo. Mientras que Ulloa y Herrera (1994) mencionaron que el nombre proviene del latín y significa “hierba, verdura u hortaliza pequeña”, debido a la apariencia de sus ascomas.

Linnaeus (1753), en la descripción del género, incluyó a *Elvela mitra*, y *Elvela pineti*. Ahora, *H. mitra* es sinónimo de *H. crispa* pero se desconoce la posición de *H. pineti*. Anderson e Ickis (1921) postularon que no se trata de una *Helvella* en el sentido actual, pero no mencionaron a qué corresponde.

Los límites de *Helvella* han sido motivo de controversia. Linnaeus (1753) no dio una definición del género, sólo de las dos especies que describió. Afzelius (1783), Buillard (1791), Fries (1823), Karsten (1871), Masee (1895) y Rhem (1896) definieron al género considerando especies con apotecio en forma de copa o lobado, y estípote liso, costillado o lagunoso, motivo por el cual incluían especies de *Gyromitra*. Posteriormente, Boudier (1907) propuso dividir al género en *Helvella* (apotecio lobado y estípote lagunoso), *Leptopodia* Boud. (apotecio lobado y estípote liso), *Cyathipodia* Boud. (apotecio en forma de copa, estípote liso y ascosporas elipsoides), *Acetabula* (Fr.) Fuckel (apotecio en forma de copa y estípote costillado), y *Macropodia* Fuckel (apotecio en forma de copa, estípote liso y ascosporas subfusiformes). Nannfeldt (1937) hizo la delimitación actual del género, retomando el concepto de incluir a las especies con apotecio en forma de copa o lobado y estípote liso, costillado o lagunoso, pero con dos tipos de tejidos en el apotecio y ascosporas unigutuladas (a excepción de *H. macropus*, que en fresco puede presentar una gútula central grande y dos pequeñas en los extremos de la ascospora). Korf (1952) definió posteriormente los dos tejidos del apotecio, como excípulo medular de “textura intricata” (hifas entrelazadas), y excípulo ectal de “textura angularis” (células isodiamétricas sin espacios intracelulares).

Desafortunadamente el concepto de Nannfeldt (1937) no fue seguido por todos los micólogos. Recientemente, Dennis (1981), y Breitenbach y Kränzlin (1984) continuaron usando *Cyathipodia*, *Leptopodia*, *Macropodia*, y *Paxina* Kuntze, para referirse a especies de *Helvella*. Mientras que otros, como Eckblad (1968), fusionaron a las especies de *Underwoodia* Peck [*U. columnaris* Peck y *U. Fuegiana* (Speg.) Gamundí] dentro del género de *Helvella*, lo cual fue seguido por Harmaja (1974), quien también agregó a *U. Beatonii* Rifai, y además transfirió a *Wynnella silvicola* (Beck) Nannf. (única especie de este género) a *Helvella*. Los estudios moleculares [O'Donnell et al. (1997), Harrington et al. (1999), Landvik et al. (1999), y Læssøe y Hansen (2007)] apoyan el concepto de *Helvella* definido por Nannfeldt, y por lo tanto es el que actualmente se utiliza.

Clasificación infragenérica

Dissing (1966) fue el primero en proponer una clasificación infragenérica siguiendo el concepto de Nannfeldt (1937), con siete secciones considerando sólo características macromorfológicas. La principal característica que usó fue la presencia o ausencia de pubescencia en la superficie estéril del apotecio: pubescentes (*Acetabulum*, *Crispae*, *Ephippium*, *Leucomelaenae* y *Macropodes*), y glabras (*Lacunosae* y *Elasticae*).

Posteriormente, Weber (1972) postuló las mismas siete de Dissing (1966), pero con emendaciones, y cambió el nombre de la sección *Crispae* por *Helvella*, debido a que en esa sección está la especie tipo de género, y ese es el nombre correcto de acuerdo a las reglas de nomenclatura. Ella consideró la forma del apotecio como la principal característica para dividir al género: apotecio lobado (*Elasticae*, *Ephippium*, *Helvella* y *Lacunosae*), y apotecio en forma de copa (*Acetabulum*, *Leucomelaenae* y *Macropodes*). La última propuesta fue hecha por Abbott y Currah (1997). Ellos propusieron seis subgéneros, también basados principalmente en la forma del apotecio: lobado (*Elasticae* y *Helvella*), en forma de copa (*Cupuliformae*, *Leucomelaenae* y *Macropodes*), y auricoide (*Silvicolae*), esta última representada sólo por el género *Wynnella* Boud.

Estudios moleculares

Los estudios filogenéticos indican que la familia Helvellaceae es monofilética, y consiste de cinco géneros: *Balsamia* Vitta., *Barssia* Gilkey, *Helvella*, *Underwoodia*, y *Wynnella* Boud. (O'Donnell et al. 1997; Hansen y Pfister 2006; Læssøe y Hansen 2007). La monofilia del género *Helvella* fue demostrada por O'Donnell et al. (1997), Harrington et al. (1999), Landvik et al. (1999), y Læssøe y Hansen (2007), con *Wynnella* como el grupo hermano. Sin embargo, en ninguno de estos trabajos se incluyeron secuencias de suficientes especies para evaluar adecuadamente las relaciones infragenéricas de *Helvella*.

OBJETIVOS

Objetivo general

- Analizar mediante estudios filogenéticos si las secciones o subgéneros que se han propuesto para el género *Helvella* tienen un sustento natural.

Objetivos particulares

- Estudiar las relaciones filogenéticas dentro del género con base en secuencias de la región LSU del ADNr.

- Evaluar el uso de características morfológicas en la construcción de árboles filogenéticos.
- Comprobar si la forma del apotecio y estípito son las características más importantes para formar secciones y subgéneros.
- Analizar si la textura de la superficie estéril del apotecio es una característica útil en la clasificación infragenerica de *Helvella*.
- Contribuir con nuevas características para la taxonomía y filogenia del género.
- Estudiar los ejemplares tipo de las especies de *Helvella*.
- Hacer un estudio de las especies del género *Helvella* registradas para México.

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Capítulo II. Landeros F, Iturriaga T, Guzmán-Dávalos L. 2012. Type studies in *Helvella* (Pezizales) 1. Mycotaxon 119: 35-63

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Type studies in *Helvella* (Pezizales) 1FIDEL LANDEROS^{1,3*}, TERESA ITURRIAGA² & LAURA GUZMÁN-DÁVALOS³¹Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro,
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ABSTRACT — Sixteen type and some additional specimens representing fifteen species assigned to *Helvella* were studied with the aim of providing new data for their improved delimitation and recognition. Specimens were received on loan from DAOM, FH, H, K, MA, MICH, S and UPS. A synoptic key to the studied species is provided to contribute to a better understanding of the genus and the taxonomy of the morphospecies. Original descriptions are emended to include data on the anatomy of the apothecial excipulum and stipe layers, apothecium and stipe reactivity to Melzer's reagent, and ascospore ornamentation. Reasons are given for maintaining *H. subglabra*, *H. atra*, *H. griseoalba*, and *H. costifera* as independent taxa and for considering *Helvella hyperborea* a synonym of *H. costifera*. Previously imprecise descriptive terms are clarified.

KEY WORDS — *Ascomycota*, holotype, isotype, lectotype, revision

Introduction

The genus *Helvella* L. includes approximately 52 species (Kirk et al. 2008). Its distribution is basically north temperate, with only one tropical species recognized (Dissing 1979). Traditional taxonomy of the genus has been based mainly on ascoma shape and color and the presence or absence of projecting hyphae on the sterile surface (ectal excipulum) of the apothecium (Dissing 1966b, Weber 1972, Abbott & Currah 1997). Characters such as ascus development (aporhynchous or pleurorhynchous), ascospore shape and size, paraphysis color, and the presence of pigment in the apothecium ectal excipulum cells have proven to be of taxonomic value in some species (Weber 1972; Harmaja 1977b, 1979; Abbott & Currah 1997).

Although Nannfeldt (1937) proposed using the term “apothecium” specifically for *Helvella* to describe the entire ascoma, Weber (1972, 1975) and

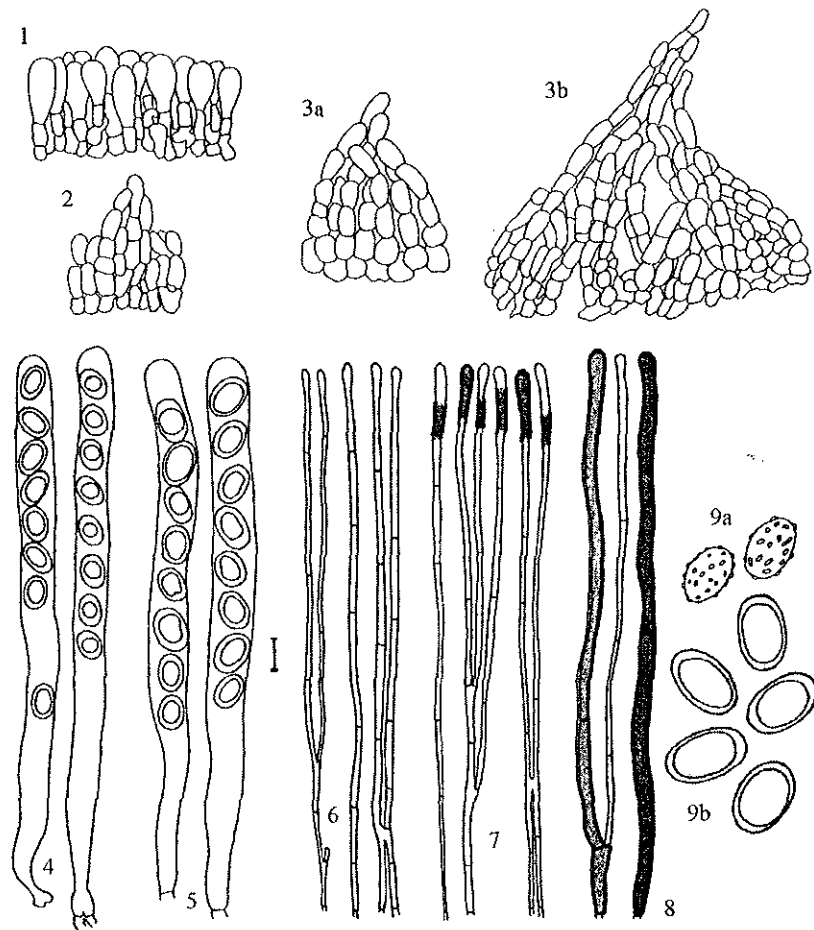
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Abbott & Currah (1988, 1997) used “apothecium” exclusively for the upper ascoma — i.e., the hymenium and its immediate supporting tissues — without the stipe. Eckblad (1968) commented that some authors carefully avoid the term apothecium for pileate forms like *Helvella*, whereas Dissing (1966b) and Calonge & Arroyo (1990) employed this term loosely, either for the complete ascoma or just for the upper part. Here, we follow Weber’s (1972) concept, applying the term apothecium only for the upper ascoma, except that where she differentiated stipe tissues with “ectal excipulum” and “medullary excipulum,” we use “outer layer” and “inner layer,” because in discomycetes “excipulum” currently is interpreted as the “tissue or tissues containing the hymenium in an apothecium” (Kirk et al. 2008).

In all *Helvella* species the medullary excipulum and stipe inner layer are composed of “textura intricata” (interwoven hyphae) while the ectal excipulum and stipe outer layer are a “textura angularis” (almost isodiametric cells without intracellular spaces) (Korf 1952, Dissing 1966, Eckblad 1968, Weber 1972). These cells are arranged in rows perpendicular to the surface. In glabrous ascomata, the ectal excipulum external layer is a palisade of clavate hyphal end-cells, ending more or less at the same level (FIG. 1) (Weber 1972). Hairy ascomata have an ectal excipulum outer layer that Eckblad (1968) described as “consisting of more or less swollen chains of cells often converging into distinct clusters.” These clusters are called “hyphal fascicles” (Weber 1972) or “chains of cells and/or fascicled hyphal chains” (Abbott & Currah 1997). Macroscopically, they give the appearance of pubescence or hairs of different lengths (FIGS 2–3) and are important in the taxonomy of the genus (Dissing 1966). Descriptive terms used in the literature — “finely pubescent,” “furfuraceous,” “granulose,” “hairy,” “pruinose,” “pubescent,” “roughened,” “velvety,” “villose” (Dissing 1966; Weber 1972, 1975; Dennis 1981; Abbott & Currah 1997) — have generated confusion through their different meanings, incorrect application, and/or the lack of consistent usage. Kaushal (1991) alone consistently uses only “pubescent” to describe the hairs; furthermore he included the hyphal fascicle length for each species.

Only three papers have described the stipe tissue: Gómez & Herrera (1965) and Weber (1972, 1975). Gómez & Herrera concluded that because stipe tissue is continuous with apothecium tissue, it is not a useful character. Although Weber (1972) described both tissues as similar in color and structure, she did indicate color differences between tissues in some species descriptions.

Pigment distribution, mainly in ectal excipulum cells (see FIGS 19–21) and paraphyses — i.e., intracellular (cytoplasmic), in the cell wall, or encrusting (deposited pigment forming an irregular crust on the wall) — is controversial. Eckblad (1968), Weber (1972), and Harmaja (1977b, 1979) considered pigmentation to be diagnostic. Eckblad (1968) wrote it is a characteristic mostly

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FIGS 1–9. 1: Ectal excipulum of a glabrous apothecium (*Helvella leucopus* var. *populina*). 2: Hyphal fascicle of the outer layer of a subpubescent stipe (*H. griseoalba*). 3: Hyphal fascicle of the ectal excipulum of a pubescent apothecium (*H. costifera*)—a: short, b: large. 4: Pleurorhynchous asci (*H. pocillum*). 5: Aporhynchous asci (*H. crassitunicata*); 6: Common paraphyses (*H. subglabra*). 7: Paraphyses with a thick-walled brown cap or collar at the apex (*H. paraphysitorquata*). 8: Thick-walled paraphyses (*H. crassitunicata*). 9: Ascospores (*H. solitaria*) —a: ornamented, b: smooth. Scale bars: 1–8 = 20 μ m, 9 = 8 μ m.

used on species level in *Pezizales*, but “[u]nfortunately too many descriptions simply state whether the paraphyses are coloured or not, not where the pigments are located.” With respect to *Helvella*, Eckblad (1968) noted, “[c]hemically and genetically it is probably a very short step from pigmented paraphyses to

hyaline ones, e.g. from the greyish-black paraphyses of *Helvella lacunosa* to the colourless paraphyses of *H. crispa*." Weber (1972) recognized two patterns of pigment distribution: 1) intracellular pigments, occurring in species with buff, tan or brown ascomata, and 2) pigments associated with hyphal walls, characteristic of gray to black species. On the other hand, Dissing (1966b) and Abbott & Currah (1997) considered pigmentation as highly variable and of limited use in circumscribing *Helvella* species. Dissing (1966b) indicated it is difficult to assess, especially in species where hymenium color variation is very large (as in *H. lacunosa* Afzel.) and hymenium color ranges from pale gray to gray brown to black due to pigments in the paraphyses. Only Dissing (1964, 1966b) went beyond just describing the colors of the structures; he also evaluated the color before and after treatment with cotton blue. Unfortunately, no further works analyze this issue.

Chemical reactions to Melzer's reagent have not been considered as diagnostic characters for structures other than ascospores or asci. Although excipulum cells in other ascomycete genera (*Perrotia*, *Hymenoscyphus*, *Epibryon*) show a hemiamyloid reaction, its taxonomic value is uncertain (Baral 1987).

Helvella ascospores have limited taxonomic value. In fact, their size is a key feature only for *H. pocillum* and *H. crassitunicata* (Weber 1975; Harmaja 1976), while the fusoid to subfusoid shape (differing from the typically ellipsoid ascospores found elsewhere) is found only in *H. macropus* (Pers.) P. Karst. (Abbott & Currah 1997) and *H. terrestris* (Velen.) Landvik (Landvik et al. 1999). Ascospore ornamentation is highly complex and a subject of controversy. Dissing (1964) and Dissing & Nannfeldt (1966) regarded ornamented ascospores in *Helvella* as immature, while Weber felt (1972) that they corresponded to the mature condition. Eckblad (1968) described ascospores with "false ornamentation," and Schumacher (pers. com.) mentioned that during the final stage of ascospore development, some secondary wall remnants might adhere to the ascospore surface, producing a highly inconsistent pattern; typically, a number of ascospores do not get such adherences at all and consequently remain smooth. On the other hand, Abbott & Currah (1997) gave to this character a high value, because they considered verruculose ascospores unique to the subgenus *Macropodes* (Dissing) S.P. Abbott.

Species concepts are similarly varied. Some authors with a narrow species concept, such as Harmaja (1976, 1977a,b, 1979), segregated species based on subtle differences. Others with a wider species concept (e.g., Abbott & Currah 1997) use fewer diagnostic characters to separate *Helvella* species. The purpose of our study was to review selected *Helvella* type specimens to delimit morphospecies and to determine which characters could be used in taxonomic and phylogenetic studies of the genus. We present five sets of types belonging to species with problematic delimitations: 1) *H. costifera* vs. *H. hyperborea*

and *H. griseoalba*; 2) *H. crassitunicata* vs. *H. pocillum*; 3) *H. subglabra* vs. *H. atra*; 4) *H. solitaria* vs. *H. queletii* and *H. ulvinenii*; and 5) *H. verruculosa* vs. *H. dryadophila*. We also add to the earlier descriptions of *H. leucopus* var. *populina*, *H. maculata*, *H. paraphysitorquata*, and *H. robusta*. Finally, we suggest a set of standard terms to clarify descriptions of *Helvella* species.

Materials & methods

Sixteen type as well as some additional specimens from eight herbaria (DAOM, FH, H, MA, MICH, O, S, UPS) were studied. Herbarium abbreviations follow Holmgren et al. (1990). Free-hand sections from apothecium and stipe were made with a razor blade directly from dry specimens. Sections and mycelium were placed first in 70% ethyl alcohol and subsequently in water to rehydrate the tissues. Specimens were examined under a Zeiss Axioskop 2 plus microscope with a drawing tube. Microphotographs were taken under a Zeiss Axioskop 40 microscope using Axio Vision 4 software. Ascospore measurements were made on mature free spores outside the asci, or on those attached to the hymenial surface, stipe, or basal mycelia. Mounts from apothecium, stipe, and mycelium were also made in Melzer's reagent (without pre-treatment in KOH) and cotton blue. We follow in part the terminology used by Baral (1987) to describe the hemiamyloid reaction in Melzer's reagent ('Melzer's'): "rr+" for hemiamyloid ("solely red") reaction and "rr-" for negative reaction. All measurements and features recorded are from type specimens. Where additional non-type specimens were studied for some species, observations that differ from those of the type are indicated under "Remarks" but not included in the technical description.

Terms used to refer to the surface of the apothecial ectal excipulum and stipe outer layer are: GLABROUS (FIG. 1), SUB-PUBESCENT (for fascicled hyphal chains < 50 µm long; FIG. 2), and PUBESCENT (for fascicled hyphal chains > 50 µm long; FIG. 3). As the hairs' length can vary in the last case, their measurements are given in the descriptions. See also "Results & discussion".

Results & discussion

We studied sixteen type specimens and present only new information or data that differs from the protologue or previous publications. In addition to the characters established by previous authors (Dissing 1966b; Calonge & Arroyo 1990; Abbott & Currah 1997), we found that pigmentation of apothecial cells, stipe tissue anatomy, and the reddish (hemiamyloid) reaction in Melzer's reagent (FIGS 10–11) are important characters that contribute to species recognition in *Helvella*. Because we found no variation in the basal mycelium of the stipe, which is universally composed of smooth-walled, hyaline, rr-, interwoven hyphae, we do not include it in the species descriptions. Nor do we make further mention of the fact that ascospores of all species have both cyanophilic cytoplasm and ornamentation (when present).

Regarding the value of pigmentation in the structures, we think it is important to study it from two perspectives: a) location and b) intensity. Concerning

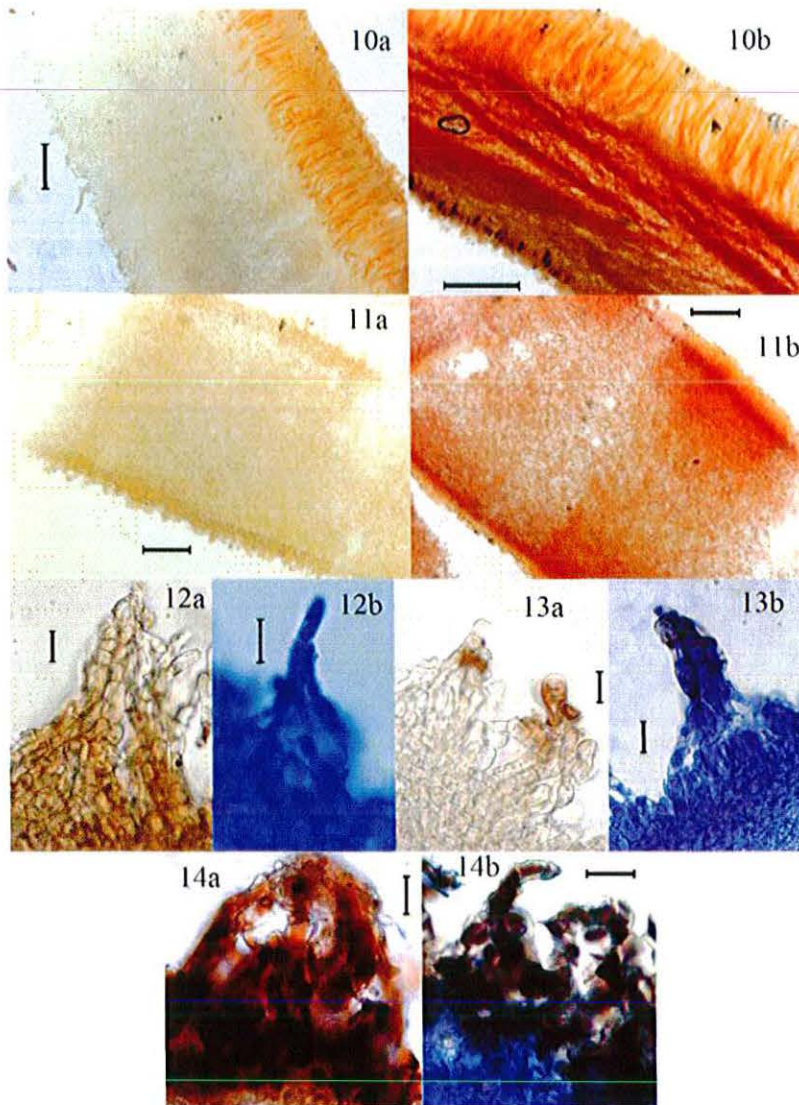
location, pigment may occur in the cytoplasm, in the wall, or encrusted on the wall (Figs 19–21). We observed that while the first two are constant within species, encrusted pigments are variable. For example, in *H. costifera* there are specimens with encrusted paraphyses and others without such incrustations. On the matter of pigment intensity, we return to cotton blue used first by Dissing (1964) to note that there are species where the cytoplasmic pigment color is so intense that it is still visible even after adding cotton blue, while others have lighter pigment no longer visible when adding the colorant (Figs 12–17). We realized that this characteristic is constant among specimens of the same species. This also happens with the pigment in the cell wall.

As indicated in the introduction, only Weber (1972, 1975) described the stipe tissue. We consider this character taxonomically valuable for the following reasons: 1) the hyphal fascicle lengths among specimens of the same species are more constant than in the apothecial sterile surface (see *H. hyperborea* remarks); 2) the pigments in the ectal excipulum and stipe outer layer can differ in water and cotton blue (see *H. ulvinenii* remarks; FIG. 22); and 3) the hemiamyloid reaction can occur in stipe tissue but not in the excipulum (e.g. *H. leucopus* var. *populina*).

As Baral (1987) noted, we know little about hemiamyloid reaction, and there indeed are few records of this reaction in tissues other than the hymenium. We report this reaction in different apothecial and stipe tissues for *H. leucopus* var. *populina*, *H. robusta*, and *H. subglabra*; we have also observed this reaction in specimens of *H. albella* Quél., *H. connivens* Dissing & M. Lange (holotype), *H. elastica* Bull., and *H. stevensii* Peck (unpublished data).

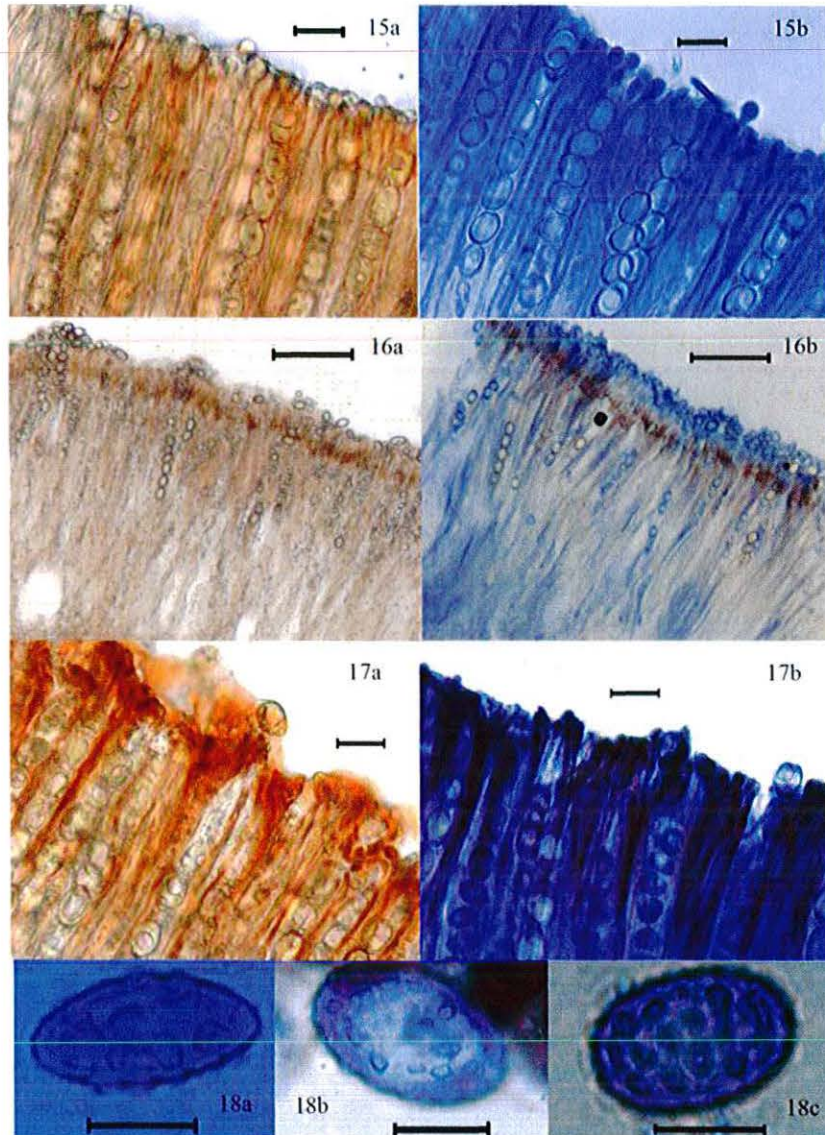
Concerning ascospore ornamentation, we make the following points. 1) Ornamented ascospores are not restricted to *H.* subgen. *Macropodes* (here represented only by *H. macropus*, FIG. 18a) as Abbott & Currah (1997) proposed. We have also observed ornamented ascospores (generally only in mature ascospores outside the asci) in the type specimens of *H. leucopus* var. *populina* (FIG. 18b), *H. paraphysitorquata* (FIG. 18c), *H. solitaria*, *H. subglabra*, and *H. ulvinenii*. 2) We agree with Weber (1972) that it is the mature *Helvella* ascospores that are verrucose, contrary to the assumption of Dissing (1964) and Dissing & Nannfeldt (1966) that ornamented ascospores are the immature ones. 3) When citing ascospore sizes, it is important to indicate what kind of spores (smooth vs. ornamented) were measured, because in some species they have different size range (FIG. 9) (see remarks under *H. queletii*).

As noted previously, many different terms have been used to describe the apothecial and stipe outer layer surfaces, giving the impression that there were different types of hairs. However, in all cases these hairs are developmentally the same: they consist of hyphal clusters that differ only in length. The tiny hairs have been especially problematic; Weber (1972) and Abbott & Currah (1997)

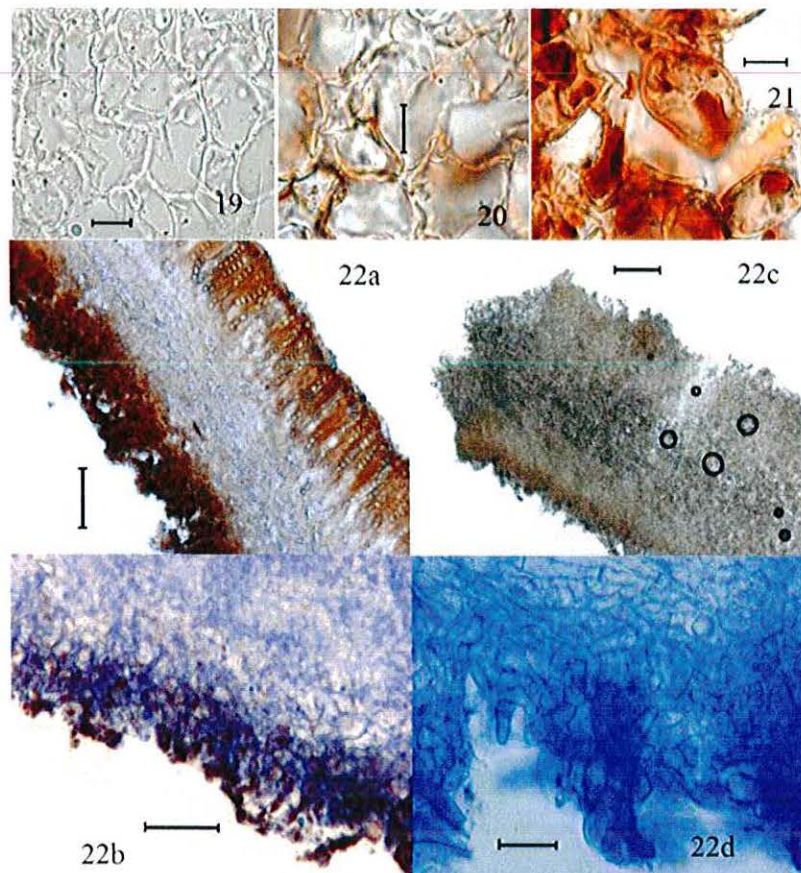
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FIGS. 10–14. 10: Reaction of the apothecial excipulum to Melzer's reagent—a: negative (*Helvella solitaria*), b: hemiamyloid in medullary excipulum (*H. robusta*). 11: Reaction of stipe tissues to Melzer's reagent—a: negative (*H. hyperborea*), b: hemiamyloid in inner layer (*H. subglabra*). 12: Apothecium hyphal fascicles (*H. costifera*)—a: brown pigments visible in water, b) pigments not visible in cotton blue. 13: Apothecium hyphal fascicles (*H. griseoalba*)—a: only terminal cells are pigmented, b: pigments visible in cotton blue. 14: Apothecium hyphal fascicles (*H. dryadophila*)—a: brown pigments visible in water, b: brown pigments visible in cotton blue. Scale bars: 10a, 11a, 11b = 200 μ m, 10b = 100 μ m, 12–14 = 20 μ m.

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FIGS. 15–18. 15: Paraphyses of *Helvella costifera*—a: brown pigments visible in water, b: pigments not visible under cotton blue. 16: Paraphyses of *H. paraphysitorquata*—a: brown pigments visible only in the thickened apices in water, b: pigments visible in cotton blue. 17: Paraphyses of *H. dryadophila*—a: brown pigments visible in water, b: pigments visible in cotton blue. 18: Ornamented ascospores in cotton blue— a: *H. macropus*, b: *H. leucopus* var. *populina*, c: *H. paraphysitorquata*. Scale bar: 15, 17 = 20 μ m, 16a = 100 μ m, 18 = 10 μ m.

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FIGS. 19–22. 19: Hyaline ectal excipulum cells in water (*Helvella griseoalba*). 20: Wall pigments in ectal excipulum cells (*H. hyperborea*). 21: Wall and cytoplasmic pigments in ectal excipulum cells (*H. dryadophila*). 22: *H. ulvinenii*—a: apothecium thin section in water, b: ectal excipulum in cotton blue, notice the brown pigments, c: stipe layers in water, d: stipe outer layer under cotton blue. Scale bar: 19–21 = 10 μm , 22a, 22b = 100 μm , 22c = 200 μm , 22d = 20 μm .

used indistinct terms such as “finely pubescent,” “furfuraceous,” “granulose,” or “granulose-roughened” — all with very different meaning. Here we propose to the term “subpubescent” to indicate that they have the same microscopic structure (i.e. are hyphal fascicles) of the hairs found on a “pubescent” surface but are simply shorter (FIG. 2). Likewise, longer hairs have been described as “pubescent” or “villose,” without considering that the terms may refer to different types of hairs. We use “pubescent” (FIG. 3) to emphasize that *Helvella* has only one hair type that varies only in length. This agrees with Kaushal’s (1991) terminology.

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Reasons to retain *H. subglabra* as independent of *H. atra* and *H. griseoalba* separate from *H. costifera* are discussed below. We agree with Harmaja (1977a) that *H. queletii* is a synonym of *H. solitaria* and with Abbott & Currah (1997) that *H. dryadophila* is a synonym of *H. verruculosa*. We also propose *H. hyperborea* as a synonym of *H. costifera*.

We present below a synoptic key of the 12 *Helvella* species considered in this paper. Although not all *Helvella* species are included, we feel that this key provides additional morphological insights into the treated species and contributes to a better understanding of the genus.

Synoptic key to species of *Helvella* included in this work

- 1) *H. costifera* (= *H. hyperborea*)
- 2) *H. crassitunicata*
- 3) *H. griseoalba*
- 4) *H. leucopus* var. *populina*
- 5) *H. maculata*
- 6) *H. paraphysitorquata*
- 7) *H. pocillum*
- 8) *H. robusta*
- 9) *H. solitaria* (= *H. queletii*)
- 10) *H. subglabra*
- 11) *H. ulvinenii*
- 12) *H. verruculosa* (= *H. dryadophila*)

APOTHECIUM SHAPE (MATURE)

- a. Cup-shaped 1, 2, 3, 7, 8, 9, 11, 12
- b. Lobed 4, 5, 6, 8, 10

APOTHECIAL STERILE SURFACE

- a. Glabrous 2, 4
- b. Subpubescent (hyphal fascicles < 50 µm long) 2, 7, 8, 9, 10, 11, 12
- c. Pubescent, with hyphal fascicles 50–150 µm long 1, 3, 5, 6, 7, 8, 9, 11, 12
- d. Pubescent, with hyphal fascicles > 150 µm long 1, 5, 6

RIBS (APOTHECIAL STERILE SURFACE)

- a. Missing or reaching up to ¼ of the surface 2, 4, 6, 7, 9, 10, 11, 12
- b. Reaching from ¼ to ¾ of the surface 1, 3
- c. Reaching from ¾ to the edge of the apothecium 1, 5, 8
- d. Simple 1, 5
- e. Bifurcated 1, 3, 5, 8
- f. Anastomosed 1, 8

STIPE (SURFACE CONFIGURATION)

- a. Even 4, 10
- b. Only ribbed 1, 2, 3, 7, 9, 11, 12
- c. Ribbed and lacunose 5, 8
- d. Consisting of 2–3 strands free or apically partly fused 6

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RIB (STIPE)

- a. Sharp-edged 5, 8
- b. Blunt-edged 1, 2, 3, 7, 9, 11, 12

STIPE (STERILE SURFACE)

- a. Glabrous 2, 3, 4
- b. Subpubescent (hyphal fascicles < 50 µm long) 2, 3, 8, 9, 10, 12
- c. Pubescent (hyphal fascicles 50–150 µm long) 1, 5, 6, 7, 8, 9, 11, 12

STIPE COLOR

- a. Light tones 1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 12
- b. Dark tones 4

STIPE CONTEXT

- a. Solid 1, 2, 3, 6, 7, 9, 10, 11, 12
- b. Hollow 4, 5, 8

ASCUS TYPE

- a. Aporhynchous 2
- b. Pleurorhynchous 1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12

ASCOSPORE SIZE

- a. Usually < 23 µm long 1, 3, 4, 5, 6, 8, 9, 10, 11, 12
- b. Usually > 23 µm long 2, 7

THICK-WALLED PARAPHYSES

- a. Absent 1, 3, 4, 5, 7, 8, 9, 10, 11, 12
- b. Present 2
- c. Thickness restricted to the apex, forming a collar or hood 6

MELZER'S REACTION (MEDULLARY EXCIPULUM)

- a. Negative 1, 2, 3, 4, 5, 6, 7, 9, 11, 12
- b. Hemiamyloid (reddish) 8, 10

MELZER'S REACTION (STIPE INNER LAYER)

- a. Negative 1, 2, 3, 5, 6, 7, 9, 11, 12
- b. Hemiamyloid (reddish) 4, 8, 10

MELZER'S REACTION (STIPE OUTER LAYER)

- a. Negative 1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12
- b. Hemiamyloid (reddish) 8

PARAPHYSES (PIGMENT TOPOGRAPHY)

- a. Absent 3
- b. In the cell wall 1, 7, 8, 10, 11
- c. In the cytoplasm 1, 2, 4, 5, 7, 9, 12
- d. Restricted to the apical collar or hood 6

PARAPHYSES (PIGMENT IN COTTON BLUE)

- a. Not visible 1, 5, 8, 10
- b. Visible in all 2, 4, 7, 9, 11, 12
- c. Visible only in thickened apices 6

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PIGMENT (ECTAL EXCIPULUM)

- a. Absent 3, 4
- b. In the cell wall 1, 2, 5, 6, 7, 8, 9, 10, 11, 12
- c. In the cytoplasm 2, 5, 7, 9, 11, 12

PIGMENT (ECTAL EXCIPULUM IN COTTON BLUE)

- a. Not visible 1, 5, 6, 8, 9, 10
- b. Visible 2, 7, 11, 12

PIGMENT (STIPE OUTER LAYER)

- a. Absent 1, 3, 11
- b. In the cell wall 2, 5, 6, 7, 8, 9, 10, 12
- c. In the cytoplasm 2, 4, 5, 12

PIGMENT (STIPE OUTER LAYER IN COTTON BLUE)

- a. Not visible 2, 4, 6, 7, 8, 9, 10, 12
- b. Visible in the cytoplasm 5

PIGMENT (APOTHECIAL HYPHAL FASCICLES)

- a. Absent 5
- b. In the cell wall 1, 2, 6, 8, 9, 10, 12
- c. In the cytoplasm 2, 7, 11, 12
- d. Restricted to the terminal cells (in the wall cell and cytoplasm) 3

PIGMENT (APOTHECIAL HYPHAL FASCICLES IN COTTON BLUE)

- a. Not visible 1, 6, 8, 9, 10
- b. Visible in the cytoplasm 7, 11, 12
- c. Visible only in the cytoplasm in apical cells 3

PIGMENT (STIPE HYPHAL FASCICLES)

- a. Absent 1, 3, 5, 11
- b. In the cell wall 2, 6, 7, 8, 9, 10, 12
- c. In the cytoplasm 2, 12

Taxonomy of type specimens

Helvella costifera Nannf., in Lundell & Nannfeldt, Fungi Exsicc. Suec.,

Fasc. 41–42: 37, 1953

FIGS 3, 12, 15, 23

= *Peziza costata* Fr., Nova Acta Reg. Soc. Sci. Uppsal., Ser. 3, 1: 120, 1851

TYPE: Sweden: Uppland, Uppsala, Botanic Garden, E.P. Fries s.n. *Peziza costata*
(Lectotype UPS [not seen]; isolectotypes S [studied], K [not seen]).

= *Helvella hyperborea* Harmaja, Karstenia 18: 57, 1978

ASCI 280–370 × 14–18 μm. PARAPHYSES 4.5–7.5 μm wide at the apex, thin-walled, hyaline, pale brown to brown in mass, pigment deposits in the cytoplasm and cell walls, few with brown pigment encrusted on the wall. MEDULLARY EXCIPULUM hyaline to light brown. ECTAL EXCIPULUM light brown, pigment deposits in the cell walls. STIPE INNER AND OUTER LAYERS hyaline. APOTHECIAL HYPHAL FASCICLES 100–230 μm long, light brown in mass, pigment deposits in the cell walls; STIPE HYPHAL FASCICLES 50–120 μm long, hyaline. The brown

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pigments of the ectal excipulum are not visible in cotton blue or Melzer's while those of the paraphysis cell walls are visible in Melzer's, but inconspicuous in cotton blue. All tissues rr–.

ADDITIONAL SPECIMENS EXAMINED: FINLAND: LAPLAND, Enontekiö, 6 Aug 1985, J. Vauras 1932 (H); NORTHERN OSTROBOTHNIA, Kuusamo, 4 Aug 1994, T. Ulvinen FO23453 (OULU); UUSIMAA, Lohja, 19 Jul 1998, U. Nummela-Salo & P. Salo 4924 (H). NORWAY: NORTHERN NORWAY, FINNMARK, 19 Aug 1995, I. Kylövuori 95-744 (H). SWEDEN: UPPLAND, 22 Jun 1948, H. Smith (UPS); 7 July 1948, A. Melderis (UPS); 9 Jul 1948, Exsiccata J.A. Nannfeldt no. 9956 (K).

REMARKS — When Nannfeldt (Lundell & Nannfeldt 1953) transferred *Peziza costata* to *Helvella*, he had to publish a nom. nov., *H. costifera*, because the epithet “*costata*” was already occupied in *Helvella* by *H. costata* Schwein. In the protologue of the replaced synonym *Peziza costata*, Fries (1851: 120) had presented two syntypes:

“In Ohio Americae borealis (*Lindblom*) — etiam copiose in Horto Botanico Upsaliensi una cum *Pez. Helvelloidis* var. *minori*, *P. sepulta* (Cfr. Summ. Veg. Sc.) *Augusto* pluvio. *El. Fries*, filius [= Elias Petrus Fries]. ... Descripti ad specimina Upsaliensia viva, a quibus exsiccatis Fungus Ohioensis non distinguendus.”

Nannfeldt (1937: 64) noted that “*Peziza costata* Fr. is represented in the Uppsala Museum by beautiful authentic material,” but Lundell & Nannfeldt (1953) cited none of Fries's specimens, noting only that the North American specimen cited by Fries is lost. Subsequently, a UPS syntype specimen collected by E.P. Fries was designated as lectotype by Dissing (1966b, as “holotype”), and accepted by Harmaja (1979, as “lectotype?”) and Abbott & Currah (1997, as “holotype”) — these errors in type terminology are correctable (McNeill et al. 2006: Art. 9.8).

The lectotype was not available for study because of the bad condition of the specimen at UPS. Dissing (1966b) described this species with narrower asci (12–15 µm) and paraphyses (3–4 µm) than we observed. Our isolectotype measurements are closer to those made by Abbott & Currah (1997; asci 313–381 × 13.3–17.1 µm, paraphyses 3.6–6.2 µm at the apex). *Helvella costifera* differs from *H. acetabulum* (L.) Qué. in being less ribbed, with blunt edged ribs, a non-lacunose stipe, grayish hymenium, and pubescent apothecium. In *H. acetabulum* the stipe is highly ribbed to lacunose with sharp edged ribs (Dissing 1966b), the hymenium has brownish tones (Weber 1972), and the sterile part of the apothecium is subpubescent to pubescent. See also discussion under *H. griseoalba* and *H. hyperborea*.

Helvella crassitunicata N.S. Weber, Beih. Nova Hedwigia 51: 30, 1975 Figs 5, 8, 24

TYPE: U.S.A.: Washington, Mount Rainier National Park, Narada Falls, on soil along a path, 10 Aug 1948, A.H. Smith 30052 (Holotype MICH, Barcode 11561).

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APOTHECIUM sterile surface subpubescent. STIPE glabrous to subpubescent. ASCI 290–340 × 18–24 μm. ASCOSPORES (21.5–)23–26(–28) × (12–)13–14.5 (–15.5) μm, ellipsoid to oblong, smooth. PARAPHYSES of two types: a) 5–7.5 μm wide at the apex, thin-walled, septate, hyaline or light brown; b) 7–9 μm wide at the apex, thick-walled, non-septate, light brown, pigment deposits always in the cytoplasm. ECTAL EXCIPULUM brown, pigment deposits in the cell wall and cytoplasm. STIPE OUTER LAYER slightly lighter than the ectal excipulum, pigment deposits in the cell wall and cytoplasm. APOTHECIAL HYPHAL FASCICLES ≤ 50 μm long, brown pigment deposits in cell walls and cytoplasm; STIPE HYPHAL FASCICLES ≤ 10 μm long, tan pigment deposits in cell walls and cytoplasm. The brown pigments of the paraphyses, ectal excipulum, and apothecial hyphal fascicles are visible in cotton blue or Melzer's; light brown pigments of the stipe outer layer and hyphal fascicles inconspicuous in cotton blue or Melzer's. All tissues rr–.

REMARKS — *Helvella crassitunicata* and *H. leucomelaena* (Pers.) Nannf. are the only two taxa with aporhynchous asci (FIG. 5) (Abbott & Currah 1997). *Helvella leucomelaena* is differentiated by mature paraphyses that are never thick-walled, slightly smaller (20–23(–25) × 10.5–14 μm) ascospores, and ascomata that fruit in spring or early summer. [However, although Weber (1972) cited *H. crassitunicata* as fruiting in the fall, Abbott & Currah (1997) noted it might fruit from May to October.] Also in *H. leucomelaena* the stipe is poorly developed or absent and the color of the paraphyses is lost in cotton blue.

Neither Weber (1972) nor we observed the following features cited for *H. crassitunicata* by Abbott & Currah (1997): 1) ectal excipulum “pubescent to densely pubescent”, 2) stipe “finely pubescent to pubescent”, and 3) asci 350–400 × 17–20 μm. It is uncertain whether the differences in wall thickness of the paraphyses should be interpreted as dimorphic (Abbott & Currah 1997) or developmental (young = thin-walled and mature = thick-walled; Weber 1975). Since a hymenium develops first as a palisade of paraphyses within which the asci develop, it would be difficult to have mature asci and immature paraphyses at the same time (Pfister pers. com.). On the other hand, we observed thin and thick-walled branches borne on the same paraphyses. See also remarks under *H. pocillum*.

Helvella dryadophila Harmaja, Karstenia 17: 58, 1977

FIGS 14, 17, 21, 25

TYPE: NORWAY: prov. Oppland, par. Lom, fjeld Høyrokampen, alt. 1400–1440 m, *Dryas octopetala* assoc., 29 Aug 1957 FE. Eckblad, p.p. (Holotype O).

= *Helvella verruculosa* (Sacc.) Harmaja, Karstenia 18: 57, 1978

ASCI 230–280 × 14–18 μm. PARAPHYSES 4–7 μm wide at the apex, thin-walled, brown, pigment deposits in the cytoplasm. MEDULLARY EXCIPULUM hyaline. ECTAL EXCIPULUM brown, pigment deposits in the cell wall and cytoplasm.

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STIPE INNER LAYER hyaline. STIPE OUTER LAYER brown, pigment deposits in cell wall and cytoplasm. APOTHECIAL HYPHAL FASCICLES 40–100 μm , brown, pigment deposits in the cell wall and cytoplasm; STIPE HYPHAL FASCICLES 30–70 μm , brown, pigment deposits in cell walls and cytoplasm. The brown pigments of the paraphyses, ectal excipulum, and apothecial hyphal fascicles are visible in cotton blue or Melzer's; brown pigments of the stipe outer layer and hyphal fascicles inconspicuous in cotton blue. All tissues rr-.

REMARKS — We agree with Abbott & Currah (1997) that *H. dryadophila* is a synonym of *H. verruculosa*, because Harmaja (1977b, 1979) used variable characters to distinguish them. 1) Both ascomata appear the same: Harmaja's own illustration (1977b: 51) (FIG. 5) shows both species with a cup-shaped apothecium and a ribbed stipe with ribs that never reach the apothecial sterile surface. 2) For the excipulum, Harmaja cited, "the outermost layer has somewhat larger cells with slightly thicker wall as *H. arctoalpina*," but gave no measurements, and we did not see such differences. 3) The paler and homogeneous contents of paraphyses in *H. dryadophila* did not appear paler to us; in fact, in cotton blue, the brown pigments are visible in the paraphyses of both species. The homogeneous content is variable and the pigment tends to be less homogeneous in immature ascomata. 4) As the presence of a fairly distinct layer of *textura angularis* in the excipulum is a generic character for *Helvella*, its occurrence should not be used to distinguish between species.

Abbott & Currah (1997) mentioned that *H. arctoalpina* Harmaja (Harmaja 1977) should also be considered a synonym of *H. verruculosa*, but as the type collection of *H. arctoalpina* is not in O, we unfortunately could not examine the holotype.

Helvella griseoalba N.S. Weber, Michigan Bot. 11: 162, 1972 Figs 2, 13, 19, 26

TYPE: U.S.A.: Michigan, Cheboygan Co., Grapevine Point, Douglas Lake, Univ. of Michigan Biol. Sta., 10 Jun 1968, N.J. Smith 982 (Holotype MICH, Barcode 14379).

ASCI 220–265 \times 12.5–16 μm . MEDULLARY & ECTAL EXCIPULA hyaline. STIPE INNER AND OUTER LAYERS hyaline. APOTHECIAL HYPHAL FASCICLES 70–120 μm long, hyaline with brown terminal cells, pigment deposits in the cell wall and cytoplasm; STIPE HYPHAL FASCICLES \leq 30 μm long, completely hyaline. The brown pigments of terminal cells of the apothecial hyphal fascicles are visible in cotton blue or Melzer's. All tissues rr-.

REMARKS — Although in fresh ascomata the hymenium and sterile surface of the apothecium are concolorous (gray to cinnamon; Weber 1972), the dried sterile surface is lighter, cream to light brown, and the hymenium is slightly darker, grayish brown. This may be one reason why dry *H. griseoalba* material can be easily confused with *H. costifera*. Both Häffner (1987) and Abbott & Currah (1997) synonymized *H. griseoalba* under *H. costifera*, noting that color

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walled, hyaline or brown, pigment deposits in the cytoplasm. MEDULLARY AND ECTAL EXCIPULA hyaline. STIPE INNER LAYER hyaline. STIPE OUTER LAYER light brown, pigment deposits in the cytoplasm. HYPHAL FASCICLES absent in the apothecium and stipe. The brown pigments of the paraphyses are visible and those of the stipe outer layer are not visible in cotton blue or Melzer's. Stipe inner layer rr+; medullary and ectal excipula and stipe outer layer rr-.

REMARKS — Persoon (1822) described *H. leucopus* Pers. as having a deflexed apothecium at both ends (lobate), bay to black in color, and a 30–40 mm long glabrous white stipe. Arroyo & Calonge (1990) distinguished variety *populina* (validated by Calonge 2000) by the darker stipe color and larger ascoma size (apothecium 40–60 × 30–45 mm; stipe 50–120 × 15–35 mm). However, Moravec (1980) previously cited larger specimens of *H. leucopus* var. *leucopus* (ascomata ≤ 150 mm high) from Slovakia. Ascoma size can be quite variable and so should be considered with caution; for example, *H. crispa* (Scop.) Fr. and *H. lacunosa* ascomata may range from 50 to 200 mm high. Arroyo & Calonge (1990) described smooth ascospores and ≤ 12 µm wide paraphyses apices, while we observed verrucose mature ascospores (more evident in cotton blue or Melzer's) and narrower paraphyses.

Helvella maculata N.S. Weber, Beih. Nova Hedwigia 51: 27, 1975

FIG. 29

TYPE: U.S.A.: Idaho, Bonner Co., south side of Hoodoo Mountain, 5 Oct 1968, H.V. Smith et N.J. Smith (N.J. Smith 2124) (Holotype MICH, Barcode 5635).

APOTHECIUM sterile surface pubescent. ASCOSPORES 18–22.5 × 10.5–12 µm. ECTAL EXCIPULUM yellowish brown, pigment deposits in cell walls and cytoplasm. STIPE INNER LAYER hyaline. STIPE OUTER LAYER brown, pigment deposits in cell walls and cytoplasm. APOTHECIAL HYPHAL FASCICLES 107–205 µm long, hyaline; STIPE HYPHAL FASCICLES 60–130 µm long, hyaline. The brown pigments of the paraphyses and ectal excipulum of the apothecium are inconspicuous and those of the stipe outer layer are very conspicuous in cotton blue or Melzer's. All tissues rr-.

REMARKS — We measured smaller ascospores than those cited by Weber (1975, 20–23 × 12–13.5 µm). *Helvella maculata* might be confused with *H. crispa*, but the mottled apothecium, grayish stipe ribs, pubescent sterile surface, and incurved and unrolling margin of *H. maculata* are diagnostic (Weber 1975; Abbott & Currah 1997). Furthermore, the brownish pigment of the stipe outer layer is evident in cotton blue in *H. maculata* but not in *H. crispa*. For Weber (1975) ascospore size could help differentiate the two species, but the size range we observed for *H. maculata* overlaps with that seen in *H. crispa* (16–20.5 × 9.8–12 µm). Another similar species, *H. fusca* Gillet, has a dark red-brown hymenium, distinctly ribbed sterile surface with some ribs reaching the apothecium margin, and vernal fructification associated with *Populus*,

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differences of the hymenial surface and absence of pigments in the apothecial ectal excipulum in *H. griseoalba* were not enough to separate them. However, we observed additional features in the types of *H. costifera* and *H. griseoalba* that support keeping them as different taxa: 1) *H. costifera* presents pubescent hyphal fascicles in the stipe while *H. griseoalba* does not (glabrous) or has shorter (subpubescent) hyphal fascicles; 2) *H. costifera* can have light brown paraphyses while *H. griseoalba* has only hyaline ones, and 3) in *H. griseoalba* the terminal cells of the apothecial hyphal fascicles have brown pigments that are visible in cotton blue (FIG. 13) while in *H. costifera* the light brown pigments in the cell walls are not visible in cotton blue (FIG. 12).

Helvella hyperborea Harmaja, Karstenia 18: 57, 1978

FIGS 11a, 20, 27

TYPE: FINLAND: prov. Kuusamo, par. Kuusamo, Juuma, western part of the gorge Jäkälävuoma, alt. ca. 205 m, on a shady shelf in the basal part of a steep dolomitic rock, among the moss *Distichium capillaceum* (etc.), accompanied by *Salix reticulata*, *Saxifraga aizoides*, *S. nivalis*, *Woodsia glabella*, *Gerronema albidum*, 27 Aug 1970, H. Harmaja (Holotype H).

= *Helvella costifera* Nannf., in Lundell & Nannfeldt, Fungi Exsicc. Suec., Fasc. 41–42: 37, 1953

ASCI 240–315 × 15–18 μm. PARAPHYSES thin-walled, hyaline, pale brown to brown in mass, pigment deposits in cytoplasm and cell walls, some with brown encrusted pigment on walls. MEDULLARY EXCIPULUM hyaline to light brown. STIPE INNER AND OUTER LAYERS hyaline. APOTHECIAL HYPHAL FASCICLES 50–160 μm long, light brown in mass, pigment deposits in cell walls; STIPE HYPHAL FASCICLES 50–100 μm long, hyaline. The brown pigments of all structures are not visible in cotton blue. All tissues rr–.

ADDITIONAL SPECIMENS EXAMINED: FINLAND: LAPLAND, Kemi, 7 Aug 1998, U. Nummela-Salo & P. Salo 5318 (H); NORTERN SAVONIA, Kuopio, 22 July 1984, J. Vauras 1638F (H); 23 Aug 1987, J. Vauras 2856 (H); VARSINAIS-SUOMEN, 4 Jul 1996, J. Vauras 11192F (H). NORWAY: NORTHERN NORWAY, TROMS, 16 Aug 1992, I. Kytövuori 92-352 (H).

REMARKS — *Helvella hyperborea* was proposed as a new species by Harmaja (1978) and accepted as distinct by Abbott & Currah (1997). After comparing its type with *H. costifera*, including eleven additional specimens from Herbaria O and UPS (labeled either *H. costifera* or *H. hyperborea*), we conclude these two species are the same. Harmaja (1979, Table 1) listed 12 characters for differentiating *H. hyperborea* from *H. costifera* but explained that only a combination of all features should be used for its identification. In fact, we think that his table is an excellent presentation of variability in *H. costifera*. Abbott & Currah (1997) used only the ribs of the apothecial sterile surface to separate the species, distinguishing *H. costifera* by branched anastomosed ribs extending up to the marginal area from *H. hyperborea* with simple unbranched

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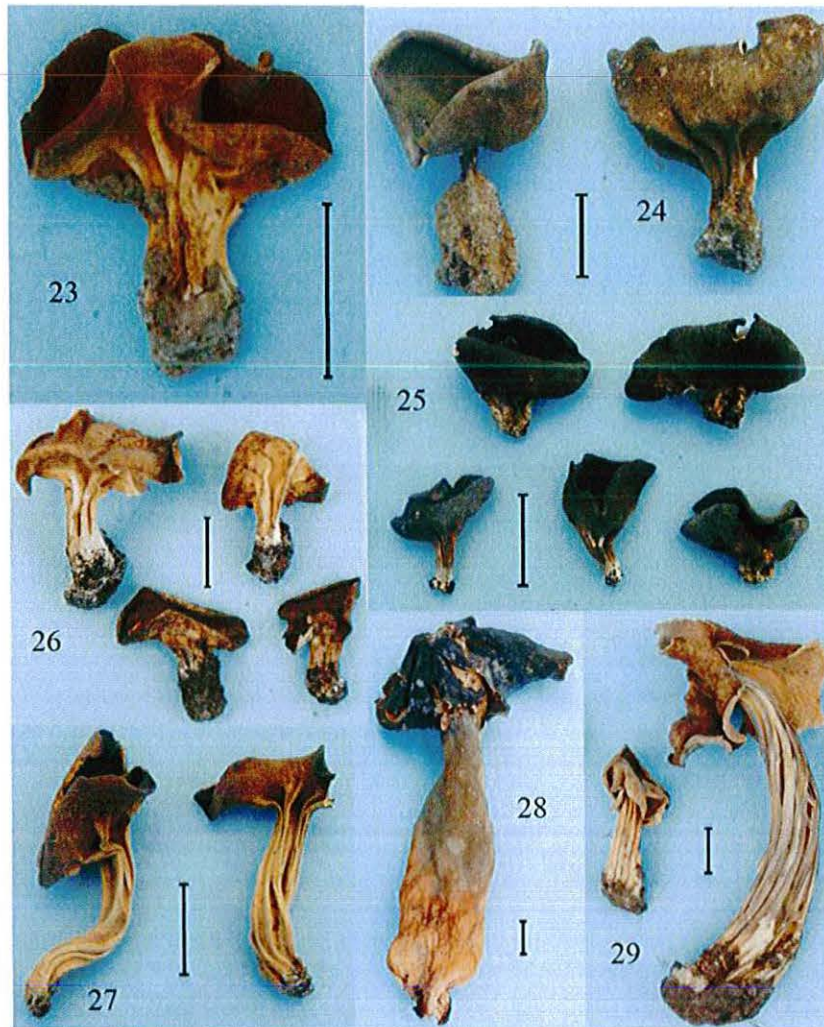
ribs extending onto the basal half. However, both isolectotype and exsiccata (J.A. Nannfeldt no. 9956) of *H. costifera* possess the same features used to identify *H. hyperborea* (see Figs 23, 27).

We provide below our evaluation of what we consider the five most important features used by Harmaja (1979) to separate these species.

- 1) A brown-grey hymenium color that is paler in *H. costifera* — we have observed that in fresh material, the color intensity of the hymenium may depend on whether the specimen is growing in a forest clearing or in a shaded area.
- 2) Ribs extending onto the sterile surface, especially in dried specimens — Although Harmaja (1979; Figs. 2–3) illustrated this feature, we found that the *H. costifera* isolectotype also has ribs on the sterile surface as, for that matter, does *H. acetabulum*.
- 3) Sterile surface of the apothecium: “with fine but almost always \pm distinct hyaline to pale brown pubescence or villosity” (*H. costifera*) versus “more or less delicate brown (mostly dark) pubescence usually appearing glabrous to bare eye” (*H. hyperborea*) — Under the microscope, the hairs of all studied specimens have the same color. However, we measured 100–230 μm long hyphal fascicles in the *H. costifera* type vs. 50–160 μm long fascicles in *H. hyperborea*. The hairs as measured in the additional specimens range from 50–240 μm long, depending on the maturity of the ascoma. In the stipe hair lengths are similar for both types — 50–120 μm long in *H. costifera*, 40–100 μm long in *H. hyperborea* — and remains relatively constant (40–120 μm) in the additional specimens.
- 4) Pigmentation of the paraphyses: “medium (rarely pale) brown wall encrustation” and more or less brown contents (*H. hyperborea*) versus hyaline, inconspicuous or pale brown encrustation and pale brown to practically hyaline contents (*H. costifera*) — We observed the same color in the paraphyses for both species, and in cotton blue the cytoplasmic pigment is inconspicuous; the cell wall pigment is variable among specimens in both species.
- 5) Distribution, “middle boreal to lower oroarctic (low alpine), optimal area apparently northern boreal zone” (*H. hyperborea*) versus “temperate to middle (oro)boreal with preference for southern and low-lying areas” (*H. costifera*) — Sequences of the 28S large subunit ribosomal DNA from three specimens identified as *H. costifera* (unpublished) from Scandinavia (two from northern boreal specimens and one from the middle boreal region) show only one or two base differences. Notably, both species were described from the Scandinavian peninsula.

Helvella leucopus var. *populina* I. Arroyo & Calonge, in Calonge, Bol. Soc. Micol. Madrid 25: 302, 2000 FIGS 1, 18b, 28
 TYPE: Spain: Guadalajara, Sigüenza, 8 May 1988, M.J. Rodríguez 888 (Holotype MA Fungus 22870).

APOTHECIUM sterile surface glabrous, even. STIPE tapering toward the apex, hollow, glabrous. ASCI pleurorhynchous. ASCOSPORES verrucose, smooth within the ascus, hyaline, uniguttulate. PARAPHYSES 3.5–4.5 μm wide at the apex, thin-

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FIGS. 23–29: Ascomata of type specimens (except when indicated) of *Helvella*. 23: *H. costifera* (Exsiccata J.A. Nannfeldt no. 9956). 24: *H. crassitunicata*. 25: *H. dryadophila*. 26: *H. griseoalba*. 27: *H. hyperborea*. 28: *H. leucopus* var. *populina*. 29: *H. maculata*. Scale bar: 1 cm.

while *H. maculata* fruits in autumn and is associated with conifers (Weber 1975); furthermore, the apothecium sterile surface of *H. fusca* is subpubescent. According to Abbott & Currah (1997), *H. maculata* could also be confused with *H. lacunosa*, which differs in having an apothecium margin attached to the stipe, black hymenium, and glabrous sterile surface of apothecium and stipe.

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Helvella paraphysitorquata I. Arroyo & Calonge, in Calonge & Arroyo, Mycotaxon
39: 210, 1990 FIGS 7, 16, 18c, 30

TYPE: Spain: within the province of Teruel, Albarracín, growing in soil under *Populus*, 3
Jun 1988, I. Arroyo & F.D. Calonge (Holotype MA-Fungi 24512).

APOTHECIUM sterile surface pubescent, even. STIPE pubescent. ASCI pleurohynchous. ASCOSPORES 16.5–19 × 11–13.5 µm, ovoid to ellipsoid, verrucose, smooth within the ascus. PARAPHYSES 5–9 µm wide at the apex, thin-walled, hyaline, with a brown thick-walled cap or collar at the apex. MEDULLARY EXCIPULUM hyaline. ECTAL EXCIPULUM hyaline to light brown, pigment deposits in cell walls. STIPE INNER AND OUTER LAYERS hyaline to light brown, pigment deposits in cell walls. APOTHECIAL HYPHAL FASCICLES 60–220 µm long, hyaline to light brown in mass, pigment deposits in the cell wall; STIPE HYPHAL FASCICLES 60–140 µm, hyaline to light brown in mass, pigment deposits in the cell wall. The brown pigments of the paraphyses are visible in cotton blue, and pigments of the ectal excipulum, apothecial hyphal fascicles, and stipe outer layer and hyphal fascicles are not visible in cotton blue or Melzer's. All tissues rr–.

REMARKS — Calonge & Arroyo (1990) described *H. paraphysitorquata* with smooth ascospores, but we also found ornamented ascospores on the hymenial surface, stipe, and basal mycelium. We observed narrower paraphyses than those recorded by Calonge & Arroyo (1990; 7–10(–15) µm), possibly due to their rehydration in 2% KOH or 10% NH₃. *Helvella paraphysitorquata* is morphologically similar to *H. pezizoides* Afzel., which differs in its totally black even stipe and paraphyses lacking the brown collar. On the other hand, in a specimen determined as *H. macropus* from Mexico (J.M. Rodríguez Canseco 12, IBUG), we also observed a few or occasional brown capped or collared paraphyses, so apparently collared paraphyses are not unique to *H. paraphysitorquata*.

Helvella pocillum Harmaja, Karstenia 15: 30, 1976 FIGS 4, 31

TYPE: Sweden: prov. Torne Lappmark, par. Jukkasjärvi, fjeld Läktatjäkko, on bare soil, 17
Aug 1946, L. Holm 472 (Holotype UPS).

APOTHECIUM sterile surface subpubescent to pubescent, concolorous with the hymenial surface, stipe ribs only reaching the apothecium basis. STIPE 1–5 × 1–3 mm, solid, costate, ribs blunt, pubescent, concolorous with the hymenial surface. ASCI 320–380 × 18–24 µm, pleurohynchous. ASCOSPORES 23–28 × 12–15.5 µm, smooth. PARAPHYSES thin-walled. MEDULLARY EXCIPULUM hyaline. ECTAL EXCIPULUM brown, pigment deposits in cytoplasm. STIPE INNER LAYER hyaline. STIPE OUTER LAYER light brown, pigment deposits in cell walls. APOTHECIAL HYPHAL FASCICLES 40–100 µm long, brown, pigment deposits in cytoplasm; STIPE HYPHAL FASCICLES 50–80 µm, hyaline to light brown in mass,

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pigment deposits in cell walls. The brown pigments of the paraphyses, ectal excipulum, and apothecial hyphal fascicles are visible and those of the stipe outer layer and hyphal fascicles are not visible in cotton blue or Melzer's. All tissues rr-.

REMARKS — *Helvella pocillum* is characterized by its very small ascoma; only *H. rivularis* Dissing & Sivertsen is as small, but with an even stipe. For Harmaja (1976) *H. pocillum* could be separated from *H. crassitunicata* by its larger ascospores, the width of the paraphyses (we found no differences in either of these characters), and the absence of thick-walled paraphyses. Besides, *H. crassitunicata* has aporhynchous asci (FIG. 5) and the sterile surfaces of apothecium and stipe are glabrous to subpubescent. Another similar species is *H. leucomelaena*, also with aporhynchous asci.

Helvella queletii Bres., Fungi trident. 1(3): 39, 1882

FIG. 32

TYPE: Italy: Bosc di lance sopra Terzolaj, May 1882, J. Bresadola (Holotype S).

= *Helvella solitaria* P. Karst., Bidr. Känn. Finl. Nat. Folk 19: 37, 1871

STIPE solid, costate, ribs blunt. ASCI 260–310 × 15–20 μm, pleurohynchous. ASCOSPORES 17.5–21.5 × 10.5–12.5 μm, broadly ellipsoidal, smooth. PARAPHYSES 3.5–7 μm wide at the apex, thin-walled, brown, pigment deposits in the cytoplasm. MEDULLARY EXCIPULUM hyaline. ECTAL EXCIPULUM brown, pigment deposits in cell walls and cytoplasm. STIPE INNER LAYER hyaline. STIPE OUTER LAYER light brown, pigment deposits in cell walls. APOTHECIAL HYPHAL FASCICLES 25–60 μm long, light brown in mass, pigment deposits in the cell wall; STIPE HYPHAL FASCICLES 40–100 μm, light brown, pigment deposits in cell walls. The brown pigments of the paraphyses are visible and pigments of the ectal excipulum, stipe outer layer, and apothecial and stipe hyphal fascicles are not visible in cotton blue or Melzer's. All tissues rr-.

ADDITIONAL SPECIMENS EXAMINED: SPAIN: MADRID, Madrid, 7 Apr 2001, A. González, J.C. Campos et al., G.P. 1395 (MA-Fungi 73836); CASTILE AND LEÓN, Valladolid, 31 Mar 2001, Herrera de Duero 1294 (MA Fungi 54822).

REMARKS — Bresadola (1882), who described *H. queletii* as having a cup-shaped apothecium, sulcate-lacunose stipe ("costate" according to Weber 1972), and ascospores measuring 17–20 × 12 μm, noted its proximity to *H. lacunosa* but without mentioning the differences with *H. solitaria*. Dissing (1966b) differentiated *H. queletii* from *H. solitaria* by the following: 1) ascospore size — 17–19.1–21 × 11–12.3–13.5 μm (*H. queletii*) vs. 19–21.7–24 × 12–13.1–15 μm (*H. solitaria*); 2) ascoma size — 20–80 mm broad apothecium, 20–60 mm high stipe (*H. queletii*) vs. 10–40 mm broad apothecium, 10–25 mm high stipe (*H. solitaria*); 3) hymenium color (pale brownish to dark greyish-brown (*H. queletii*) vs. greyish to greyish-brown (*H. solitaria*); 4) stipe rib number — 4–7 in *H. queletii* vs. 2–5 in *H. solitaria*; 5) fruiting time — April–October in *H. queletii* vs. February–June in *H. solitaria*.

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Harmaja (1977a) suggested that *H. queletii* be recognized as a synonym of *H. solitaria* based on the variability of ascoma size, color, pubescence, and stipe rib number. Abbott & Currah (1997) also considered them synonymous (but see below under *H. solitaria*). The following list summarizes our observations of both holotypes and other original descriptions.

- 1) The *H. solitaria* holotype has smooth ascospores and a spore range (18–20 × 9.5–12 µm) matching that of the *H. queletii* holotype and as reported by Dissing (1966b). We also found smaller (15–17.5 × 9.5–11.5 µm) verrucose ascospores more closely matching measurements given by Karsten (1871, 14–16 × 10 µm) but never matching that cited by Dissing (1966b).
- 2) Ascoma size, highly variable in *Helvella*, is not a good taxonomic criterion for a widespread species,
- 3) Ascoma color is highly variable in *H. queletii* with tones very similar to *H. solitaria*, as noted in Dissing (1966a) and Dissing & Nannfeldt (1966),
- 4) Among materials cited as *H. queletii* by Dissing (1966b) is a specimen collected in March (Velenovsky s.n., Mar 1923, PRC), while among his *H. solitaria* materials are specimens collected in July (Eftesøl s.n., 8 Jul 1956, O; Berg s.n., 15 Jul 1957, O), August (Bresadola s.n., Aug 1893, S; Hakelier s.n., 28 Aug 1962, UPS), September (P. Karsten s.n., 21 Sep 1866, H), October (Toft s.n., 21 Oct 1965, C), and November (Bresadola s.n., Nov 1896, S; Arwidsson s.n., 1 Nov 1943, S). Thus, the time of fruiting is not diagnostic.
- 5) Both holotypes are anatomically similar, except that the brown cytoplasmic pigment in the paraphyses is lighter in *H. solitaria*.

Helvella robusta S.P. Abbott, in Abbott & Currah, Mycotaxon 33: 242, 1988

Figs 10b, 33

TYPE: CANADA: Calgary, Nose Hill area, 30 Aug 1972, R.M. Danielson 459 (Holotype DAOM-143869).

APOTHECIUM irregularly cupulate with a large central depression to irregularly bi-lobed, margin free, covering the stipe; sterile surface subpubescent to pubescent, ribbed, ribs sharp. STIPE gradually expanding toward the apothecium, lacunose, ribs sharp, subpubescent to pubescent. PARAPHYSES hyaline to light brown, pigment deposits in cell walls. MEDULLARY EXCIPULUM hyaline. ECTAL EXCIPULUM light brown, pigment deposits in cell walls. STIPE INNER LAYER hyaline. STIPE OUTER LAYER light brown, pigment deposits in cell walls. APOTHECIAL HYPHAL FASCICLES 38–80 µm long, hyaline to light brown, pigment deposits in cell walls; STIPE HYPHAL FASCICLES 40–90 µm long, hyaline to light brown, pigment deposits in cell walls. The brown pigment of the paraphyses, ectal excipulum, apothecial hyphal fascicles, and stipe outer layer is not visible in cotton blue or Melzer's. Medullary excipulum and stipe inner and outer layers rr+; ectal excipulum rr–.

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REMARKS — Abbott & Currah (1988, 1997) described *H. robusta* with apothecium that is irregularly cupulate or centrally depressed with reflexed margins; in addition to this type, we observed an irregularly bi-lobed apothecium covering the stipe, with the apothecial edges curved towards the stipe, thus fully exposing the hymenium. The peculiar shape of the ascoma makes *H. robusta* easy to recognize, although Abbott & Currah (1988) noted that it could be confused with some species of section *Acetabulum*, although members of that section have a well-defined cup-shaped apothecium in all stages of development. In addition to its peculiar apothecial shape, *H. robusta* has a strong reddish reaction in the apothecial medullary excipulum and stipe inner layer and moderately reddish reaction in the stipe outer layer in Melzer's.

Helvella solitaria P. Karst., Bidr. Känn. Finl. Nat. Folk 19: 37, 1871 Figs 9, 10a, 34

TYPE: Finland: Mustiala, in horto, ad marg. rivula, 21 Sep 1866, P. Karsten PAK 3288 (Holotype H).

= *Helvella queletii* Bres., Fungi trident. 1(3): 39, 1883

ASCOSPORES a) smooth: 18–20 × 9.5–12 µm, broadly ellipsoidal; b) verrucose: 15–17.5 × 9.5–11.5 µm, ellipsoidal. PARAPHYSES 4–7 µm wide at the apex, thin-walled, light brown, pigment deposits in the cytoplasm. MEDULLARY EXCIPULUM hyaline. ECTAL EXCIPULUM brown, pigment deposits in cell walls and cytoplasm. STIPE INNER LAYER hyaline. STIPE OUTER LAYER light brown, pigment deposits in cell walls. APOTHECIAL HYPHAL FASCICLES 40–90 µm long, light brown, pigment deposits in cell walls; STIPE HYPHAL FASCICLES 35–90 µm, light brown in mass, pigment deposits in cell walls. The brown pigments of the paraphyses are visible, and pigments of the ectal excipulum, stipe outer layer, and apothecial and stipe hyphal fascicles are not visible in cotton blue or Melzer's. All tissues rr–.

REMARKS — *Helvella solitaria* can be confused with *H. pocillum*, *H. ulvinenii*, and *H. verruculosa* because of its cup-shaped apothecium, costate stipe with ribs extending only to the base or a short distance onto the apothecium, and pleurohynchous asci. *Helvella pocillum* has larger ascospores (22–30 × 13–17 µm). *Helvella ulvinenii* has brown, sepia to black apothecial sterile surface (never with grayish tones), brown pigment of the apothecial hyphal fascicles visible in cotton blue and hyaline stipe hyphal fascicles. *Helvella verruculosa* differs in the visibility of the brown cytoplasmic pigments in the ectal excipulum and apothecial hyphal fascicles in cotton blue, and its arctic and alpine distribution contrasts with the boreal and temperate distribution for *H. solitaria* (Abbott & Currah 1997).

Paraphysis widths cited here match those by Karsten (1871) but not those by Abbott & Currah (1997), who cited paraphyses with 7–8 µm wide apices. Karsten (1871) gave 14–16 × 10 µm for *H. solitaria* ascospores but did not

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mention whether they were smooth or ornamented. We agree with Harmaja (1977a,b) that mature and immature ascospore sizes differ in some species, but in view of the greater size variation in *H. solitaria*, we consider it important to list the sizes of both immature and mature ascospores.

Although Dissing (1966b) recognized *H. solitaria* and *H. queletii* as different species, we agree with Harmaja (1977a) that they are synonyms, with the name *H. solitaria* having priority (see discussion under *H. queletii*).

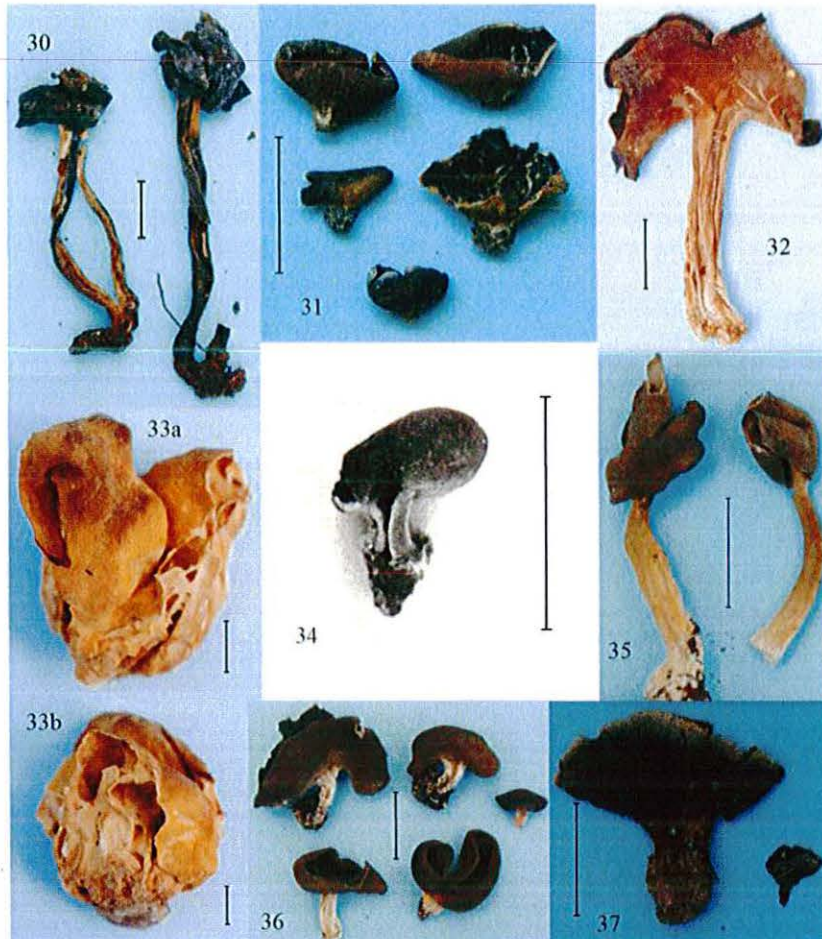
According to Abbott & Currah (1997), *H. solitaria* sensu Dissing (1966b) corresponds to *H. leucomelaena*. We do not agree with this because of the following: 1) *H. leucomelaena* has aporhynchous asci; Dissing (1966b) did not mention the ascus base, and 2) the specimens studied by Dissing do not seem to correspond to a single species. Harmaja (1977a) designated one Dissing *H. solitaria* specimen as holotype of *H. confusa* Harmaja (also considered a synonym under *H. leucomelaena* by Abbott & Currah, 1997), while other Dissing specimens correspond to different species, among them *H. leucomelaena* and *H. solitaria* (Harmaja 1979). As Dissing's concept of *H. solitaria* was very broad, it cannot be attributed to a particular taxon.

Helvella subglabra N.S. Weber, Michigan Bot. 11: 179, 1972 Figs 6, 11b, 35

TYPE: U.S.A.: Michigan, Washtenaw, Co., Stinchfield Woods, near Dexter, 13 Oct 1968,
N.J. Smith 2145 (Holotype MICH, Barcode 14381).

ASCI 224–324 × 15–17 μm, pleurorhynchous. ASCOSPORES 15–19 × 10–11.5 μm, smooth, few verrucose. PARAPHYSES thin-walled, hyaline to pale brown, pigment deposits in the cell wall. STIPE OUTER LAYER brown, pigment deposits in the cell wall. APOTHECIAL & STIPE HYPHAL FASCICLES ≤ 30 μm long, scattered; hyaline to brown, pigment deposits in cell walls. The brown pigments of all structures are not visible in cotton blue. Medullary excipulum and stipe inner layer rr+; ectal excipulum and stipe outer layer rr–.

REMARKS — Häffner (1987) and Abbott & Currah (1997) synonymized *H. subglabra* under *H. atra* J. König. They considered that the differences listed by Weber (1972) were not enough to separate them, because other species (*H. lacunosa*, *H. albella*, *H. latispota* Boud.) also accommodate such variability. Distinctions noted by Weber (1972) are: 1) hymenium surface color— dark gray to brownish gray or drab (*H. subglabra*) vs. black to grayish black (*H. atra*); 2) color of stipe and apothecial sterile surface — drab to gray (*H. subglabra*) vs. black or dark gray (*H. atra*); 3) pigments in cells of the ectal excipulum — scattered hyphal cells with brown walls (*H. subglabra*) vs. most hyphal cells with brown walls (*H. atra*); and 4) apothecial sterile surface texture — subpubescent (*H. subglabra*) vs. completely glabrous (*H. atra*). We add here two more characters that separate *H. subglabra* from *H. atra*: 1) tissues in Melzer's — ascoma negative (*H. atra*) vs. apothecial medullary excipulum

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FIGS. 30–37: Ascomata of type material of *Helvella*. 30: *H. paraphysitorquata*. 31: *H. pocillum*. 32: *H. queletii*. 33: *H. robusta*. 34: *H. solitaria* (scanned image of the picture contained in the type specimen). 35: *H. subglabra*. 36: *H. ulvinenii*. 37: *H. verruculosa*. Scale bar: 1 cm.

weakly reddish and stipe inner layer strongly reddish (*H. subglabra*); 2) the brown cell wall pigment in the paraphyses, ectal excipulum, and stipe outer layer is visible in cotton blue in *H. atra*.

Helvella ulvinenii Harmaja, Karstenia 19: 42, 1979

FIGS 22, 36

TYPE: Finland: prv. Enontekiön Lappi, par. Enontekiö, Kilpisjärvi, NE slope of W peak of fjeld Pikku-Malla, alt. ca. 650 m, H. Harmaja, 25 Aug 1979 (Holotype H).

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APOTHECIUM sterile surface subpubescent to pubescent. STIPE solid, costate, ribs blunt, pubescent. ASCI 240–300 × 14–17 µm. ASCOSPORES 14.5–18.5 × 10.5–12(–13.5) µm, broadly ellipsoid, smooth and verrucose. STIPE INNER & OUTER LAYERS hyaline. APOTHECIAL HYPHAL FASCICLES 40–105 µm long, brown, pigment deposits in the cytoplasm; STIPE HYPHAL FASCICLES 60–140 µm, hyaline. The brown pigments of the paraphyses, ectal excipulum, and apothecial hyphal fascicles are visible in cotton blue or Melzer's. All tissues rr–.

REMARKS — Harmaja (1979) did not mention ascospore ornamentation for *H. ulvinenii*; we observed both smooth (immature), and verrucose (mature) ascospores with the same size and shape. *Helvella ulvinenii* shares cup-shaped apothecia and costate stipes with ribs that do not reach the sterile apothecial surface with *H. solitaria* and *H. verruculosa*. We agree with Harmaja (1979) that *H. ulvinenii* is distinguished from *H. solitaria* by 1) a darker sterile surface that is never grayish, 2) shorter ascospores, and 3) ectal excipular hyphae with distinctly dark pigments, present only in the cell wall and not in the cytoplasm. Additional distinctions include: 1) the stipe outer layer and hyphal fascicles are hyaline in *H. ulvinenii* and light brownish (on the cell walls) in *H. solitaria*, and 2) the apothecial hyphal fascicle pigments are deposited in the wall in *H. solitaria* and occur both in the cytoplasm and in the cell wall in *H. ulvinenii*.

Harmaja (1979) differentiated *H. verruculosa* (as *H. dryadophila*) from *H. ulvinenii* based on 1) apothecial shape, 2) longer ascospores, and 3) very long paraphysis end cells. Although we did measure longer ascospores (17.5–22 × 10.5–13 µm) for *H. verruculosa*, both types had cup-shaped apothecia and ribbed stipes and the paraphysis end cells appeared the same. In addition, we observed that *H. verruculosa* has pigmented stipe hyphal fascicles. Probably, *H. ulvinenii* is a variety of *H. verruculosa*.

The *H. ulvinenii* type demonstrates particularly well the differences between the structure of the ectal excipulum and apothecial hyphal fascicles and of the stipe outer layer and hyphal fascicles; cells are pigmented in the apothecium and hyaline in the stipe (FIG. 22).

Helvella verruculosa (Sacc.) Harmaja, *Karstenia* 18: 57, 1978

FIG. 37

TYPE: Russia: Madagan Obl., Chukotski Peninsula, Arakamchene Island by the Bearing Strait, Stony Hills, 11 Aug ca. 1885, Wright, Herb. U.S.N. Pacif. Expl. Exped. No. 369 (Holotype K, Isotype FH, both studied).

= *Geopyxis verruculosa* Sacc., *Sylogae fungorum* 8: 68, 1889

= *Helvella dryadophila* Harmaja, *Karstenia* 17: 58, 1977

PARAPHYSES 4–8 µm wide at the apex, thin-walled, brown, pigment deposits in the cytoplasm. MEDULLARY EXCIPULUM hyaline. ECTAL EXCIPULUM brown, pigment deposits in cell walls and cytoplasm. STIPE INNER LAYER hyaline.

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STIPE OUTER LAYER brown, pigment deposits in cell walls and cytoplasm. APOTHECIAL HYPHAL FASCICLES 70–150 µm, brown, pigment deposits in cell walls and cytoplasm; STIPE HYPHAL FASCICLES 50–130 µm, brown, pigment deposits in cell walls and cytoplasm. The brown pigments of the paraphyses, ectal excipulum, and apothecial hyphal fascicles are visible and those of the stipe outer layer and hyphal fascicles are not visible in cotton blue or Melzer's. All tissues rr-.

REMARKS — Abbott & Currah (1997) described this species with a “villose margin” of the apothecium (sometimes with distinct white hairs), the stipe as having few chambers, and with stipe ribs extending onto basal half of apothecial sterile surface. We did not observe the marginal hairs, perhaps because the hairs have been lost due to age or handling. Furthermore, we observed neither stipe chambers nor ribs on the sterile surface of the apothecium. In fact, *H. verruculosa* is more easily confused with *H. solitaria* and *H. ulvinenii*, which do not have ribs on the sterile surface (see differences under the remarks of these species) than with *H. acetabulum*, *H. costifera*, and *H. griseoalba*.

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We appreciate the thorough reading and helpful comments from Donald H. Pfister (Harvard University, USA) and Trond K. Schumacher (University of Oslo, Norway) who acted as presubmission reviewers. Shaun Pennycook, Mycotaxon Nomenclature Editor, kindly helped us to make clearer the *H. costifera* nomenclatural remarks. We especially thank Lorelei Norvell, Mycotaxon Editor-in-Chief, who made an excellent work to improve the text. Thanks are given to the curators of the herbaria DAOM, FH, H, K, MA, MICH, S and UPS for the loan of type specimens. The first author thanks the Universidad Autónoma de Querétaro for its support and CONACYT for a scholarship grant for his doctoral studies. Virginia Ramírez Cruz (Universidad de Guadalajara, Mexico) is acknowledged for her valuable help inking the drawings, Greg Bonito (Duke University, USA) for literature on *Helvella*, and Dick Korf for his advice on the typification of *H. costifera*. Funds were obtained from Universidad de Guadalajara (projects 72640, 88682, 108721, PIFI-2008-2009).

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Capítulo III. Landeros F, Korf RP. 2012. Nomenclatural notes 13. An incorrect neotype designation and provision of a lectotype and an epitype for *Helvella fusca*. Mycotaxon 119: 431-438

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<http://dx.doi.org/10.5248/119-431>

Volume 119, pp. 431–438

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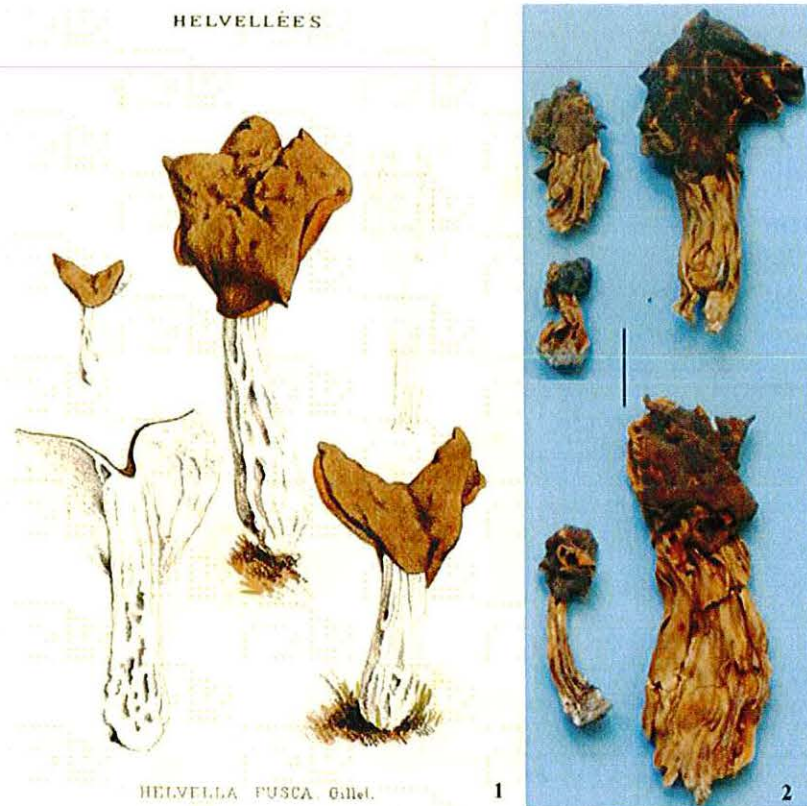
Nomenclatural notes 13. An incorrect neotype designation and provision for a lectotype and an epitype for *Helvella fusca*FIDEL LANDEROS^{1,2} & RICHARD P. KORF³¹*Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Avenida de las Ciencias s/n, Santiago de Querétaro, Qro., 76270, Mexico*²*Departamento de Botánica y Zoología, Universidad de Guadalajara, Apartado postal 1-139, Zapopan, Jal., 45101, Mexico*³*Plant Pathology Herbarium, Cornell University, Ithaca, NY 14853, USA*CORRESPONDENCE TO *: *landeros@uaq.mx, ³info@mycotaxon.com

ABSTRACT — A neotype designation for *Helvella fusca* proposed in 1997 proves to have been erroneous because an illustration accompanying the original description was overlooked. Such illustrations normally have served as the lectotype when all known specimens of the author's taxon have been lost. The authors of that neotype designation should instead have designated the illustration as a lectotype and a specimen as an epitype, which is done in this paper. The so-called neotype specimen is now selected as the epitype specimen. A full description, illustrations and remarks about synonyms and a non-synonym are also provided.

KEY WORDS — International Code of Botanical Nomenclature

Helvella fusca was described by Gillet (1879: 9), but unfortunately his description did not specify any specimen or figure to represent that species, making typification more difficult. Dissing (1966b) wrote about this species: "I have not seen any authentic specimen of *H. fusca* Gillet, whereas the many Bresadola-collections of *H. fusca* in the herbarium in Stockholm (S) make it possible to get a precise concept of Bresadola's species." With respect to the type specimen of *H. fusca*, Dissing (1966b) wrote only, "not seen." Later, in their seminal paper on the northern and northwestern *Helvellaceae* of North America, Abbott & Currah (1997) made a minor but (we believe) critical error by designating a neotype specimen for *H. fusca*, even though that species does not occur in North America. They overlooked the excellent illustration in Gillet's paper (pl. 4, not cited in the species description but referenced mistakenly in one plate listing as pl. 14 and correctly in the other as pl. 4). They may have been unaware that such an illustration, if one upon which it can be shown that the description

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FIGS. 1–2. 1: Type of *Helvella fusca*, reproduced from Gillet (1879). 2: Part of *Helvella fusca* epitype (Bresadola's specimen 05 21 1898, S). Scale bar = 1 cm.

or diagnosis validating the name was based, is considered part of the original material (McNeill et al. 2006: Vienna Code Art. 9 Note 2) and becomes eligible as a lectotype (sometimes informally referred to an “iconotype”) of the species name (FIG. 1). An interesting article by Ross (2002) brings into question whether an illustration accompanying an original description is always part of the original material and thus eligible as a lectotype when all specimens are lost or missing. At the XVIII International Botanical Congress in 2011 one proposal attempting to clarify such situations (Art. 9, Prop E (215); see McNeill & Turland 2011, Perry 2010) regrettably was rejected by a card vote (McNeill et al. 2011). We feel that this case should be corrected at a future Congress but now proceed under the assumption that Gillet's plate was drawn from living specimens now lost and that the illustration is part of the original material that can and should be designated as a lectotype.

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A neotype may only be proposed when ALL original material is lost [Vienna Code]:

Art. 9.6. A neotype is a specimen or illustration selected to serve as nomenclatural type if no original material is extant, or as long as it is missing.”

Also pertinent is Art. 9.7:

An epitype is a specimen or illustration selected to serve as an interpretative type when the holotype, lectotype, or previously designated neotype, or all original material associated with a validly published name, is demonstrably ambiguous and cannot be critically identified for purposes of the precise application of the name of a taxon.

The senior author pointed out this discrepancy to the junior author, and we have chosen instead to propose as epitype the same specimen designated as neotype by Abbott & Currah (1997) from the Bresadola collection in the Naturhistorische Rijksmuseum in Stockholm, Norway —Al Deserto, [Italy], collected by Bresadola, 05 21 1898 (FIG. 2). This specimen is also illustrated by Dissing (1966b). Oddly, Abbott & Currah failed to cite (or were unaware of) Bresadola's careful description, which clearly cited Gillet's figure and provided a superb plate of his own collection (Bresadola 1900: 100, tab. CCXII) (FIG. 3). That plate and description was reissued (Bresadola 1933: 1174, pl. 1174) with the headers and footers of the plate in different typeface and numbering and with a number of emendations of the text —notably eliminating Bresadola's 1900 acknowledgement that Boudier had informed him that specimens Bresadola had sent to him were identical with Gillet's species. The 1933 plate renders the figures in paler colors throughout.

Since Gillet's plate does not provide enough information for modern identification, an epitype is in order. The CODE requires that if an illustration is the only surviving element of the original material, that illustration should be designated as a lectotype, which we do in this paper. The confused information that already exists on the morphology of this species in the literature can be resolved with an epitype specimen. Gillet (1879) described *H. fusca* with spherical to subspherical ascospores, and he did not mention any other useful microscopic character. Bresadola (1900) described ascospores as ellipsoidal, 18–20 × 12–13 µm (but he did not indicate whether those measurements correspond to smooth or to verrucose ascospores), and a glabrous, sterile outer surface of the apothecium. Dissing (1966b) mentioned ascospores 17–18.4–21 × 11–12–13 µm, with pustules when young, and the outside of the apothecium naked or very delicately pubescent. The senior author studied Bresadola's specimen 05 21 1898 (now the epitype) and observed that smooth (young) ascospores were larger, while verrucose (mature) were smaller (FIG. 5a) (see species description), with the hyphal fascicles of the apothecium absent or ≤ 50 µm in length (FIG. 5b), corresponding to a glabrous to subpubescent surface.

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Inasmuch as the incorrect neotypification appeared in MYCOTAXON (Abbott & Currah 1997: 61), we have chosen that same journal in which to rectify their action and to propose both the new lectotype and new epitype for the name.

The corrected typifications and full description

Helvella fusca Gillet, Champignons de France, Discom.: 9, pl. 4, 1879. FIG. 5

TYPE: Pl. 4, in Gillet, Champignons de France, Discom., 1879 (Lectotype, designated here); Bresadola 05.21.1898, Al Deserto, Italy (S) (Epitype, designated here).

= *Helvella fusca* var. *bresadolae* Boud., Icon. Mycol. (Paris),

Tome 2: pl. 230, 1910; Tome 4: 121, 1911.

= *Helvella fusca* var. *gyromitroides* Chenant., in Pelé & Chenantais,

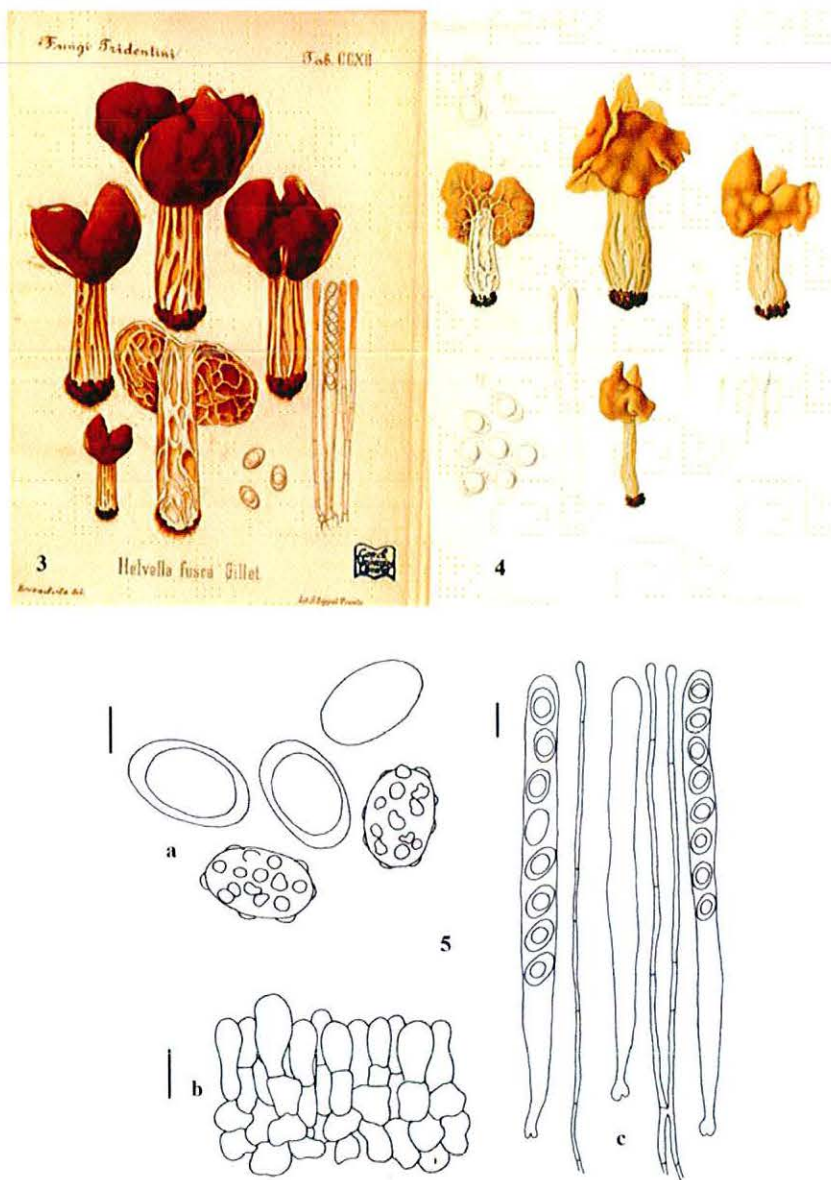
Bull. Soc. Sci. Nat. Ouest, Sér. 4, 1: 75, 1921.

≠ *Helvella sulcata* a *fusca* Afzel., K. Vetensk.-Acad. Handl. 4: 305, Tab. X, fig. 1, 1783.

APOTHECIUM 6–25 mm diam., 4–25 mm high, irregularly lobed or irregularly saddle shaped, margin fused to the stipe or rarely free, hymenium pale brown, tawny, to dark brown when dry, outside glabrous to subpubescent, whitish, yellowish, to pale brown, ribs branched or unbranched, extending near to the marginal zone of the excipular surface. STIPE 8–45 mm high, 3–15 mm broad, equal or slightly wider at the base, whitish or pale brown, glabrous to subpubescent, lacunose, internally chambered.

ASCI 260–320 × 14–15.5 μm, pleurorhynchous. ASCOSPORES young, smooth: (17–)18.5–21 × 11–13 μm; mature, verrucose: 15.5–18.5 × 11–12.5 μm. PARAPHYSES clavate, 5–8 μm wide at the apex, simple or branched, septate, thin-walled, yellowish brown, pigmented deposits in the cytoplasm. MEDULLARY EXCIPULUM hyaline. ECTAL EXCIPULUM yellowish brown, pigmented deposits usually in the cell wall and in a few cells in the cytoplasm. INNER LAYER OF THE STIPE hyaline. OUTER LAYER OF THE STIPE yellowish brown, pigmented deposits usually in the cell wall and in few cells in the cytoplasm. HYPHAL FASCICLES of the apothecium and stipe up to 50 μm long, light brown in mass, pigmented deposits in the cell walls. None of the pigmented deposits in any of the structures are visible in cotton blue mounts. All tissues are “rr-.”

REMARKS — *Helvella fusca* can be confused with *H. lacunosa* Afzel., because both have lobed apothecia, a lacunose stipe, glabrous to subpubescent excipular surface with the outer surface of the stipe similar, but *H. fusca* has a pale brown hymenium and grows associated with *Populus* spp., while *H. lacunosa* has a black or greyish hymenium and has a global distribution with no particular association with *Populus*. Boudier (1904) first introduced *H. fusca* var. *bresadolae* as a nomen nudum for a plate he planned to issue later. As pointed out by Korf (1986: 213, footnote; 1988: 213, footnote), Boudier (1907) soon after abandoned the variety, citing his plate as merely *H. fusca*. Boudier (1910), who eventually validly proposed *H. fusca* var. *bresadolae* (FIG. 4) based on apothecia

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FIGS. 3–5. 3: *Helvella fusca* reproduced from Bresadola (1900, from Boudier's book deposited in Cornell University Library). 4: Type of *H. fusca* var. *bresadolae* reproduced from Boudier (1910, Tome 2, pl. 230). 5: *Helvella fusca* (epitype), a: ascospores, b: ectal excipulum, c: paraphyses and asci. Scale bar: 5a = 8 μm ; 5b, 5c = 20 μm .

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that Bresadola sent him (but unfortunately not cited in the description), wrote “Hæc varietas typo simillima, differt tantummodo pediculo non albido, sed pileo concolore.” Boudier (1911) later expanded the description. Dissing (1966a) considered this variety as invalid, because this specimen is possibly part of the Bresadola material that he studied and determined as “in all details identical.” We also do not recognize the variety, because Gillet did not describe the stipe color only as white but as “dessous pâle, blanc sale ou lég[è]rement fuligineux.” Furthermore, in *Helvella* stipe coloration varies too greatly within a species to be considered useful for recognizing varieties. For example the stipe of *H. lacunosa* can vary from whitish to grayish to black. Chenantais (Pelé & Chenantais 1921) proposed *H. fusca* var. *gyromitroides*, but the features that he used to recognize the variety (multilobed, fawn and free apothecial margin, and lacunose and yellowish stipe) are within the range of variation of the species. We do not consider *H. fusca* a synonym of *H. sulcata* α *fusca*, because Afzelius recognized *H. sulcata* with “sulcis regularibus,” i.e., only longitudinal ribs on stipe (Afzelius 1783, Tab. X, fig.1; this figure is also in Dissing (1966b, fig. 27c), while *H. fusca* and *H. lacunosa* have longitudinal and transverse ribs (lacunose stipe) [i.e., in the words of Afzelius: “lacunis sulcisque irregularibus”]. DNA sequences support *H. sulcata* as a distinct species (unpublished data), contrary to the opinions by Dissing (1966b) and Abbott & Currah (1997), who considered it a synonym of *H. lacunosa*. Persoon (1801) described *H. sulcata* α *fusca* with “pileo nigro.” *Helvella fusca* has more recently been reported from Europe, North America, and Asia (Dissing 1966b, Ceccaldi 2006, Kempton & Wells 1970; Kaushal 1991). Abbott & Currah (1997) doubted the existence of *H. fusca* in North America because their study indicated that such reports were probably *H. maculata* N.S. Weber. On the other hand, Kaushal (1991) recorded *H. fusca* from the Himalayas, but as his description mentioned hyphal fascicles of the apothecium measuring ≤ 105 µm long, it is unclear whether that report corresponds to *H. fusca*. Based on the above information, we can say that its distribution outside of Europe remains doubtful.

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as the Internet Archive (<http://www.archive.org/>) for uploading invaluable literature for taxonomists on their websites.

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Capítulo IV. Landeros F, Iturriaga T, Rodríguez A, Vargas-Amado G, Guzmán-Dávalos L. 2012. *Helvella* (Pezizales: Ascomycota): phylogeny and taxonomy based on morphological data and LSU rDNA sequences. Fungal Diversity

Helvella (Pezizales: Ascomycota): phylogeny and taxonomy based on morphological data and LSU rDNA sequences

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Abstract. The phylogenetic relationships of species of the genus *Helvella* were investigated, using both morphological and molecular (LSU rDNA) characters. The analyses contributed to the understanding of its taxonomy, and also allowed the recognition of two new cryptic species, the first related to *H. leucomelaena*, and the second allied to *H. sulcata* for their glabrous to subpubescent ascoma. Unfortunately, few major clades have support (bootstrap and posterior probabilities) in the topologies resulted from the phylogenetic analyses, so it is not possible to completely discern which of the previous traditional classifications based on morphological data has to be followed. The morphological and molecular data support to divide *Helvella* in two subgenera, *Leucomelaenae* and *Helvella*, and the recognition of the following sections: *Elasticae* Dissing emend. N.S. Weber, *Helvella*, *Lacunosae* Dissing, within subgenus *Helvella*, and the section *Leucomelaenae* Dissing emend. N.S. Weber in the subgenus *Leucomelaenae*.

Key words. Type specimens, keys, generic delimitation

Introduction

The current delimitation of the genus *Helvella* L. was made by Nannfeldt (1937), considering characteristics of the excipulum and the ascospores. He described the excipulum formed of intricate interwoven hyphae and almost isodiametrical cells, which later Korf (1952) named as medullary excipulum of *textura intricata* and ectal excipulum of *textura angularis* or *prismatica*. Also Nannfeldt (1937) described the ascospores of this genus with a large central guttula (sometimes with small apical guttulae) and tetra-nucleated (two nucleus at each end). Currently, *Helvella* contains approximately 52 species (Kirk et al. 2008).

Phylogenetic studies indicate the family Helvellaceae is monophyletic consisting of five genera: *Balsamia* Vitta., *Barssia* Gilkey, *Helvella*, *Underwoodia* Peck, and *Wynnella* Boud. (O'Donnell et al. 1997; Hansen and Pfister 2006; Læssøe and Hansen 2007). Specifically, O'Donnell et al. (1997), Harrington et al. (1999), Landvik et al. (1999), and Læssøe and Hansen (2007) showed *Helvella* is a monophyletic genus and *Wynnella* (monotypic genus) as the sister group.

Several infrageneric classifications have been proposed based on morphological characteristics (fig.1). Dissing (1966b) proposed seven sections based only in macromorphological features. He considered the presence or absence of pubescence on the apothecium sterile surface as the starting point to make his classification. Weber (1972) used the same seven sections of Dissing (1966b), but using the kind of ascus (aporhynchous or pleurorhynchous) besides the macromorphological characteristics; she

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considered the apothecium shape as the starting point to separate the sections. Some sections have different delimitation as the ones defined by Dissing (1966b). The most recent infrageneric classification of *Helvella* was written by Abbott and Currah (1997). They proposed six subgenera, based on macro and micromorphological features, two of them monotypic [*Macropodes* (Dissing) S.P. Abbott and *Silvicolae* (S.P. Abbott) S.P. Abbott], and following Weber (1972), they considered the apothecium shape as the first characteristic to split the genus.

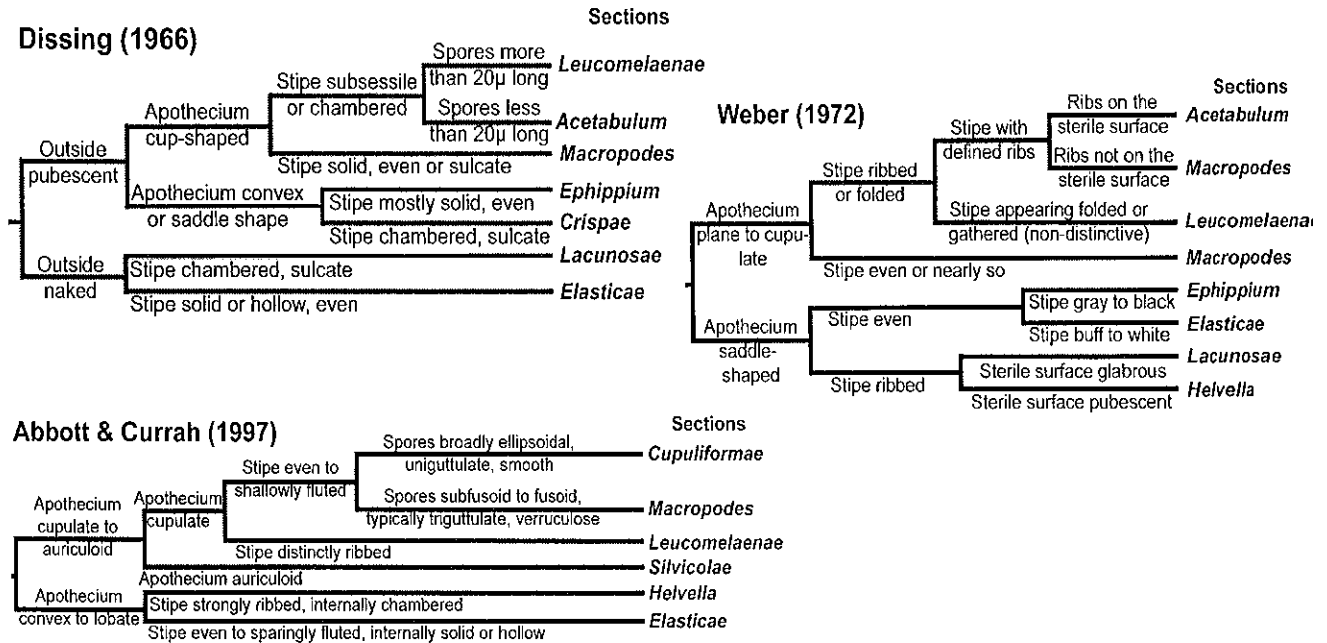


Fig. 1 Traditional infrageneric classification of *Helvella*.

Phylogenetics studies cited above have not included enough sequences of *Helvella* species to evaluate the infrageneric traditional classifications proposed with morphological data, therefore this study aims to clarify the phylogenetic relationships within the genus *Helvella* using morphological data and DNA sequences of the nLSU region. The morphologic characters were re-evaluated in the light of the phylogenetic analyses, allowing to understand the taxonomy of the genus, and validating some infrageneric groups. Representative collections of all known sections were examined (including type material) from thirteen countries of America, Europe, Asia and Oceania.

Material and methods

Morphological studies

Eighteen type specimens and additional specimens, from sixteen herbaria: DAOM, ENCB, FCME, H, IBUG, K, MICH, NY, O, OSC, OULU, PRM, S, TAAM, UPS and WTU were studied. Herbaria abbreviations follow Holmgren et al. (1990). The specimens were studied following the methodology described by Landeros et al. (2012), which basically consist in making free-hand sections from apothecium and stipe with a razor blade directly from the dry ascoma. Tissues sections were placed first in 96% ethyl alcohol and subsequently in water to rehydrate the tissues, Melzer's reagent or cotton blue. The authors of the species are not indicated in the text but in the head of each species description, except for the ones not described.

Phylogenetic protocols

Taxon sampling. DNA nrLSU sequences were generated from 39 specimens, representing 25 taxa of *Helvella* plus one sequence of *Wynnella silvicola* (Beck) Nannf. as outgroup. From them, 15 sequences were from type specimens. Five extra sequences were obtained from GenBank, two of which correspond to taxa for which we were unable to obtain sequences (*H. albella* and *H. atra*). The 45 sequences used in this study are of specimens from 12 countries. A list of all specimens included in the molecular analyses is presented in Table 1.

DNA extraction. The protocol of proteinase K (Aljanabi and Martinez 1997) with some modifications was used. A small part (ca 4 mg) of apothecium was placed in an Eppendorf tube of 2 ml, then the tube was immersed in a container with liquid nitrogen, and the tissue was macerated with an acrylic rod inside the tube, to prevent loss of material. Next, 400 µl of saline buffer (NaCl 0.4 M, Tris-HCl 10 mM, EDTA 2 mM) with 1% PVP were added, slowly mixed by inversion and 40 µl of 20% SDS and 8 µl of proteinase K (20 mg/ml) were aggregated. This was mixed by inversion and incubated (in a water bath) for one hour at 65°C. Then, 300 µl of NaCl 6 M was incorporated and slowly mixed for 30 sec and centrifuged at 12000 rpm for 30 min at 24°C. The supernatant was transferred to a new tube of 2 ml and the same amount of cold isopropanol was put on. It was gently mixed by inversion, incubated for one hour at -20°C (only in this step the protocol can be stopped, incubating overnight). After, it was centrifuged at 4°C for 30 min at 12000 rpm, decanting and throwing the supernatant. Then, 1000 µl of 70% cold ethanol was added, mixed by inversion each five minutes at least three times. It was centrifuged at 12000 rpm for 10 min at 4°C and decanted. The washing was repeated two times and centrifuged at 12000 for 10 min at 4°C and decanted. It is important to wait until the ethanol evaporates completely. Finally, the DNA pellet was diluted in 100–500 µl of TE (Tris 10 mM pH 7.4, EDTA 0.2 mM), to ambient temperature during overnight, and stored at -20°C until use.

PCR amplification. Polymerase chain reaction (PCR) was performed to amplify the D1 and D2 domains of the large subunit (LSU) of the rDNA, because the most informative region for this taxonomic group is in the first 500 pb. Taq DNA polymerase Recombinant Kit (Invitrogen, Catalog Number 10342–053) was used. PCR-mix (25 µl) and primer-Taq (1.15 µl) were prepared separately. PCR-mix contained 18.3 µl of HPLC water, 3 µl of 10X PCR buffer without Mg⁺⁺, 1.5 µl magnesium chloride (50 mM), 0.7 µl of dNTP's (10 mM) and 1.5 µl of 2% BSA (bovine serum albumin). Primer-Taq consisted of 0.5 µl of each primer, and 0.15 µl Taq DNA polymerase. Each 27.15 µl PCR reaction contained 25 µl of PCR-mix, 1.15 µl of primer-Taq, and 1 µl of DNA template (diluted 1:10); negative controls, without DNA template, were included to detect contamination in the reagents. Primer pairs LROR–LR3 (White et al. 1990) were used to amplify the first 600 pb. Unfortunately in many ascomata the DNA was deteriorated, mainly from the type specimens, therefore we designed four additional internal primers, using the software Lasergene Primer Select v:7.1.0 (44) (DNASTAR, Inc.), to amplify shorter segments of 300 pb (see fig. 2): LSUHeF1 (AGCGGAGGAAAGAAACCAACAG), LSUHeR1 (CTCTACTTGTGCGCTATCGGTCT), LSUHeF2 (AGACCGATAGCGCACAAGTAGAG), and LSUHeR2 (TCCCA-ACAGCTATGCTCCTACTC).

PCR amplifications were performed in an Eppendorf Mastercycler Personal 5332 thermocycler using the protocol of White et al. (1990) with some modifications. The amplification program was the following: denaturation at 95°C for 5 min, then 35 cycles of denaturation at 95°C for 1 min, annealing at 52–54°C for 1:30 min, and extension at 72°C for 1:45 min, at the end of cycles a final extension of 72°C for 10 min and hold at 4°C. Amplification products were separated by electrophoresis in 1.5%

agarose gels in a solution of 1X TBE, stained in an ethidium bromide solution and visualized on a UV trans-illuminator. GFX PCR DNA columns and Gel Band Purification Kit (GE Healthcare) were used to purify the PCR products, following the instructions described by the provider.

DNA sequencing. Volume used for the sequencing reaction was of 20 μ l: 4 μ l of BigDye^R Terminator v3.1 (Applied Biosystems), 2 μ l of 5X buffer (Applied Biosystems), 0.5 μ l of selected primer (except for LROR, the others five primers resulted good to sequence the samples), 7–10 μ l of PCR product (depending on the quantity of DNA obtained in the PCR), and HPLC water to complete 20 μ l. The thermocycler conditions were 24 cycles of denaturation at 96°C for 30 sec, annealing at 50°C for 15 sec, and an extension at 60°C for 4 min, and hold at 4°C. Sequencing products were purified using an AutoSeq G–50 Dye Terminator Removal Kit (GE Healthcare), following the indications of the provider. The samples were sequenced on an ABI–Prism 310 Genetic Analyzer.

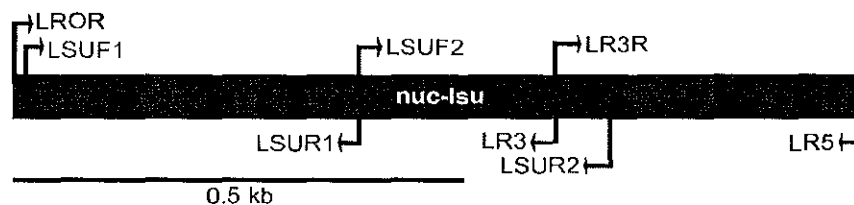


Fig. 2 Location of the primers used in this work. Primers designed specifically for *Helvella* are in greyish.

Phylogenetic analysis with molecular data. Sequence data were edited and contigs assembled with Chromas Pro vs. 1.41 (Technelysium Pty, Ltd, Tewantin, Qld, Australia). Every sequence was subjected to a BLAST search in GenBank and doubtful sequences (the ones that did not correspond to *Helvella*) were removed. Alignments were checked by eye and manually corrected when necessary using MacClade 4.0 (Maddison and Maddison 2000). Only *Wynnella silvicola* was used as outgroup, because sequences of other taxa of the family Helvellaceae deposited in GenBank (*Balsamia*, *Barssia* and *Underwoodia*) were very different, provoking many ambiguous regions and this caused loss of valuable information by elimination of these regions. A matrix with 45 sequences and 491 pb were obtained, and of 472 pb when excluding ambiguous regions (bases 62–65, 141–149, 450–455).

Analyses were made with Maximum Parsimony (MP), Maximum Likelihood (ML), and Bayesian inference. MP was conducted in PAUP 4.0b10 (Altevec) (Swofford 2002), with the following parameters: gaps as missing characters, heuristic searches with changes among character states having equal weights, with 1000 replicates, tree-bisection-reconnection (TBR) as the branch swapping algorithm, and branches collapsed if maximum branch length is zero. MP bootstrap support (BS-MP) was obtained from 1000 replications (Felsenstein 1985). RAxML 7.2.6 (Stamatakis 2006) implemented on raxmlGUI 0.93 (Silvestro and Michalak 2010) was used for the ML search, consisting in 100 replicates to find the best ML tree using the GTRGAMMA model; bootstrap support (BS-ML) was made with 1000 replicates using the same model. Bayesian analyses were conducted in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003), with the following parameters: GTR model, rates=invgamma, ngen=20000000, nruns=4, samplefreq=100, and the first 50% of the samples were discarded. In this case the support of the clades is indicated with the posterior probabilities (PP). Only values over 50% of BS-MP and BS-ML, and 95% of PP in the branches are shown.

Analysis with molecular and morphological data. A matrix of 45 specimens (corresponding to the DNA sequence matrix) with 472 pb and 15 morphological and chemical characters were used. Appendix 1 shows the character codification and Appendix 2 the morphological and chemical matrix.

It resulted in a matrix of 45 specimens with 487 data. Also MP, ML and Bayesian analysis were made; MP in PAUP 4.0b10 as described above, ML in RAxML 7.2.6 implemented on raxmlGUI 0.93, adding separated each matrix, with the GTR model for morphological and chemical data and GTRGAMMA for molecular data, and using the parameters described above. For Bayesian method also MrBayes 3.1.2 was used, for morphological and chemical data with the following parameters: nst=1, which is the basic model, and rates=gamma, while for the molecular data the parameters described above.

Amount of variation in the DNA sequences. We used the option "pairwise base differences" of PAUP 4.0b10, in order to study the amount of variation (measured in the number of different bases) among specimens of the same species, and between species, with the purpose of using this information as an additional criterion for species recognition.

Results

Molecular phylogeny

Analyses of the LSU dataset. From the 472 characters 353 were constant, 39 parsimony-uninformative, and 80 parsimony-informative. A total of 611 trees were recovered, with the following features: 277 steps, CI = 0.588 and CR = 0.440. The strict consensus obtained from the MP analysis (fig. 3) shows only two major clades with support (BS-MP, BS-ML, and/or PP), clade (1), with BT-ML = 70%, BT-MP = 73% and PP = 95%, formed by *Helvella calyx*, *H. leucomelaena*, *H. melaleuca*, and *H. sp. 1*, and clade (2), with BT-ML = 63%, BT-MP = 83% and PP = 97%, including the remaining species of *Helvella*.

Unfortunately, the branches at the next inferior level are not supported. However, in the most nested subclades of clade (2) there are three monophyletic groups with some kind of support: a) *H. crispa* and *H. maculata* (BS-ML = 86%, BS-MP = 85%, PP = 100%); b) *Helvella sp. 2*, *H. sulcata*, and *H. aff. sulcata* (BS-ML = 67%, BS-MP = 52%, PP = 98%), and c) *H. albella*, *H. compressa*, *H. connivens*, *H. elastica*, and *H. stevensii* (BS-ML = 68%, BS-MP = 58%, PP = 99%).

Molecular and morphological phylogeny

Analysis combining sequences and morphological data. From the 487 characters 353 were constant, 39 parsimony-uninformative, and 95 parsimony-informative. A total 2146 trees were recovered, with the following features: 331 steps, CI = 0.541 and CR = 0.403. The phylogram of the ML tree (fig. 4) shows also two major clades as in the analysis using only molecular data, clade (1) supported by BS-ML = 71%, BS-MP = 72%, and PP = 95%; and clade (2) with BS-ML = 71%, BS-MP = 88%, and PP = 99%. Also, the branches at the next level are not supported. However, better resolution was obtained in the nested subclades, listed above, group (a) with BS-ML = 94%, BS-MP = 87%, PP = 100%; (b) with BS-ML = 70%, BS-MP = 53%, PP = 98%; and (c) with BS-ML = 70%, BS-MP = 59%, PP = 98%. Besides, subclade (b) is joined to a supported group (b') with *H. fusca* and *H. lacunosa*, with BS-ML = 60%, BS-MP = 67%, PP = 100%. This is also present in fig. 3, but without support. Unfortunately, from several species its affinity could not be elucidated, they are: *H. acetabulum*, *H. atra*, *H. costifera*, *H. cupuliformis*, *H. ephippium*, *H. griseoalba*, *H. macropus*, *H. pallidula*, *H. robusta*, *H. subglabra*, and *H. ulvinenii*. Although some of them form supported clades with another species: *H. atra* with *H. subglabra* (BS-ML = 71%, BS-MP = 77%, PP = 98%), and *H. cupuliformis* with *H. pallidula* (BS-ML = 93%, BS-MP = 95%, PP = 100%).

Table 1. Sequenced specimens of *Helvella* and outgroup

Species	Infrageneric ubication	Collection data, date (Herbarium)	Internal control key	Country of origin	GenBank (accession no.)
<i>Helvella acetabulum</i>	D, W – <i>Acetabulum</i> ; A & C – <i>Leucomelaenae</i>	M.A. Hernández 164, 3 November 1994 (IBUG) Bellis Kullman, 21 May 2001 (TAA179637, TAAM)	He191 -----	Mexico Estonia	^{1,2} AJ972414
<i>H. albella</i>	D – <i>Ephippium</i> ; W, A & C – <i>Elasticae</i>	A. Jakobson et al., 14 September 2001 (TAA175705, TAAM)	-----	Estonia	¹ AJ972411
<i>H. atra</i>	D, W – <i>Ephippium</i> ; A & C – <i>Elasticae</i>	TAA179690 (TAAM)	-----	Estonia	³ AJ972413
<i>H. calyx</i>	D, W, A & C – <i>Leucomelaenae</i>	P.A. Saccardo, without date [Isotype , K (M): 15990]	He286	Italy	
<i>H. compressa</i>	D – <i>Ephippium</i> ; W, A & C – <i>Elasticae</i>	D.E. Stuntz 12143, 30 October 1960 (WTU)	He162	USA	
<i>H. connivens</i>	D – <i>Ephippium</i> ; W, A & C – <i>Elasticae</i>	A.H. Smith 25872, 21 July 1947 (Holotype , MICH)	He284	USA	
<i>H. costifera</i>	D, W – <i>Acetabulum</i> ; A & C – <i>Leucomelaenae</i>	T. Ulvinen, 4 August 1994 (OULU) U. Nummela-Salo & P. Salo 5318, 7 August 1998 (H) I. Kytövuori 92-352, 16 August 1992 (H)	He292 He301 He302	Finland Finland Norway	
<i>H. aff. costifera</i>	D, W – <i>Acetabulum</i> ; A & C – <i>Leucomelaenae</i>	M. Medina & I. García 1104, 3 August 1975 (ENCB) F. Landeros 3358, 27 September 2009 (IBUG) F. Tapia 2301, 22 August 2004 (IBUG)	He257 He193 He226	Mexico Mexico Mexico	
<i>H. crispa</i>	D ⁴ , W, A & C – <i>Helvella</i>	L. Guzmán-Dávalos 10453, 24 August 2008 (IBUG) F. Landeros 3355, 26 September 2009 (IBUG) DSH97-050 (FH)	He177 He230 -----	Mexico Mexico USA	¹ AY789399
<i>H. cupuliformis</i>	D, W – <i>Macropodes</i> ; A & C – <i>Cupuliformae</i>	T. Eriksson & R. Morander, 21 July 1948 (Paratype , UPS)	He258	Sweden	
<i>H. elastica</i>	D, W, A & C – <i>Elasticae</i>	L. Guzmán-Dávalos 7554, 11 September 1998 (IBUG)	He189	Mexico	
<i>H. ephippium</i>	D, W – <i>Ephippium</i> ; A & C – <i>Elasticae</i>	O. Rodríguez 1022, 19 August 1994 (IBUG)	He221	Mexico	
<i>H. fusca</i>	W – <i>Lacunosae</i> ; D ⁴ , A & C – <i>Helvella</i>	G. Bresadola, 21 May 1898 (Epitype , S)	He270	Italy	
<i>H. griseoalba</i>	D, W – <i>Acetabulum</i> ; A & C – <i>Leucomelaenae</i>	N.J. Smith 982, 10 June 1968 (Holotype , MICH)	He164	USA	
<i>H. lacunosa</i>	D, W – <i>Lacunosae</i> ; A & C – <i>Helvella</i>	L. Guzmán-Dávalos 9002, 18 October 2003 (IBUG) A. Castro-Castro, 7 October 2010 (IBUG) N.S. Weber 6373, 10 November 1990 (OSC)	He244 He323 -----	Mexico Mexico USA	¹ U42681
<i>H. leucomelaena</i>	D, W, A & C – <i>Leucomelaenae</i>	P. Billekens & J. Legarde, 22 May 1982 (H) F.D. Calonge 15990, 11 May 1980 [K, ex herb. MA-Fungi 15990]	He324 He287	Netherlands Spain	

<i>H. macropus</i>	D, W, A & C – <i>Macropodes</i>	O. Rodríguez 3409, 24 August 2008 (IBUG) F. Landeros 3396a, 9 October 2010 (IBUG) F. Landeros 3396c, 9 October 2010 (IBUG)	He208 He321 He322	Mexico Mexico Mexico	
<i>H. maculata</i>	D ⁴ , W, A & C – <i>Helvella</i>	N.J. Smith 2124, 5 October 1968 (Holotype , MICH)	He165	USA	
<i>H. melaleuca</i>	D, W, A & C – <i>Leucomelaenae</i>	Beaglehole & Fuhrer (Beaton 333), 23 July 1966 (Holotype , K)	He273	Australia	
<i>H. pallidula</i>	D, W – <i>Macropodes</i> ; A & C – <i>Cupuliformae</i>	N.J. Smith 397, 24 July 1967 (Holotype , MICH)	He168	USA	
<i>H. robusta</i>	D, W – <i>Acetabulum</i> ; A & C – <i>Leucomelaenae</i>	R.M. Danielson 459, 30 August 1972 (Holotype , DAOM)	He163	Canada	
<i>H. stevensii</i>	D – <i>Ephippium</i> ; W, A & C – <i>Elasticae</i>	Stevens, 23 June 1905 (NY)	He281	USA	
<i>H. subglabra</i>	D, W – <i>Ephippium</i> ; A & C – <i>Elasticae</i>	N.J. Smith 2145, 13 October 1968 (Holotype , MICH)	He166	USA	
<i>H. sulcata</i>	D, W – <i>Lacunosae</i> ; A & C – <i>Helvella</i>	C.T. Rogerson, 29 July 1962 (NYS)	He274	USA	
<i>H. aff. sulcata</i>	D, W – <i>Lacunosae</i> ; A & C – <i>Helvella</i>	De Ávila 13B, without date (ENCB) F. Landeros 1848, 7 August 2004 (Holotype , IBUG)	He320 He224	Mexico Mexico	
<i>H. ulvinenii</i>	D, W – <i>Acetabulum</i> ; A & C – <i>Leucomelaenae</i>	H. Harmaja, 25 August 1979 (Holotype , H)	He248	Finland	
<i>H. sp. 1</i>	D, W, A & C – <i>Leucomelaenae</i>	M. Korhonen 5421, 22 August 1983 (H) U. Söderholm 2916, 17 June 1999 (Holotype , H)	He297 He296	Sweden Austria	
<i>H. sp. 2</i>	D, W – <i>Acetabulum</i> ; A & C – <i>Leucomelaenae</i>	P. Marstad 128-93, 22 July 1993 (Holotype , O) Anders & Wollan 34, 31 August 2007 (O)	He290 He289	Norway Norway	
<i>Peziza subclavipes</i>	D, W, A & C – <i>Macropodes</i>	N.A.F. Ellis, 27 September 1882 (Lectotype , NYS)	He315	USA	
<i>Wynnella silvicola</i>	Outgroup	N.S. Weber 6219 (OSC)	He328	USA	

Simbology: D – Dissing (1966b), W – Weber (1972), A & C – Abbott & Currah (1997). ¹Specimen with sequence in GenBank and included in the morphological study.

²Specimen with sequence in GenBank as “*H. leucomelaena*”. ³Specimen with sequence in GenBank, but not morphologically studied. ⁴As Sect. *Crispa*. In the case of the species not included by D, W and A & C, the ubication is in accordance with the characteristics of the section.

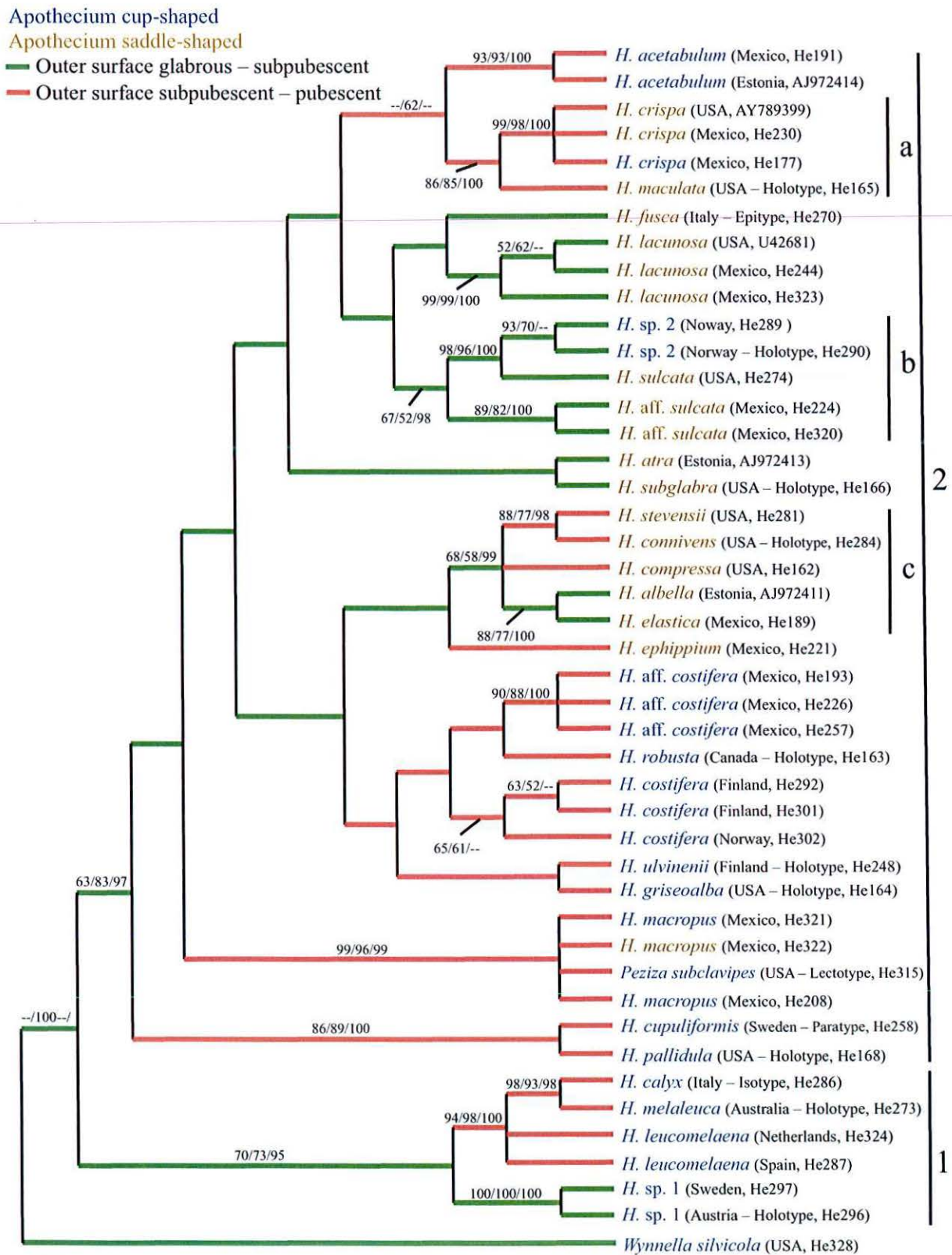


Fig. 3. Phylogeny of *Helvella* based on Maximum parsimony analysis of large nuclear subunit rDNA sequences, showing the strict consensus of 611 trees. Maximum likelihood bootstrap support (BML) and parsimony bootstrap support (BMP) >50%, and Bayesian posterior probability (PP) values >95% are given at the internodes (BML/BMP/PP).

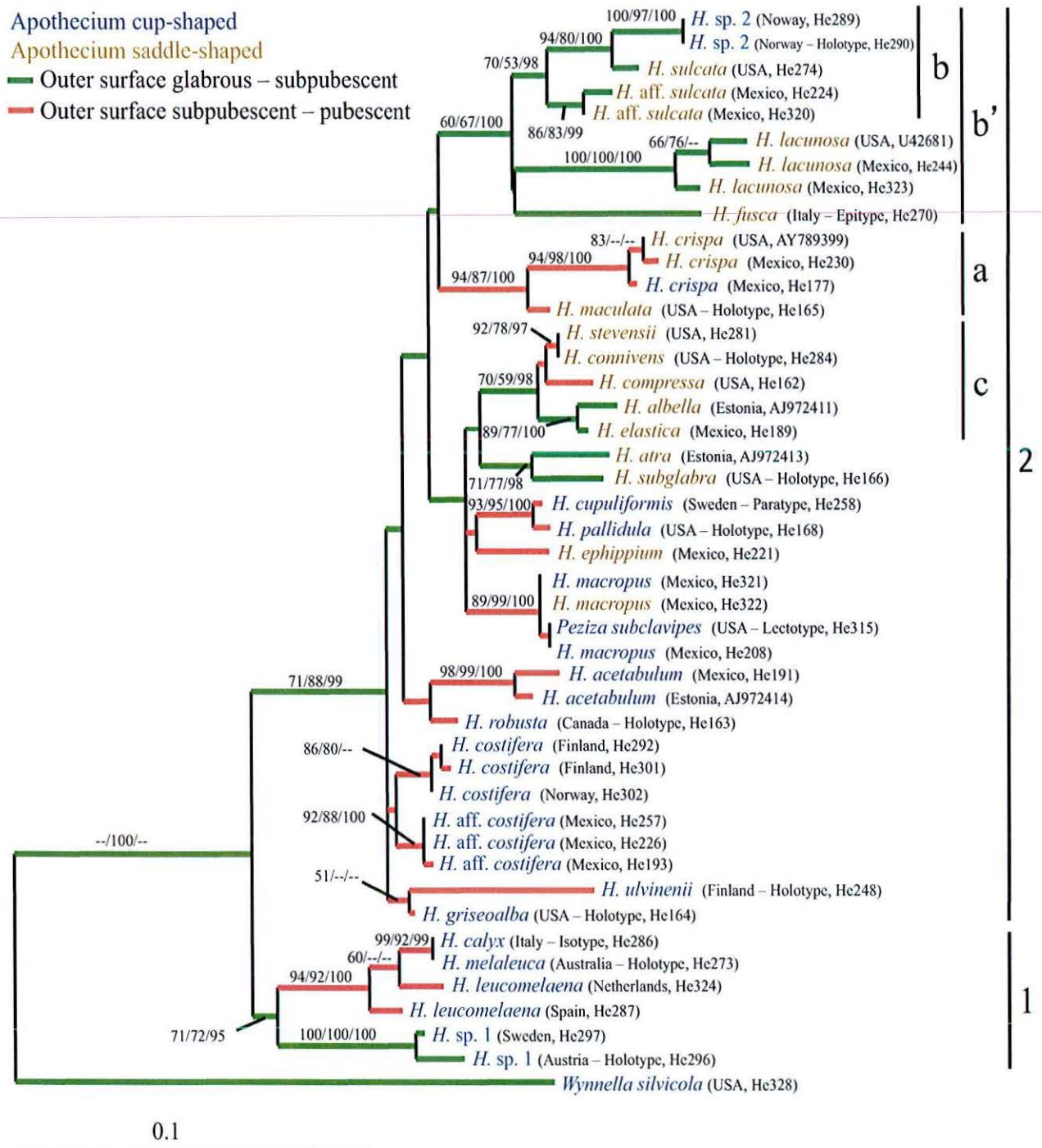


Fig. 4. Phylogeny of *Helvella* generated from Maximum likelihood analysis of large nuclear subunit rDNA sequences and morphological data. Maximum likelihood bootstrap support (BML), parsimony bootstrap support (BMP) >50%, and Bayesian posterior probability (PP) values >95% are given at the internodes (BML/BMP/PP).

New species. *Helvella* sp. 1 is related to *H. leucomelaena* in the clade (1), while *Helvella* sp. 2 is to the sister taxon of *H. sulcata* in subclade (b) of the clade (2).

Amount of intraspecific and interspecific variation

The species that showed less intraspecific variation were: 1) *H. macropus* and *Helvella* sp. 2 (the sequences of their specimens did not differ between them), 2) *H. costifera* (its three specimens varied from one to two bases among themselves), and 3) *H. crispa* (one to two differing bases among three specimens). The species that showed greater intraspecific variation were *H. lacunosa* (eight bases of difference among three specimens), and 2) *H. leucomelaena* (the four specimens, including the specimens of *H. calyx* and *H. melaleuca*, have between eight and ten different bases). On the other hand, the species that showed less intraspecific variation relating to its closest species were: 1) *H. elastica* has only four different bases with respect to *H. albella*, and 2) *H. robusta* varied in five or six bases with the specimens of *H. costifera* and *H. aff. costifera*. The species that showed greater intraspecific variation considering its closest species were: 1) *H. ulvinenii* varied in at least 16 bases from *H. griseoalba*, 2) *H. fusca* had at least 20 bases of difference with respect to *H. costifera*, and 3) *H. leucomelaena* (including the specimens of *H. calyx* and *H. melaleuca*) varied at least in 21 bases with respect to *H. sp. 1*. For a complete detail of the amount of variation among specimens of one species and through species of *Helvella* see the Table 2.

TaxonomyThe misunderstood concept of *Helvella*

Nannfeldt (1937) considered that *Acetabula* (Fr.) Fuckel, *Cyathipodia* Boud., *Leptopodia* Boud., *Macropodia* Fuckel, and *Paxina* Kuntze were untenable, because microscopically all these genera were similar, and they should be included in *Helvella*. These genera were described based only in macroscopic characteristics, like apothecium and stipe shape, e.g. *Macropodia* with cup-shaped apothecium; however, it is common to find species in *Helvella* which have cup-shaped apothecium when young, and later lobed. Recent phylogenetic studies (e.g. O'Donnell et al. 1997; Harrington et al. 1999; Landvik et al. 1999; Læssøe and Hansen 2007) have shown the Nannfeldt's concept of *Helvella* is correct, because it is a monophyletic group.

Some authors did not follow the Nannfeldt's concept of *Helvella*. Dennis (1981) and Breitenbach and Kränzlin (1984) continued using the names *Cyathipodia*, *Leptopodia*, *Macropodia*, and *Paxina*, in as well as *Helvella*. On the other hand, others added species of the genera *Underwoodia* and *Wynnella* to *Helvella*, and this has led to some confusion on the definition of the genus. Eckblad (1968) placed *U. columnaris* Peck and *U. fuegiana* (Speg.) Gamundi under *Helvella*, and this was followed by Harmaja (1974), who proposed *H. beatonii* (Rifai) Harmaja (= *U. beatonii* Rifai). However, Dissing (1966b, 1972), Rifai (1968), Korf (1972), Ainsworth et al. (1973), Abbott and Currah (1997), and Gamundi (2010) considered *Underwoodia* as an independent genus. Phylogenetic studies have corroborated the last point of view (O'Donnell et al. 1997; Hansen and Pfister, 2006; Læssøe and Hansen, 2007). Although *Underwoodia* has medullary excipulum of *textura intricata* and ectal excipulum of *textura angularis* as all species of *Helvella*, and this character was used by Eckblad (1968) to consider *Underwoodia* as a synonym of *Helvella*, the apothecium of *Underwoodia* is fully adhered to the stipe, unlike to any apothecium seen in *Helvella*; also, the ascospores ornamentation is very evident inside of the asci, and some species have hooked paraphyses (*U. columnaris* and *U. beatonii*), while all the species of *Helvella* have straight paraphyses.

The taxonomic position of *Wynnella* was controversial when Harmaja (1974), considering microscopic features, transferred *W. silvicola* to *H. silvicola* (Beck) Harmaja. Abbott and Currah (1988, 1997),

following Harmaja, created in *Helvella* the section *Silvicolae* (Abbott and Currah 1988) to place this species, and subsequently raised it to subgenus (Abbott and Currah 1997). But other authors (Dissing 1966b, 1972; Eckblad 1968; Korf 1972; Ainsworth et al. 1973; Dissing et al. 2000; Parslow and Spooner 2009) recognized *Wynnella* as an independent genus of *Helvella*, which was corroborated by phylogenetic studies of the family placing it as the sister genus of *Helvella* (O'Donnell et al. 1997; Harrington et al. 1999; Landvik et al. 1999; Hansen and Pfister 2006; Læssøe and Hansen 2007). As mentioned above, the LSU sequence of *W. silvicola* has more variation (50-61 bases) in comparison with the species of *Helvella*, than the infrageneric variation among *Helvella* (4-46 bases) (see Table 2). As in *Underwoodia* and *Helvella*, *Wynnella* has medullary excipulum of *textura intricata* and ectal excipulum of *textura angularis*, but its apothecium is auriculoid (like a rabbit's ear), unlike any apothecium seen in *Helvella*. We include below a complete delimitation of the genus *Helvella* based mainly on the works of Nannfeldt (1937), Dissing (1966b, 1972), and Rifai (1968).

Generic description

Helvella (as *Elvela*) L., Species Plantarum 2: 1180, 1753.

Type species: *Elvela mitra* L., l.c. = *H. crispa* (Scop.) Fr., Systema Mycologicum 2: 14, 1822.

Generic description. Ascoma epigeous, stipitate, occasionally sessile, solitary to gregarious. Apothecium cupulate, plane, convex, saddle-shaped, bi-, tri- or irregularly lobed, but never auriculoid, or completely fused with the stipe; hymenium white, cream, buff, brown, grey, red brown, dark brown or black, occasionally mottled (shades of grayish brown); apothecium sterile surface smooth or ribbed, glabrous, subpubescent or pubescent, same color as hymenium or lighter. Stipe terete, or with clefts, costate or lacunose, white, cream, buff, brown, grey or black, glabrous, subpubescent or pubescent, internally solid, hollow or chambered; base with white mycelium. Asci cylindrical, hyaline, operculate, base pleurorhynchous or aporhynchous, non-amyloid, 8-spored. Ascospores ellipsoid, broadly ellipsoid, subglobose, subfusoid or fusoid, normally with a central guttule or rarely triguttulate, hyaline, non-amyloid, smooth or verrucose, tetranucleate at maturity, de Bary bubbles absent. Paraphyses straight, clavate, septate, simple or branched, normally thin-walled, rarely thick-walled, or with a thick-walled cap or collar at the apex, hyaline, light brown or dark brown, pigments in the wall, cytoplasm and/or encrusted on the wall, pigments visible or not under cotton blue. Apothecial tissues separated into medullary and ectal excipulum; stipe tissues also separated in outer and inner layer. Medullary excipulum and stipe inner layer of *textura intricata*, hyaline or light brown, some species with hemiamyloid reaction under Melzer's solution. Ectal excipulum and stipe outer layer of *textura angularis*, hyaline, light brown or dark brown, pigments in the wall, cytoplasm and/or encrusted on the wall, pigments visible or not under cotton blue, some species with hemiamyloid reaction under Melzer's solution. Hairs of the apothecium sterile surface and of the stipe with the same structure under the microscope in all species presenting them, forming hyphal clusters or fascicles, hyaline, light brown or dark brown, pigments in the wall, cytoplasm and/or encrusted on the wall, pigments visible or not under cotton blue, some species with hemiamyloid reaction under Melzer's solution. Mycelial hyphae septate, hyaline, without reaction to Melzer's solution.

Habitat and distribution. Mostly solitary, some scattered, in soil of coniferous and angiosperms forests. Common in temperate and arctic habitats, only one species is reported from a tropical region (*H. papuensis* Dissing from Papua New Guinea); the genus is almost exclusively distributed in the northern hemisphere, except *H. papuensis*. Some species were cited from Argentina and Australia, where they probably have been introduced.

Taxonomic informative features

Apothecium. The apothecium shape is considered by Weber (1972) and Abbott and Currah (1997) as one of the most important features to recognize sections or subgenera. Species with cup-shaped apothecium throughout their entire development are: *H. acetabulum*, *H. cupuliformis*, *H. costifera*, *H. ulvinenii*, *H. verruculosa* (Sacc.) Harmaja, or with lobed apothecium: *H. albella*, *H. compressa*, *H. elastica*, *H. lacunosa*. The problem is that some species (e.g., *H. crispa*, *H. ephippium*, *H. macropus*) have cupulate when young and lobed apothecia when mature, and sometimes the cupulate forms can be already mature, having completely formed ascospores. This issue makes hard their classification based on the apothecium shape. These exceptions make desirable to re-evaluated this feature studying various collections to determine the degree of variation. Also it is important to consider if the apothecium margin is attached to the stipe; this feature is almost exclusive of section *Lacunosae*, and outside this section *H. robusta* is the only species presenting it.

Stipe. The stipe kind is considered by Weber (1972) and Abbott and Currah (1997) as another important feature to divide the genus. Weber (1972) wrote a glossary where she described the stipe, with the following terms: costate, even, lacunose, and sulcate. The first three are easy to distinguish, but the last one is hard to differentiate from costate. For this reason, we consider both terms as synonyms and meaning the stipe has only longitudinal ribs. Sometimes species with even stipe can develop folds or clefts mainly in old ascomata [e.g. *H. atra*, *H. corium* (O. Weberb.) Masee, *H. pezizoides* Afzel., *H. stevensii*], but they never look like true ribs as in *H. costifera*, *H. acetabulum* and *H. sulcata*. On another hand, there are species with costate stipe and one or two transversal ribs (e.g. *H. costifera*, *H. palustris* and *H. sulcata*), giving the appearance to be somehow lacunose, but it never looks like a true lacunose stipe as in *H. lacunosa*. On the other hand, we have only seen specimens of *H. acetabulum* and *H. crispa* with both, costate or lacunose stipes, for this reason we believe important to know the degree of variation among and inside species.

Hymenium and stipe color. Weber (1972) considered the hymenium and stipe color as valuable features to propose her infrageneric classification, while Abbott and Currah (1997) did not used this feature to describe their sections. We agree with Weber (1972) that hymenium and stipe color are useful characteristics; in fact, for section *Elasticae* Dissing sensu Weber two of its defining features are its tan to gray-brown hymenial surface and buff to nearly white stipe. The color is also helpful for identifying species, for example, *H. griseoalba*, in fresh specimens, has a hymenium with grayish tones which separates it from *H. costifera*, which has brownish tones.

Ribs. The edge of the ribs is particularly useful to distinguish *H. acetabulum*, with sharp ribs, from *H. costifera* and *H. griseoalba*, with blunt ribs. Another feature to evaluate is how far the ribs reach in the apothecium sterile surface; we only recognize 1) if they are missing or only reach up to a quarter of the sterile surface, 2) if they reach half or the edge of the apothecium, because in the same ascoma of *H. costifera* or *H. acetabulum* it is posible to see ribs arriving to the half, some to three quarters and others to the edge of the apothecium sterile surface. The ribs can be simple, bifurcated or anastomosed. The last two should be considered with especial care; Harmaja (1978) proposed *H. hyperborea* as a new species different of *H. costifera* based on the rib features, but a study of the type specimens (Landeros et al. 2012) demonstrated both are synonyms. In fact, *H. acetabulum* shows a wide range of variation, from simple, bifurcated to anastomosed ribs. Curiously, for the same reason Abbott and Currah (1997) considered *H. griseoalba* as a synonym of *H. costifera*, but not of *H. hyperborea*.

Asci. Weber (1972) was the first to propose the kind of ascus (aporrhynchous vs. pleurorrhynchous) as a useful character. Indeed, she restricted Sect. *Leucomelaena* for only species with aporrhynchous asci. In this work we corroborated that Sect. *Leucomelaena* Dissing sensu Weber is monophyletic (figs. 3-4), being the aporrhynchous asci the synapomorphy.

Ascospores. Normally the ascospores have little taxonomic value, except to *H. crassitunicata* N.S. Weber, and *H. pocillum* Harmaja due to its large ascospores (Landeros et al. 2012), and to *H. macropus* and *H. terrestris* (Velen.) Landvik for their fusoid to subfusoid ascospores (Abbott and Currah 1997, Landvik et al. 1999). On the other hand, Abbott and Currah (1997) established the ornamentation (verrucose) as an important taxonomic feature. However, it is broadly variable in *Helvella*, because it is not constant among ascospores of the same species. The verrucose appearance is due to remnants of the secondary wall of the ascospores, which might adhere to the wall (Schumacher, pers. com.). It is common in many ascospores of the same specimen that such remnants do not adhere, and therefore the ascospores remain smooth. For this reason Eckblad (1968) described the ascospores of *Helvella* with a “false ornamentation”.

Paraphyses. All species have septate, simple or branched and straight paraphyses, in at least one stage of their development, contrary to observations of Vite-Garín et al. (2006), who described species with non septate and/or unbranched paraphyses. Eckblad (1968) transferred *Underwoodia columnaris* to *Helvella*, but this species has hooked paraphyses. Therefore, the paraphyses shape (except their pigmentation, see comments below) is useful at generic level, but not to separate species.

Hyphal fascicles. The hairs in the apothecium surface microscopically are formed by hyphal fascicles, for this reason we only used the terms: 1) glabrous, when such hyphal fascicles are absent; 2) subpubescent, when hyphal fascicles measure less than 50 µm long; and 3) pubescent, when hyphal fascicles measure more than 50 µm long (see discussion in Landeros et al. 2012). Dissing (1966b) considered the hairs in the apothecium sterile surface as an important criterium in his infrageneric classification. Undoubtedly, there are sections where this condition is present in all species, e.g. all species of Sect. *Lacunosae* are glabrous–subpubescent, while all species of sections *Helvella* and *Macropodes* are pubescent; however, in Sect. *Elasticae* there are species with glabrous, subpubescent and pubescent ascomata. Also this feature is useful to recognize some species, as *Helvella* sp. 1, *H. albella*, *H. elastica*, and *H. fusca*, which have glabrous to subpubescent surface.

Pigments. There is a controversy if the presence of pigments in different parts of the ascoma is a valuable taxonomical feature (Landeros et al. 2012). When present this characteristic has to be evaluated from three points of views: 1) color: dark brown vs. light brown, 2) position: paraphyses, cells of ectal excipulum, cells of stipe outer layer, apothecial hyphal fascicles, and stipe hyphal fascicles, and 3) where the pigments are: in the wall, cytoplasm and/or encrusted on the wall. We recommend to use cotton blue to evaluate if the pigments are visible or not under this colorant. It is important to clarify that the encrusted pigment on the wall (mainly in the paraphyses) is variable between ascomata of the same species, and when it is present is always visible under cotton blue.

Hemiamyloid reaction (rr+). “Solely red” reaction under Melzer’s reagent following Baral (1987). This is a meaningful characteristic from the taxonomic and phylogenetic perspectives. All species of Sect. *Elasticae* have at least one hemiamyloid tissue. But this feature is not exclusive of this section, e.g., *H. acetabulum*, *H. robusta*, and *H. subglabra*, also have at least one hemiamyloid tissue and it can be used to recognize such species. This reaction is especially evident in stipe tissues, for this reason it is

important to look for it in the whole ascoma and to describe in which tissue is present (Landeros et al. 2012).

Cell length in the ectal excipulum and stipe outer layer. We noticed that the cell length in both structures of one ascoma is equal, and they are independent of where the cut is made. But the thickness of the ectal excipulum may vary slightly, being thinner towards the edge and wider in the apothecium center, while in the stipe outer layer is equal. This feature is important to recognize to *Helvella* sp. 1, because in this species the size of its cells in the ectal excipulum and in the stipe outer layer is totally different to other species.

Key to the species of *Helvella*

As far as possible the arrangement of the key has been done considering the phylogenetic relationships attained in this study. We also include some species that was not possible to obtain its DNA sequence, but for which we review specimens (in some cases the type specimen). The key comprises a total of 34 species, being the most comprehensive to date. In addition, for some species we mention important synonyms.

- | | |
|---|---|
| 1.- Asci aporhynchous | 2 |
| 1.- Asci pleurorhynchous | 4 |
| 2.- Paraphyses thick-walled present | <i>H. crassitunicata</i> |
| 2.- Paraphyses thick-walled absent | 3 |
| 3.- Apothecium sterile surface subpubescent to pubescent; cells of ectal excipulum and stipe outer layer 5–30 µm long; ectal excipulum 50–120 µm wide; stipe outer layer 40–80 µm wide | <i>H. leucomelaena</i> (= <i>H. calyx</i> , <i>H. confusa</i> , <i>H. melaleuca</i> , <i>H. pedunculata</i>) |
| 3.- Apothecium sterile surface glabrous to subpubescent; cells of ectal excipulum and stipe outer layer 20–60 µm long; ectal excipulum 140–250 µm wide; stipe outer layer 100–200 µm wide | <i>H. sp. 1</i> |
| 4.- Ascospores always fusoid or subfusoid within asci | 5 |
| 4.- Ascospores ellipsoid within asci | 6 |
| 5.- Apothecium cup-shaped or lobed; ascospores 18–24 x 10–13.5 µm, subfusoid or subfusoid within asci, and then slightly ellipsoid when mature | <i>H. macropus</i> |
| 5.- Apothecium cup-shaped; ascospores 50–65 x 12–15 µm, always fusoid | <i>H. terrestris</i> |
| 6.- Stipe terete, sometimes with slight folds, but never true ribs | 7 |
| 6.- Stipe ribbed or lacunose | 19 |
| 7.- Apothecium cup-shaped, irregularly lobed or saddle-shaped | 8 |
| 7.- Apothecium only cup-shaped | 18 |
| 8.- Stipe buff to white | 9 |
| 8.- Stipe gray to black | 14 |
| 9.- Apothecium ectal excipulum glabrous to subpubescent | 10 |
| 9.- Apothecium ectal excipulum pubescent | 13 |
| 10.- Hymenium dark brown, blackish brown or black | 11 |
| 10.- Hymenium whitish or pale brown | 12 |
| 11.- Ascospores 21–24 x 13–15 µm | <i>H. leucopus</i> |
| 11.- Ascospores 17.5–21 x 10.4–12 µm | <i>H. albella</i> |
| 12.- Apothecium margin not curving towards the hymenium when young; stipe hollow; ascospores 18–22 x 11–13.5 µm | <i>H. elastica</i> |
| 12.- Apothecium margin curving towards the hymenium when young; stipe solid; ascospores 18–22 x 14–18 µm | <i>H. latispora</i> |
| 13.- Distribution West USA; ectal and medullary excipulum hemiamyloid | <i>H. compressa</i> |

13.- Distribution East USA and Europe; ectal excipulum non hemiamyloid, medullary excipulum hemiamyloid	<i>H. stevensii</i> (= <i>H. connivens</i>)
14.- Apothecium ectal excipulum glabrous to subpubescent	15
14.- Apothecium ectal excipulum pubescent	16
15.- Hymenium drab to brownish gray, never black; apothecium sterile surface subpubescent; medullary excipulum and stipe inner layer hemiamyloid	<i>H. subglabra</i>
15.- Hymenium dark gray to black; apothecium sterile surface glabrous; medullary excipulum non hemiamyloid, stipe inner layer hemiamyloid	<i>H. atra</i>
16.- Paraphyses with brown thick-walled apical collar or cap	<i>H. paraphysitorquata</i>
16.- Paraphyses without brown thick-walled apical collar or cap	17
17.- Ascoma relatively small (apothecium up to 15 mm diam. and stipe up to 25 x 3 mm)	<i>H. ephippium</i>
17.- Ascoma relatively large (apothecium 15–55 mm diam. and stipe 20–60 x 3–15 mm)	<i>H. pezizoides</i>
18.- Apothecium diameter equal or greater than stipe length	<i>H. cupuliformis</i>
18.- Apothecium diameter less than stipe length	<i>H. fibrosa</i> (= <i>H. pallidula</i>)
19.- Apothecium cup-shaped	20
19.- Apothecium lobed, irregularly lobed or saddle-shaped	28
20.- Ribs with sharp-edge	21
20.- Ribs with blunt-edge	22
21.- Hymenium tan to light brown; apothecium margin often bending towards the stipe wrapping it; stipe robust, more than 3 cm wide	<i>H. robusta</i>
21.- Hymenium dark brown; apothecium margin regular or wavy, but never bending towards the stipe; stipe small and slender, less than 2 cm wide	<i>H. acetabulum</i>
22.- Ribs on apothecium sterile surface	23
22.- Ribs absent on apothecium sterile surface or extending only onto basal portion	24
23.- Hymenial surface gray; paraphyses hyaline; stipe glabrous to subpubescent; brown pigments in terminal cells of apothecium hyphal fascicles visible under cotton blue	<i>H. griseoalba</i>
23.- Hymenial surface brown or grayish brown; paraphyses hyaline and light brown; stipe pubescent; brown pigments in terminal cells of apothecium hyphal fascicles not visible under cotton blue.....	<i>H. costifera</i> (= <i>H. hyperborea</i>)
24.- Ascospores 22–30 µm long	<i>H. pocillum</i>
24.- Ascospores 14–22 µm long	25
25.- Apothecium sterile surface glabrous to subpubescent	<i>H. sp. 2</i>
25.- Apothecium sterile surface pubescent	26
26.- Brown pigments of paraphyses, cells of ectal excipulum and stipe outer layer, and hyphal fascicles not visible under cotton blue	<i>H. solitaria</i> (= <i>H. queletii</i>)
26.- Brown pigments visible under cotton blue at least in one structure (paraphyses, cells of ectal excipulum and stipe outer layer, or hyphal fascicles).....	27
27.- Ascospores 17.5–22 x 10.5–13 µm; hyphal fascicles of stipe pigmented	<i>H. verruculosa</i>
27.- Ascospores 14.5–18.5 x 10.5–12 µm; hyphal fascicles of stipe hyaline	<i>H. ulvinenii</i>
28.- Apothecium sterile surface glabrous to subpubescent	29
28.- Apothecium sterile surface pubescent	32
29.- Stipe mainly ribbed	<i>H. sulcata</i>
29.- Stipe mainly lacunose	30
30.- Hymenium whitish to cream	<i>H. lactea</i>
30.- Hymenium with other colors	31
31.- Hymenium light brown, tan or brown	<i>H. fusca</i>

31.- Hymenium black, grayish or dark brown	<i>H. lacunosa</i>
32.- Tropical distribution	<i>H. papuensis</i>
32.- Temperate distribution	33
33.- Hymenial surface pale cream to pale pinkish buff, non-mottled; apothecium hyphal fascicles 50–130 µm long; pigments of stipe outer layer not visible under cotton blue	<i>H. crispa</i>
33.- Hymenial surface mottled, with greyish brown patches on a cream blackground; apothecium hyphal fascicles 107–205 µm long; pigments of stipe outer layer visible under cotton blue	<i>H. maculata</i>

Main proposals to the infrageneric classification of *Helvella*

Dissing (1966b) was the first to propose an infrageneric classification according to the Nannfeldt's concept of *Helvella*, with seven sections based only in macromorphological features (fig. 1). The first feature that he used was the presence or absence of pubescence on the apothecium sterile surface. Therefore, we can divide his sections in two groups: A) pubescent, with five sections: 1) *Acetabulum* Dissing, chambered stipe, gradually widen into the apothecium, outside with sharp or blunt ribs, and normally less than 20 µm long ascospores; 2) *Crispae* Dissing, convex or irregularly saddle-shaped apothecium, and lacunose stipe; 3) *Ephippium* Dissing, involute to saddle-shaped apothecium, and even and mostly solid stipe; 4) *Leucomelaenae* Dissing, cup-shaped apothecium, subsessile or with a short and sulcate stipe, and normally more than 21 µm long ascospores; and 5) *Macropodes* Dissing, cup-shaped apothecium, solid, even or sulcate stipe, and ribs not continuing on the outside of the apothecium. B) Glabrous, with two sections: 1) *Lacunosae* Dissing, convex or irregularly saddle-shaped apothecium, and lacunose stipe; and 2) *Elasticae* Dissing, saddle-shaped apothecium, even, sometimes with grooves near to the base, solid or hollow, and glabrous to subpubescent stipe.

Later, Weber (1972) also postulated the same seven sections of Dissing, but with a different delimitation [except to the sections *Helvella* (= *Crispae*) and *Lacunosae*], considering macromorphological characteristics and the kind of ascus (aporhynchous or pleurorhynchous) (fig. 1). She did not consider the presence or absence of pubescence as the first feature to separate her sections, but she initiated with the apothecium shape. We again can divide her sections in two groups: A) cupulate to plane at maturity apothecium, with three sections: 1) *Acetabulum* Dissing emend. Weber, subsessile to stipitate, stipe with definite ribs, which continue on the apothecium sterile surface, pleurorhynchous asci; 2) *Leucomelaenae* Dissing emend. Weber, subsessile to stipitate, base of the ascome appearing “folded or gathered”, ribs not distinctive from the rest of the apothecium, aporhynchous asci; and 3) *Macropodes* Dissing emend. Weber, terete stipe or with a few low rounded ribs, which do not continue on the apothecium sterile surface. B) saddle-shaped, convex or irregularly lobed and folded at maturity apothecium, with four sections: 1) *Elasticae* Dissing emend. Weber, even and terete or compressed stipe, occasionally with a few basal clefts, gray to gray-brown hymenial surface, buff to nearly white stipe; 2) *Ephippium* Dissing emend. Weber, even and terete or compressed stipe, occasionally with a few basal clefts, gray to black or occasionally drab hymenial surface, gray to black, rarely drab stipe; 3) *Helvella*, ribbed throughout its length stipe, variable in cross section, buff to umber-brown hymenial surface, pubescent when young apothecium sterile surface; and 4) *Lacunosae* Dissing, ribbed throughout its length stipe, variable in cross section, gray to black hymenial surface, glabrous apothecium sterile surface.

Finally, Abbott and Currah (1997) did the most recent infrageneric classification of *Helvella* (fig. 1). They proposed six subgenera, and for the first time many micromorphological features were used; also they considered the apothecium shape as the start point to their classification, like Weber (1972). We

can divide their subgenera in two groups: A) convex to irregularly lobed apothecia, with two subgenera: 1) *Elasticae* (Dissing) S.P. Abbott, terete to sparingly fluted, internally solid or hollow stipe; and 2) *Helvella*, strongly ribbed, internally chambered stipe. B) Cupulate to auriculoid apothecia (like a rabbit's ear), with four subgenera: 1) *Cupuliformae* S.P. Abbott, cupulate apothecium, terete to shallowly fluted stipe, broadly ellipsoid, uniguttulate, smooth (finely rugose under SEM) ascospores; 2) *Leucomelaenae* (Dissing) S.P. Abbott, cupulate apothecium, distinctly ribbed stipe; 3) *Macropodes* (Dissing) S.P. Abbott, cupulate apothecium, terete to shallowly fluted stipe, subfusoid to fusoid, typically triguttulate (rarely uniguttulate), verruculose (verrucose under SEM) ascospores; and 4) *Silvicolae* (S.P. Abbott) S.P. Abbott, auriculoid apothecium. Two of these subgenera are monotypic (*Macropodes* and *Silvicolae*).

With the results obtained in this work from the phylogenetic analyses with morphological and molecular data, we can only recognize the following four sections: *Elasticae* Dissing emend. N.S. Weber, *Helvella*, *Leucomelaenae* Dissing emend. N.S. Weber, and *Lacunosae* Dissing.

Species description by section

Below only additional information or the one that differs from the protologue or previous publications is presented. Species included in Landeros et al. (2012) and Landeros and Korf (2012) are not described; only some remarks to recognize it are mentioned.

Section *Leucomelaenae* Dissing emend. N.S. Weber, Mich. Bot. 11: 157, 1972.

≠ Section *Leucomelaenae* Dissing, Dansk Botanisk Arkiv 25: 36, 1966b.

≠ Subgenus *Leucomelaenae* (Dissing) S.P. Abbott, in Abbott & Currah, Mycotaxon 62: 62, 1997.

Type species: *Helvella leucomelaena* (Pers.) Nannf., in Lundell & Nannfeldt, Fungi exsicc. upsal. 21: 952, 1941.

Dissing (1966b) proposed the section *Leucomelaenae* for species with pubescent ascoma, cup-shaped apothecium, regular, short to sessile, sulcate stipe, and normally more than 20 µm long ascospores. Later, Weber (1972) made some restrictions to this section, considering some of the Dissing's features, but also aporhynchous asci (in fact we consider this characteristic as the most important to delimit this section), and the ascospores size was eliminated as a relevant characteristic for the section. With such definition (Weber, 1972), *H. solitaria* P. Karst. recognized by Dissing (1966b) as a species of this section, was out. For us the distinctive characteristic of this section are: cup-shaped apothecium; distinctive, short to sessile and costate stipe; ellipsoid ascospores; aporhynchous asci; and all tissues negative under Melzer's reagent. The apothecium and stipe sterile surfaces are very variable among the species of this section, they can be glabrous to pubescent; and paraphyses are thin- or thick-walled. We only recognize three species in this section: *H. crassitunicata*, *H. leucomelaena* and *Helvella* sp. 1. This section corresponds to clade (1) (figs. 3-4), with the addition of *H. crassitunicata*, and with aporhynchous asci as the synapomorphy.

***Helvella leucomelaena* (Pers.) Nannf.**, in Lundell & Nannfeldt, Fungi exsicc. upsal. 21: 952, 1941.

= *Acetabula calyx* Sacc., Mycotheca veneti: no. 168, 1873.

= *H. confusa* Harmaja, Karstenia 17: 43, 1977.

= *H. melaleuca* Rifai (specimen labeled as holotype at K, but not references were found in Rifai 1968, Index fungorum or Mycobank).

= *H. pedunculata* Harmaja, Karstenia 18: 57, 1978.

= *Peziza debeauxii* Roum., Rev. Myc. 4: 156, 1882.

Lectotype: L 8945–6, Netherlands (Herbarium Persoon in Leiden, not seen).

Asci 240–410 x 14–21 μm . **Ascospores** (17–) 18–24 x 11–14.5 μm . **Paraphyses** 4–10 μm wide at the apex, thin-walled, hyaline, pale brown to brown in mass, pigmented deposits in the wall, in the cytoplasm and few with yellowish brown pigment encrusted on the wall. **Medullary excipulum** hyaline. **Ectal excipulum** 50–120 μm wide, with 5–30 μm long cells, yellowish brown, pigmented deposits in the wall and in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** 40–80 μm wide, with 4–25 μm long cells, yellowish brown, pigmented deposits in the wall and in the cytoplasm. **Apothecial hyphal fascicles** 40–150 μm long, yellowish brown, pigmented deposits in the wall and in the cytoplasm; **stipe hyphal fascicles** 20–80 μm long, yellowish brown, pigmented deposits in the wall and in the cytoplasm. Pigments of all structures not visible under cotton blue, except for the encrusted pigment in the paraphyses. All tissues rr–.

Material examined: ALGERIA: Oran, bois de pins a terre, April 1882, O. Debeaux s.n. [K (M) 163795, isotype of *Peziza debeauxii*]. AUSTRALIA: Victoria, Lower Glenelg, 23 July 1966, Beaglehole and Fuhrer (Beaton 333) [K(M) 163797, holotype of *Helvella melaleuca*]. DENMARK: Jylland, near Thisted, Klitmøller plantage, 15 May 1965, K. Toft and H. Dissing (H, holotype of *Helvella confusa*). FINLAND: Kuusamo, Kansallispuisto, 11 July 1968, AM. Jakkula (OULU F026213, as *H. pedunculata*), 17 July 1991, M. Ohenoja and E. Ohenoja (OULU F023450); Kuusamo, Oulanka National Park, 24 August 1979, T. Ulvinen (OULU F026124, as *H. pedunculata*); Pohjois-Pohjanmaa, Kiiminki, 4 September 1971, M. Ohenoja (OULU, F026210, as *H. pedunculata*), 19 July 1975, T. Ulvinen (OULU F026211, as *H. pedunculata*), 10 August 1978, T. Ulvinen (OULU F026212, as *H. pedunculata*); Pohjois-Pohjanmaa, Kiiminki, Keskikylän, 2 July 1975, E. Ohenoja (OULU F026209, as *H. pedunculata*). ITALY: Padova, P.A. Saccardo [ex herb. MC. Cooke] [K(M) 163791, isotype of *Acetabula calyx*]. NETHERLANDS: Abbert Bos, Bij Dronten, 22 May 1982, P. Billekens and J. Lagarde (H). NORWAY: Rana, Dunderlandsdalen, 11 September 1976, W. Jakowlev and T. Ulvinen (OULU F026707, as *H. pedunculata*). SPAIN: Madrid, Puerto Canencia, 11 May 1980, F.D. Calonge [K(M) 15990]. SWEDEN: Uppland, Älvkarleby parish ca. 3 km of Gärdskär, 30 June 1965, O. Eriksson 2780 and N. Lundqvist (F. Suec. 3268) [K(M) 163792].

Comments: *Helvella leucomelaena* is probably the species that has generated more problems in its delimitation. Harmaja (1977a, 1977b, 1978) described three similar species, *H. confusa*, *H. oblongispora* Harmaja, and *H. pedunculata*, and latter compared and distinguished among the three (Harmaja 1979, Table 2). Abbott and Currah (1997) synonymized *H. confusa* and *H. pedunculata* under *H. leucomelaena*, considering only *H. oblongispora* as a valid species. They mentioned that the Harmaja's table was in fact a good representation of the variation of *H. leucomelaena*. We checked the holotype of *H. confusa* and agree with Abbott and Currah (1997), because we did not find any difference with respect to other specimens identified as *H. leucomelaena*. The table constructed by Harmaja (1979) presents continuous features overlapping among the species and representing the concept of *H. leucomelaena*. Unfortunately, we could not study the other two type specimens, but we examined very good collections of *H. pedunculata* deposited in OULU, some of them determined by Harmaja, and we did not find any difference with respect to other specimens, for this reason, we also consider this name as a synonym of *H. leucomelaena*. Also, after checking the type specimens, we agree with Dissing (1966b) that *Acetabula calyx* and *Peziza debeauxii* are synonyms of *H. leucomelaena*. Likewise, *H. melaleuca* has to be considered as a synonym too, as was proposed by Abbott and Currah (1997). There is only pending the taxonomic status of *H. oblongispora*.

Specimens sequenced from various parts of the world (type specimen of *A. calyx* from Italy, type specimen of *H. melaleuca* from Australia, and *H. leucomelaena* from Netherlands and

Spain) are grouped in a clade (figs. 3–4) with BS-ML = 94, BS-MP = 92–98, PP = 100. These and the studied specimens (Africa, Australia, Europe: Denmark, Finland, Italy, Netherlands, Spain, Sweden) for the morphological part show *H. leucomelaena* has a wide distribution. We only recognize three species with aporhynchous asci, *H. crassitunicata*, *H. leucomelaena*, and *Helvella* sp. 1. *Helvella leucomelaena* is distinguished of *H. crassitunicata* because the last one has thin- and thick-walled paraphyses. For recognition from *Helvella* sp. 1 see the comments under this species.

***Helvella* sp. 1** sp. nov.

Fig. 5

MycoBank:

Apothecium cup-shaped, stipe ribbed, ribs arriving at the base or 1/4 of the apothecium, apothecium sterile surface and stipe glabrous to subpubescent, asci aporhynchous, ectal excipulum 140–250 µm wide, stipe outer layer 100–200 µm long, cells of the ectal excipulum and of the stipe outer layer up to 60 µm long.

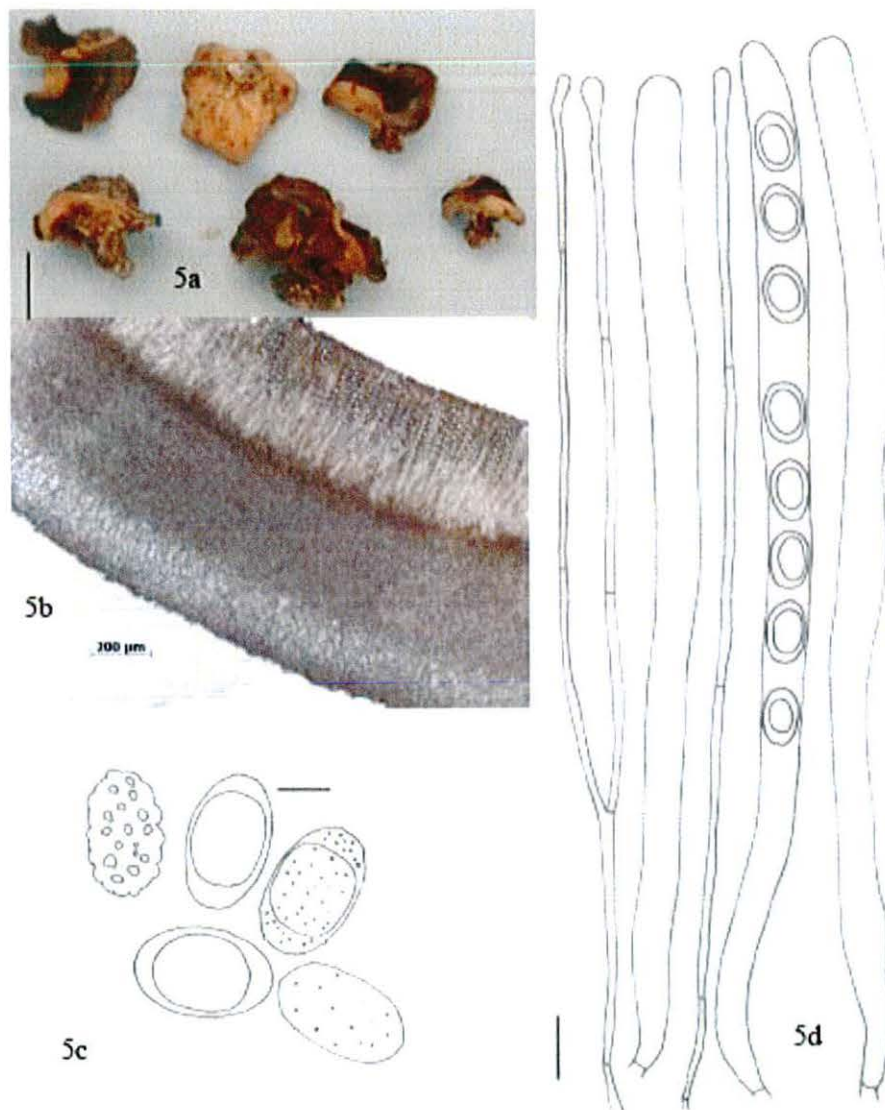


Fig. 5. *Helvella* sp. 1, a: ascomata of the type material (U. Söderholm 2916, H), b: apothecium thin section in water, c: ascospores, d: aporhynchous asci and paraphyses. Scale bars: 5a: 1 cm; 5b: 200 µm; 5d: 20 µm; 5c: 10 µm.

Holotypus: U. Söderholm 2916, 17 June 1999, Rinteessä 800 masl, grid 27°E, Hiekkainen tienreuna kuusivalt, Zell Am See, Austria (H).

Etymology: Tentatively this species will be dedicated to John Axel Nannfeldt (1904–1985), Swedish mycologist, for his contribution to the genus *Helvella*.

Apothecium 10–50 mm diam., 3–20 mm high, cupulate, hymenium brown to dark brown when dried, sterile surface brown to yellowish brown, glabrous to subpubescent, ribs absent or extending onto basal quarter only. **Stipe** 5–22 x 2–8 mm, tapering to the base or nearly equal, whitish to cream, glabrous to subpubescent, solid or chambered, ribbed, ribs blunt-edged at the base of the stipe, becoming slightly sharp-edged to the apex of the stipe. **Asci** 260–360 x 14–18 µm, aporhynchous. **Ascospores** 19–23.5 x 11–13.5 µm, ellipsoid, hyaline, smooth or finely verrucose, uniguttulate. **Paraphyses** 4–9 µm wide at the apex, thin-walled, yellowish brown to pale brown, pigmented deposits in the wall, in the cytoplasm and sometimes encrusted on the wall. **Medullary excipulum** hyaline. **Ectal excipulum** 140–250 µm long, cells 20–60 µm long, yellowish brown to pale brown, pigmented deposits in the wall, and sometimes in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** 100–200 µm long, cells 20–60 µm long, yellowish brown to pale brown, pigmented deposits in the wall, and sometimes in the cytoplasm. **Apothecial and stipe hyphal fascicles** up to 50 µm long, light brown in mass, pigmented deposits in the wall. Pigments of all structures not visible under cotton blue. All tissues rr–.

Material examined: AUSTRIA: holotype. FINLAND: Parainen, Simonby, 1 August 1981, J. Vauras 1019F (H, as *H. oblongispora* by Harmaja). SWEDEN: Medelpad, Borgsjö, 22 August 1983, M. Korhonen 5421 (H).

Comments: *Helvella* sp. 1 is distinguished of *H. leucomelaena*, because the first one has the ectal excipulum very wide, almost the same broad as the medullary excipulum, also the stipe outer layer is wide, both composed by very large cells, and the apothecium and stipe are glabrous to subpubescent, while *H. leucomelaena* has narrower ectal excipulum and stipe outer layer, with smaller cells, and subpubescent to pubescent apothecium and stipe. The phylogeny (figs. 3–4) corroborated our position to consider *Helvella* sp. 1 as a new taxon and related to *H. leucomelaena*. It is important to mention that this species cannot be *H. oblongispora* (Harmaja, 1978), because Harmaja (1979) described it with: 1) ribs on the lowest fourth to third part of apothecium sterile surface, and 2) “[e]ctal excipulum: width of ± elongated cells of *t. angularis*” 5–17 (–22) µm.

Section *Elasticae* Dissing emend. N.S. Weber, Mich.Bot. 11: 191, 1972.

≠ Section *Elasticae* Dissing, Dansk Botanisk Arkiv 25: 128, 1966b.

≠ Subgenus *Elasticae* (Dissing) S.P. Abbott, in Abbott & Currah, Mycotaxon 62: 46, 1997.

Type species: *Helvella elastica* Bull., Herb. Fr. 6: Pl. 242, 1785.

Dissing (1966b) proposed this section for species with saddle-shaped apothecium, even stipe (sometimes with grooves near to the base), and glabrous to subpubescent ascoma, considering the latter characteristic as one of the most important to recognize this section from the Sect. *Ephippium*, which is similar, but with pubescent ascoma. Later, Weber (1972) eliminated the restriction of the section to have glabrous-subpubescent ascoma, and considered the tan to gray-brown hymenium and the buff to nearly white stipe as the most important features to recognize it from Sect. *Ephippium* (which she described with gray to black or occasionally drab hymenial surface and gray to black, rarely drab stipe). We follow in part the concept of Sect. *Elasticae* Dissing sensu Weber (1972), because it is supported by molecular and morphological data (figs. 3–4), but with some changes, we do not consider the hymenium color as an important characteristic to define this section, e.g. *H. albella* has an almost

black hymenium, while the light colored stipe is a characteristic that all species of this section have in common; we also found that species of this section have hemiamyloid tissue in at least one of their layers, mainly in the stipe. The distinctive characteristics of the section are apothecium deflexed to saddle-shaped or lobed; hymenial surface pale tan, brown, grayish brown, dark brown or blackish brown; apothecium sterile surface glabrous, subpubescent or pubescent, cream color or pale tan; stipe terete, even, sometimes with slight folds, but never with ribs, whitish or pale buff, glabrous, subpubescent or pubescent; asci pleurorhynchous; ascospores ellipsoid, uniguttulate; paraphyses thin-walled; and one of the ascoma tissues rr+ under Melzer's reagent. We consider members of this section to *H. albella*, *H. compressa*, *H. elastica*, *H. leucopus*, and *H. stevensii*. The inclusion of *H. latispora* and *H. capucina* in this section is pending, until the review of the hemiamyloid reaction of their tissues. This section corresponds to clade (2-c) (figs. 3-4), with saddle-shaped apothecium and tissues rr+ as homoplastic synapomorphies. *Helvella leucopus* is not included in the phylogenetic analyses, but due to its morphological characters (Landeros et al. 2012) it belongs to this section.

Helvella albella Quél., Compt. Rend. Assoc. Franç. Avancem. Sci. 24(2): 621, pl. 6, fig. 16, 1895 (1896). Fig. 6a

Lectotype: pl. 6, fig. 16, Compt. Rend. Assoc. Franç. Avancem. Sci. 24(2) (selected here).

Asci 230–300 x 13–17 µm. **Ascospores** 17.5–20 x 10.5–13 µm, smooth and verrucose. **Paraphyses** 4–10 µm wide at the apex, hyaline and light brown, pigmented deposits in the wall and in the cytoplasm, some with brown pigment encrusted on the wall. **Medullary excipulum** hyaline. **Ectal excipulum** yellowish, yellowish brown to light brown, pigmented deposits in the wall and in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** yellowish, yellowish brown to light brown, pigmented deposits in the wall and in the cytoplasm. **Apothecial hyphal fascicles** absent; **stipe hyphal fascicles** up to 50 µm long. Pigments of all structures not visible under cotton blue, except the encrusted in the paraphyses. Medullary excipulum and stipe inner layer slightly rr+; ectal excipulum and stipe outer layer rr–.

Material examined: ESTONIA: Hiiu Co., Kõrgessaare Comm., Kõpu Peninsula, Puski, 14 September 2001, A. Jakobson et al. (TAA179705, TAAM). MEXICO: Edo. de México, Municipality of Ocoyoacac, road México-Toluca, near to La Escondida, 13 August 1967, M. Frías 9 (ENCB); Michoacán, Municipality of Zitácuaro, Los Gallineros-El Cielito, 30 August 1998, E. Pellicer-González 63 (FCME, 15010).

Comments: *Helvella albella* for its lobed apothecium, dark brown to blackish hymenium, whitish stipe and glabrous apothecium sterile surface can be mixed up with *H. leucopus* Pers., but the last one has larger ascospores (21–24 x 13–15 µm), hollow stipe and different time of fruiting (July–October for *H. albella*, and February–June for *H. leucopus*) (Dissing, 1966b). In addition, cytoplasmic pigments of paraphyses are visible under cotton blue in *H. leucopus* (Landeros et al., 2012). In the Mexican specimens the medullary excipulum is rr– but the stipe inner layer is rr+, while in the Estonian specimen the reaction rr+ is more evidente in the medullary excipulum, and little evident in the stipe inner layer.

Helvella compressa (Snyder) N.S. Weber, Beih. Nova Hedwigia 51: 35, 1975.

= *Paxina compressa* Snyder, Mycologia 28(5): 486, 1936.

Type: L.C. Snyder, 5 May 1934, Eaton, Wahington, USA (WTU, holotype; NY, isotype).

Ascospores 17.5–21.5 x 11–13.5 µm. **Paraphyses** hyaline and light brown, pigmented deposits in the cytoplasm. **Medullary excipulum** hyaline. **Ectal excipulum** yellowish brown to light brown, pigmented deposits in the wall and in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** yellowish, yellowish brown to light brown, pigmented deposits in the wall and in the cytoplasm. **Apothecial hyphal fascicles** 50–320 µm long; **stipe hyphal fascicles** 50–120 µm long. Pigments of all structures not visible under cotton blue. Medullary excipulum, ectal excipulum, apothecial hyphal fascicles and stipe inner layer rr+; stipe outer layer and stipe hyphal fascicles rr–.

Material examined: USA: holotype (WTU), isotype (NY); California, Santa Barbara Co., Figueroa Mountains, 22 April 1978, W. Burke 152 (NY); Friday Harbor, San Juan Island, 12 November 1960, D.E. Stuntz 12223 (WTU), 21 April 1957, S.G. Brough 56 (WTU), 5 May 1957, S.G. Brough 67 (WTU), 30 October 1960, D.E. Stuntz 12143 (WTU), 5 November 1960, D.E. Stuntz 1273 (WTU).

Comments: *Helvella compressa* was described by Snyder (1936) as *Paxina compressa*, and later transferred to *Helvella* by Weber (1975). She considered the ascospore measure as an important feature to separate it of *H. stevensii*. She mentioned ascospores 19–25 x 13–15 µm or 19.5–21 x 12–14 µm, respectively in her key and in the description of *H. compressa*, and 17–20 x 11–13 µm or 18–21 x 11–13 µm, respectively in her key and in the description of *H. stevensii*. On the other hand, Snyder (1936) reported ascospores 23–25 x 13–19 µm, and Abbott and Currah (1997) 19.7–23.8 x 11.4–14.8 µm. Based on the above, we do not consider the spore size as a feature to distinguish *H. compressa* from *H. stevensii*, as was proposed by Weber (1972). Abbott and Currah (1997) wrote that pubescence and distribution (endemic to West Coast of USA) are the distinctive features of *H. compressa*. We consider the follow features to pull apart *H. compressa* of *H. stevensii*: 1) hymenium color (medium to dark brown or grayish brown in *H. compressa*, and cinnamon to pale tan in *H. stevensii*); 2) length of the pubescence of the apothecium sterile surface (50–320 µm in *H. compressa*, and 30–120 µm in *H. stevensii*); 3) hemiamyloid reaction (rr+ in medullary excipulum, ectal excipulum, apothecial hyphal fascicles, and stipe inner layer for *H. compressa*, and rr+ only in medullary excipulum and stipe inner layer in *H. stevensii*); and 4) distribution (West Coast of the USA for *H. compressa*, and East Coast of the USA and Europe for *H. stevensii*). These two species form a clade (fig. 4), although without support, indicating their phylogenetic relationship. Landeros and Guzmán-Dávalos (2012) reported this species from Mexico.

Helvella elastica Bull., Herb. Fr. 6: tab. 242, figs. A–B, D–G, 1785; description in Hist. Champ. Fr. 1: 299–300, 1791 Fig. 6b

Lectotype: Herb. Fr. 6: tab. 242, figs. A–B, D–G, Herb. Fr. 6 (selected here).

Asci 250–305 x 16–18 µm. **Ascospores** 18–22 x 10.5–13 µm, verrucose and smooth. **Paraphyses** 5–10 µm wide at the apex, thin-walled, hyaline, pale brown to yellowish brown in mass, pigmented deposits in the wall and in the cytoplasm, few with brown pigment encrusted on the wall. **Medullary excipulum** hyaline. **Ectal excipulum** light brown, pigmented deposits in the wall. **Stipe inner layer** hyaline. **Stipe outer layer** yellowish, pigmented deposits in the wall. **Apothecial hyphal fascicles** absent; **stipe hyphal fascicles** up to 10 µm long, hyaline. Pigments not visible under cotton blue and Melzer's reagent. Medullary excipulum and stipe inner layer rr+; ectal excipulum, stipe outer layer, and apothecial and stipe hyphal fascicles rr–.

Material examined: MEXICO: Edo. de Mexico, Municipality of Naucalpan, Lerma, Las Rajas, km 29 road México-Toluca via Naucalpan 15 August 1968, E. González 78 (ENCB); Edo. de Mexico, Municipality of Zinacantepec, Loma Alta, road Toluca-Temascaltepec, km 3 of the deviation to shelter

of Nevado de Toluca, 19 September 1982, L. Guzmán-Dávalos 526 (ENCB); Jalisco, Municipality of Zapotlán el Grande, slopes of Nevado de Colima, El Floripondio, 11 September 1998, L. Guzmán-Dávalos 7554 (IBUG); Jalisco, Municipality of Zapopan, forest “La Primavera”, km 1.5 of the housing to Autódromo, 8 October 2001, O. Rodríguez 2433 (IBUG). USA: Massachusetts, Conway, Bear River, 5 October 1968, H.E and M.E Bigelow 5263 (NY).

Comments: *Helvella elastica* can be identified for its light brown to dark brown, lobed apothecium, glabrous apothecium sterile surface, and even, whitish, glabrous to subpubescent, and hollow stipe. A similar species is *H. capucina* Quélet., which was recognized by Dissing (1964), but then (Dissing, 1966b) considered it as a synonym of *H. elastica*, and *H. capucina* sensu Dissing (1964) as a synonym of *H. albella*. Kempton and Wells (1970) wrote that there is a inconsistency in the Dissing’s works, because Dissing (1964) reported ascospores $21\text{--}24\text{--}27 \times 12\text{--}14.1\text{--}16.5 \mu\text{m}$ for *H. capucina*, but later (Dissing 1966b) considered it as a synonym of *H. albella*, but he described smaller ascospores, of $19\text{--}20.5\text{--}22 \times 11\text{--}12.1\text{--}14 \mu\text{m}$ for this species, and $18\text{--}19.2\text{--}21 \times 11\text{--}12\text{--}13.5 \mu\text{m}$ for *H. elastica*. Quélet (1877) described *H. capucina* with ascospores $20\text{--}25 \mu\text{m}$ long, while Karsten (1871: 35) was the first to defined the ascospores size to *H. elastica* of $18\text{--}22 \times 12\text{--}15 \mu\text{m}$. More recently, Dissing et al. (2000) recognized *H. capucina* as an independent species, but more related to *H. albella*. Unfortunately, we have not studied specimens to corroborate the taxonomic status of *H. capucina*, and for this reason we cannot consider it as a synonym, until a complete review with authentic material is done.

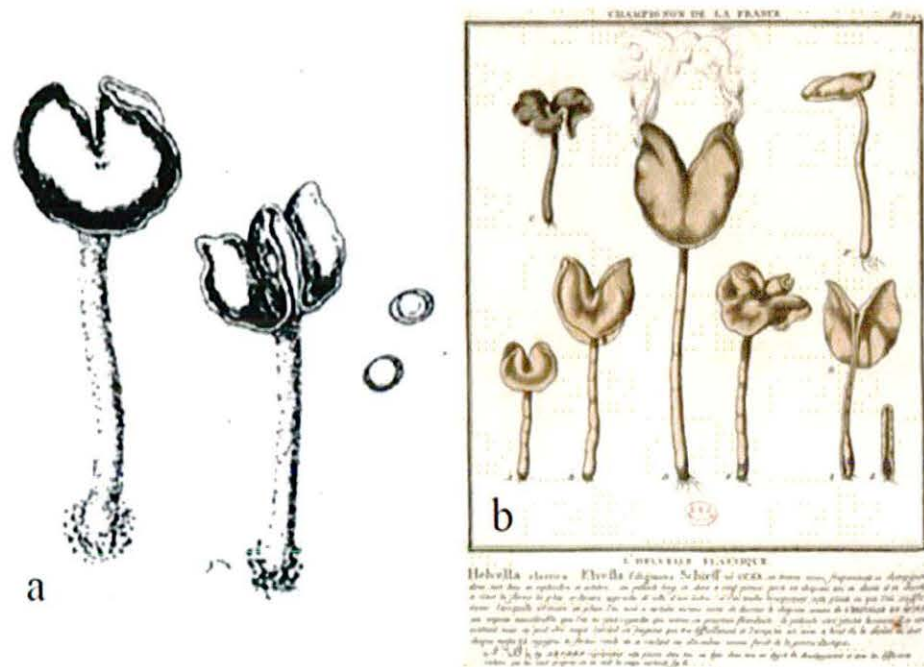


Fig. 6. a: Lectotype of *H. albella*, reproduced from Quélet (1895), b: Lectotype of *H. elastica*, reproduced of Bulliard (1780)

Helvella stevensii Peck, Bull. Torrey bot. Club 31: 182, 1904.

Holotype: R.L. Stevens 6 1903, Detroit, Michigan, USA (NYS, not seen).

= *H. connivens* Dissing & M. Lange, Mycologia 59: 351, 1967.

Asci $220\text{--}300 \times 13\text{--}17 \mu\text{m}$. **Ascospores** $17\text{--}20 \times 10\text{--}12.5 \mu\text{m}$. **Paraphyses** $5\text{--}8 \mu\text{m}$ wide at the apex, hyaline and yellowish to light brownish, pigmented deposits in the cytoplasm. **Medullary excipulum**

hyaline. **Ectal excipulum** yellowish to light brown, pigmented deposits in the wall and few with pigments in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** yellowish to light brown, pigmented deposits in the wall. **Apothecial hyphal fascicles** 30–120 μm long; **stipe hyphal fascicles** 30–110 μm long. Pigments of all structures not visible under cotton blue. Medullary excipulum and stipe inner layer rr+; ectal excipulum, outer layer, and apothecial and stipe hyphal fascicles rr--.

Material examined: USA: Iowa, Boone county, Ledges State Park, along des Moines River, 25 June 1983, C.T. Rogerson (NY), 25 June 1983, R.E. Halling 3824 (NY); Massachusetts, Mt. Tobi, 6 August 1958, H.E. and M.E. Bigelow and F. Witham 2427 (NY), 30 August 1958, H.E. and M.E. Bigelow 2474 (NY); Michigan, Detroit, 23 June 1905, R.L. Stevens (NY); Michigan, Cross Village, along roadside, 21 July 1947, A.H. Smith 25872 (MICH, *H. connivens*, holotype).

Comments: *Helvella stevensii* was considered as a synonym of *H. latispora* by Häffner (1987) and Abbott and Currah (1997), but we agree with Dissing (1966b) in consider both species as independent taxa. The following features support our point of view: 1) *H. stevensii* was described with ascospores 20 x 12 μm by Peck (1904: 182), and recorded by Dissing (1966b) as 18–18.4–19.5 x 11.5–12.3–13 μm , while *H. latispora* was defined with wider ascospores, 18–20 x 15–17 by Boudier (1907: 16, pl. III, fig. IIe), similar to those mentioned by Dissing (1966b) of 18–19.4–21 x 13.5–14.8–18 μm . However, Abbott and Currah (1997) recorded ascospores of (16.5–) 18.6–19.9 (–20.8) x (10.9–) 11.4–12.4 μm for *H. latispora*, but such measures are more like to *H. stevensii*; and 2) Peck (1904) described the apothecium sterile surface of *H. stevensii* as “pruinose velvety”, while Boudier (1907) reported *H. latispora* as glabrous. Abbott and Currah (1997) described *H. latispora* as “finely pubescent to pubescent”, and such feature correspond to *H. stevensii*. In fact, Dissing (1966b) considered *H. stevensii* in Sect. *Ephippium* and *H. latispora* in Sect. *Elasticae*, because the first one is pubescent and the second glabrous. Such discrepancies are rare, because Abbott and Currah (1997) reported that they studied the type of both species, but Dissing (1966b) cited the type of *H. latispora* as “*Helvella* pl. nr. 480, *latispora* Boud (Hb. Boudier), Typus PC” doing reference to a plate, and Abbott and Currah (1997) mentioned the type as “France, Boudier Herbarium Mycologique, PC (holotype)”, referring to a specimen. Boudier (1907) in his description of *H. latispora* wrote “Rarissimé reperi in Sylva Carnelle dièta. Septembre 1889 et 1896”, i.e., he did not cite any reference specimen, therefore *H. latispora* do not have a type, and the specimen Abbott and Currah (1997) studied as the holotype of *H. latispora* could represent a different species. *Helvella stevensii* can be confused with *H. compressa* (see remarks under this species).

We studied authentic material of *H. stevensii* and the holotype of *H. connivens* and we did not find any difference, in fact their DNA sequences are identical, therefore, we agree with Weber (1972) and Abbott and Currah (1997) that *H. connivens* has to be consider as a synonym of *H. stevensii*.

Section *Helvella* in Dissing, Dansk Botanisk Arkiv 25: 85, 1966b (as Section *Crispae*).

= Section *Crispae* Dissing, Dansk Botanisk Arkiv 25: 85, 1966b, invalid name.

≠ Subgenus *Helvella* in Abbott & Currah, Mycotaxon 62: 54, 1997.

Type species: *Helvella crispae* (Scop.) Fr., Syst. Myc. (Lundae) 2(1): 14, 1822.

Dissing (1966b) described Sect. *Crispae* for species with pubescent ascoma with convex to irregularly saddle-shaped apothecium, and lacunose or sulcate stipe. According to Weber (1972), it is an invalid section name because it harbors the type species of the genus, and for this reason must bear the name of the genus (Art. 22, *International Code of Botanical Nomenclature*); although she followed Dissing's (1966b) delimitation. Abbott and Currah (1997) proposed the Subgen. *Helvella* for species with irregularly lobed to lobed apothecium, costate or lacunose stipe, and glabrous or pubescent

apothecium sterile surface, as they wrote “subgenus *Helvella* corresponds closely to the genus *Helvella* in its most restricted sense (e.g., Boudier 1885, 1907; Breitenbach and Kränzlin 1981)” for such reason they considered *H. crispa*, *H. lacunosa*, *H. fusca*, *H. lactea*, and *H. maculata* as members of this subgenus. In other words, they put together the species of the Dissing’s sections *Crispa* and *Lacunosa* in their subgenus. Our phylogenetic results do not support this hypothesis (figs. 3-4), but they back up the viewpoint of Dissing (1966b) and Weber (1972). Dissing (1966b) considered only three species in this section, *H. crispa*, *H. fusca* (cited by him as “Gill. sensu Bres.”), and *H. queletiana* Sacc. & Traverso, and then he (Dissing 1979) added *H. papuensis* (a species with tropical distribution), while Weber (1972) contemplated only one species, *H. crispa*, because it was the only species distributed in her study area, and later (Weber 1975) included besides *H. maculata*. We reviewed the Bresadola’s specimen of *H. fusca* (Bresadola 21.V.1898, S), which correspond to fig. 23 in Dissing’s manuscript, and was considered by Abbott and Currah (1997) as the neotype of *H. fusca* (see comments in *H. fusca*) and we did not find pubescent ascomata, rather they are glabrous to subpubescent, therefore this species would be more related to *H. lacunosa* than to *H. crispa*, and the phylogenetic results (figs. 3-4) corroborated our observations. With respect to *H. queletiana*, we did not study any specimen of this species. We consider the characteristics given for Dissing (1966b) are enough to define this section. The species that we recognize for this section are: *H. crispa*, *H. maculata*, and *H. papuensis*, it remains pending the affinity of *H. queletiana*.

Helvella crispa (Scop.) Fr., Syst. Mycol. (Lundae) 2(1): 14, 1822.

= *Phallus crispus* Scop., Fl. carniol., Edn 2 (Wein) 2: 475, 1772.

= *Helvella mitra* L., Sp. Pl. 2: 1180, 1753.

Lectotype: in Micheli, Nov. Pl. Gen. 204, Tab. 86, Fig. 7, 1729.

Asci 220–325 x 12.5–18 µm. **Ascospores** (14.5–) 16–20 (–22) x 9.5–12.5 µm. **Paraphyses** hyaline and yellowish, pigmented deposits in the wall, in the cytoplasm, and rarely encrusted on the wall. **Medullary excipulum** hyaline. **Ectal excipulum** yellowish, pigments usually deposited in the wall and rarely in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** yellowish, pigmented deposits usually in the wall and rarely in the cytoplasm. **Apothecial hyphal fascicles** 30–120 µm long, yellowish, pigmented deposits usually in the wall and rarely in the cytoplasm; **stipe hyphal fascicles** 30–90 µm long, yellowish, pigmented deposits usually in the wall and rarely in the cytoplasm. Pigments of all structures not visible under cotton blue. Stipe inner layer slightly rr+, more evident in young ascomata; ectal and medullary excipulum, stipe outer layer, and apothecial and stipe hyphal fascicles rr–.

Material examined: MEXICO: Jalisco, Municipality of Ahualulco, Piedras Bolas, 24 August 2008, L. Guzmán-Dávalos 10453 (IBUG); Municipality of Mazamitla, cerro El Tigre, to 4 km of Mazamitla, October 2009, V. Ramírez-Cruz 1115 (IBUG); Municipality of Tapalpa, to NE to the town, of 14 August 1982, G. Nieves 37 (IBUG), 15 September 2009, F. Landeros 3344 (IBUG); Municipality of Tecolotlán, Sierra de Quila, km 8 of road of Quila to Árbol de la Lira, 26 September 2009, F. Landeros 3355 (IBUG); Municipality of Tequila, volcán de Tequila, road to microwave station, 21 August 1990, O. Rodríguez 599 (IBUG); Municipality of Zapopan, 6 km to south of forest “La Primavera”, 3 September 1992, O. Rodríguez s.n. (IBUG); Municipality of Zapotlán el Grande, slopes of Nevado de Colima, El Floripondio, 7 September 1996, MR. Sánchez-Jácome 939 (IBUG).

Comments: *Helvella crispa* can be confused with *H. maculata* (see comments under this species) and *H. papuensis*. Dissing (1979) mentioned the following, features to recognize it from *H. papuensis*: 1) hymenium color in fresh condition, oxide yellow to brownish yellow in *H. papuensis*, white, cream or

pale cream in *H. crispa*; 2) pubescence, “much more villose” in *H. papuensis* according to Dissing [but we measured the apothecial hyphal fascicles (60–160 µm long) and stipe hyphal fascicles (50–120 µm long) of *H. papuensis* and did not find any significance difference with those observed in *H. crispa*]; and 3) distribution, tropical, only known of Papua New Guinea for *H. papuensis*. Furthermore, we found another feature: in the holotype of *H. papuensis* all tissues are rr–.

Helvella maculata N.S. Weber, Beih. Nova Hedwigia 51: 27, 1975.

Holotype: H.V. Smith and N.J. Smith (N.J. Smith 2124), 5 October 1968, Bonner Co., south side of Hoodoo Mountain, Idaho, USA (MICH, Barcode 5635).

Material examined: USA: holotype.

Comments: *Helvella maculata* has lobed apothecium, lacunose stipe, and pubescent apothecium and stipe sterile surfaces. It might be confused with *H. crispa*, but *H. maculata* have the following distinctive features (Weber, 1975, Landeros et al., 2012): 1) mottled apothecium; 2) grayish ribs in the stipe; 3) apothecial hyphal fascicles of 107–205 µm long, and stipe hyphal fascicles 60–130 µm long; 4) incurved and unrolling apothecium margin; and 5) brownish pigments in the cells of the stipe outer layer evident under cotton blue. See description and more comments in Landeros et al. (2012).

Section *Lacunosae* Dissing, Dansk Botanisk Arkiv 25: 98, 1966b.

≠ Subgenus *Helvella* in Abbott & Currah, Mycotaxon 62: 54, 1997.

Type species: *Helvella lacunosa* Afzel. K. Vetensk-Acad. Handl. 4: 304, 1783.

Dissing (1966b) described section *Lacunosae* to harbor species with glabrous ascomata, convex, hemispheric, lobed or discoid apothecium, and sulcate or chambered stipe. This concept was followed by Weber (1972). Abbott and Currah (1997) joined this section with Sect. *Helvella* in their Subgen. *Helvella*, as was discussed above. Our phylogenetic results support the Dissing (1966b) and Weber (1972) viewpoint. Species that we recognized under this section are *H. fusca*, *H. lactea*, *H. lacunosa*, *H. palustris*, *H. phlebophora*, *H. philonotis*, *H. sulcata*, and *Helvella* sp. 2.

Helvella fusca Gillet, Champignons de France, Discom. 1: 9, Pl. 4, 1879.

Lectotype: Pl. 4, in Gillet, Champignons de France, Discom., 1879.

Epitype: Bresadola 5 21 1898, Al Deserto, Italy (S).

Material examined: ITALY: epitype (S).

Comments: *Helvella fusca* can be recognized by its brown to pale brownish hymenium, glabrous to subpubescent apothecium sterile surface, and lacunose stipe. Morphological and molecularly it is close to *H. lacunosa*, differing for its black or greyish black hymenium. Dissing (1966b) placed *H. fusca* in its Sect. *Crispae*, because he considered this species with pubescent ascoma, but we agree with Bresadola (1892) and Ceccaldi (2006), who described the ascoma as glabrous or almost, i.e., more related to *H. lacunosa*, and DNA sequences corroborate this observation. Kaushal (1991) reported *H. fusca* from the Himalayas, but he described “pubescent hairs up to 105 µm”, so it is probably a different species. Also *H. fusca* was reported from Alaska and Oregon (Kempton and Wells, 1970; Larsen and Denison, 1978), but Abbott and Currah (1997) did not find any specimen representing this species during their study. Therefore, we consider *H. fusca* is only known from Europe and its distribution elsewhere is doubtful. See a complete description and more comments in Landeros and Korf (2012).

Helvella lacunosa Afzel., K. Vetensk-Acad. Handl. 4: 304, 1783.

Type: Unknown.

Asci 220–420 x 13–16 μm . **Ascospores** 17.5–21 x 10.5–13.5 μm , smooth or slightly verrucose. **Paraphyses** 5–10 μm wide at the apex, thin-walled, brownish, pigmented deposits in the cytoplasm, in the wall, and encrusted on the wall. **Medullary excipulum** hyaline. **Ectal excipulum** yellowish brown, pigmented deposits usually in the wall and sometimes in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** brown, pigments usually deposited in the wall, and few cells with pigmented deposits in the cytoplasm. **Apothecial hyphal fascicles** absent or up to 50 μm long, light brown in mass, pigmented deposits in the wall; **stipe hyphal fascicles** absent or up to 50 μm long, light brown in mass, pigmented deposits in the wall. Only encrusted pigments on the wall of paraphyses visible on cotton blue. Everything rr–, except apothecial medullary excipulum slightly rr+ on Melzer's reagent.

Material examined: MEXICO: Edo. de Mexico, Nevado de Toluca slopes, Cerro Prieto, 18 October 2003, L. Guzmán-Dávalos 9002 (IBUG); Jalisco, Municipality of Autlán, Sierra de Manantlán, 1 km to S of Estación Las Joyas, 12 September 2002, G. Zarco 144 (IBUG); Municipality of Guadalajara, around the city, without date, J. Manzi 514 (IBUG); Municipality of Tequila, volcán de Tequila, km 14-15 road to microwave station, 21 September 1986, M. Garza 257 (IBUG), km 3-6.5, 24 August 1986, O. Rodríguez 240 (IBUG); Municipality of Zapotlán el Grande, Nevado de Colima, 7 October 2010, A. Castro-Castro (IBUG); Michoacán, Coeneo, Cerro El Salto, 1.5 km before to San Marcos Matugeo, 30 August 1996, O. Rodríguez 1561 (IBUG); Querétaro, Cadereyta, Chavarrías, 8 August 2004, F. Tapia 2229 (IBUG); San Joaquín, Ranas, 20 September 2004, F. Landeros 883 (IBUG); Tamaulipas, Miquihuana, without date, G. Guevara 1061 (ITCV); Tlaxcala; road Apizaco to Chignahuapan, to N of Tlaxco, 19 September 1974, R. Grada y R. Cerrato 33-T (ENCB); Veracruz, La Perla, 27 September 1996, F. Tapia 1403 (XAL). USA: Oregon, Polk Co., S fork of Peede Creek, N of Peeds, 10 November 1990, NSW 6373 (OSC).

Comments: *Helvella lacunosa* was described by Afzelius (1783), and since then there is confusion in its definition, specifically with *H. sulcata*. Afzelius (1783) described *H. lacunosa* with lacunose stipe, i.e., with longitudinal and transversal septa, and *H. sulcata* with costate stipe, i.e., with mainly longitudinal septa. Fries (1823) recognized both species as separate taxa. However, Dissing (1966a, b) considered *H. sulcata* as a synonym of *H. lacunosa*, because for him this separation was subjective. In fact, Dissing (1966a) cited the Boudier's figures (1910, pls. 228-229) to illustrate this situation. We regard that Boudier's figures are an unfortunate representation to distinguish *H. sulcata* of *H. lacunosa*, because both figures represent *H. lacunosa*. We disagree to consider *H. sulcata* as a synonym of *H. lacunosa*. We recognize the stipe type as the best way to distinguish both species, as it was described by Afzelius (1783), and molecular results completely support such separation.

Helvella sp. 2 sp. nov.

Fig. 7

MycoBank:

Apothecium cup-shaped, dark brown to black, stipe greyish to black, ribbed, ribs never arriving to the apothecium sterile surface, apothecial hyphal fascicles up to 50 μm long and stipe hyphal fascicles up to 30 μm long.

Holotypus: P. Marstad 128–93, 22 Jul 1993, Grimsdale, Dovre, Oppland, Norway (O).

Etymology: Tentatively this species will be the name of the country where it was collected.

Apothecium 5–12 mm diam., 1.5–6 mm high, cupulate, hymenium dark brown to black when dried, sterile surface dark brown to black, whitish edge, glabrous to subpubescent, ribs absent. **Stipe** 1–7 x 1–2.5 mm, tapering to the base or nearly equal, greyish to black, glabrous to subpubescent, solid, ribbed, ribs blunt-edged. **Asci** 230–330 x 14–22 μm , pleurorhynchous. **Ascospores** 17.5–20 x 10.5–13 μm , ellipsoid, hyaline, smooth or finely verrucose, uniguttulate. **Paraphyses** 5–10 μm wide at the apex, thin-walled, brown, pigmented deposits in the wall, in the cytoplasm, and sometimes encrusted on the wall. **Medullary excipulum** hyaline. **Ectal excipulum** with basal cells hyaline with yellowish pigments in the wall, outer cells brown, pigmented deposits in the wall and in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** brown, pigmented deposits in the wall and in the cytoplasm. **Apothecial hyphal fascicles** up to 50 μm long, brown, pigmented deposits in the wall and in the cytoplasm; **stipe hyphal fascicles** up to 30 μm , pigmented deposits in the wall and in the cytoplasm. Pigments of all structures visible under cotton blue. Medullary excipulum and stipe inner layer slightly rr^+ (more evident in young ascomata and in the stipe inner layer), ectal excipulum and stipe outer layer rr^- .

Material examined: NORWAY: holotype (O); Oppland, Lom, Høyrokampen v. Bøvertun, 31 August 2007, Anders and Wollan 34 (O).



Fig. 7. *Helvella* sp. 2, a: ascomata of the type material (P. Marstad 128–93, O), b: ectal excipulum, c: ascospores, d: pleurorhynchous asci and paraphyses. Scale bars: 7a: 1 cm; 7b, 7d: 20 μm ; 7c: 10 μm .

Comments: *Helvella* sp. 2 is recognized by its cup-shaped apothecium and glabrous to subpubescent ascoma; in fact, this species along with *H. philonotis* Dissing are the only two species of the section *Lacunosae* with cup-shaped apothecia. *Helvella* sp. 2 can be distinguished of *H. philonotis*, because in the last one the stipe ribs continue on the apothecium sterile surface and its apothecium is lobed at maturity (Dissing 1964: 117). Other species which can be mistaken with *Helvella* sp. 2 are *H. dovrensis* T. Schumach., *H. solitaria*, *H. ulvinenii*, and *H. verruculosa*, because of the cup-shaped apothecium, ribbed stipe, and ribs never arriving to the apothecium sterile surface, but these species are subpubescent to pubescent. Schumacher (1992) described the apothecial hyphal fascicles of 40–120 μm long for *H. dovrensis*, and Landeros et al. (2012) mentioned 40–90 μm long for *H. solitaria*, 40–105 μm long for *H. ulvinenii*, and 70–150 μm long for *H. verruculosa*. The studied specimens were determined as *H. dovrensis* at O, but they did not correspond to this species (Schumacher, pers. com.).

Helvella sulcata Afzel., K. Vetensk-Akad. Handl. 4: 305, 1783, Tab. 10, Fig. 1.
Lectotype: Tab. 10, Fig. 1, K. Vetensk-Akad. Handl. 4 (selected here).

Fig. 8a

Apothecium 10–13 mm diam., 5–9 mm high, lobed, attached in two points to the stipe, hymenium dark brown to black when dried, sterile surface cream to brownish, glabrous to subpubescent, ribs absent or reaching one quarter. **Stipe** 13–20 x 2–2.5 mm, tapering to the base or nearly equal, blackish, glabrous to subpubescent, solid, ribbed, ribs sharp-edged. **Asci** 240–340 x 13–18 μm , pleurorhynchous. **Ascospores** 16–20 x 9.5–12 μm , ellipsoid, hyaline, smooth or finely verrucose, uniguttulate. **Paraphyses** 4–10 μm wide at the apex, thin-walled, brownish, pigmented deposits in the wall, in the cytoplasm, and sometimes encrusted on the wall. **Medullary excipulum** hyaline. **Ectal excipulum** with brown pigmented deposits in the wall and sometimes encrusted on the wall, yellowish pigmented deposits in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** with brown pigmented deposits in the wall and sometimes encrusted on the wall, yellowish pigmented deposits in the cytoplasm. **Apothecial and stipe hyphal fascicles** absent. Only encrusted pigments on the wall of paraphyses, and ectal excipulum and stipe outer layer cells visible under cotton blue. Medullary excipulum slightly rr+ (after 15 minutes), ectal excipulum, and stipe outer and inner layer rr–.

Material examined: MEXICO: Jalisco, Municipality of Bolaños, Sierra de los Huicholes, km 30 Bolaños-Tuxpan de Bolaños, 24 August 2004, I. Álvarez 2195 (IBUG); Municipality of Tecolotlán, Sierra de Quila, 2 km to N of La Ciénega, 26 September 2009, F. Landeros 3353 (IBUG); Municipality of Tequila, km 15 trail from Tequila to microwave station, 10 October 2009, F. Landeros 3360 (IBUG); Morelos, Municipality of Hueyapan, 1980, De Ávila 13B (ENCB); Querétaro, Municipality of San Joaquín, Nuevo San Joaquín, 7 August 2004, F. Landeros 1848 (IBUG); Municipality of San Joaquín, Ranas, 15 September 2004, F. Landeros 883 (IBUG). USA: Michigan, Cheboygan Conty, Carp. Creek Gorge, University of Michigan, Biological Station, Douglas Lake, 29 July 1962, C.T. Rogerson (NY); New York, Baergen Swamp, 1 September 1946, W.C. Muenscher and B. Brown (NY).

Comments: *Helvella sulcata* has been controversial in its recognition; in modern works only Weber (1972) distinguished it as independent of *H. lacunosa*. Its mostly ribbed stipe instead of lacunose helps in their recognition (see comments under *H. lacunosa*). Similar species to *H. sulcata* is *H. palustris* Peck. The latter was described by Peck (1880: 31) as "[p]ileus irregular, at first blackish and slightly adnate, then grayish-brown or mouse-colored and free", but the Peck's drawings (figs. 16–17) are an excellent representation that this species has a free apothecium. Also Abbott and Currah (1997), who studied the holotype, described "... discoid to convex

apothecium which remains free from the stipe", while *H. sulcata* always has the apothecium attached to the the stipe in two points.

Helvella sulcata was described from Europe, and is also present in USA. The sequence of US specimen (labeled as *H. sulcata* in the tree) is very different with respect to *H. aff. sulcata* (which are Mexican specimens), so its necessary to study if it is a species complex.

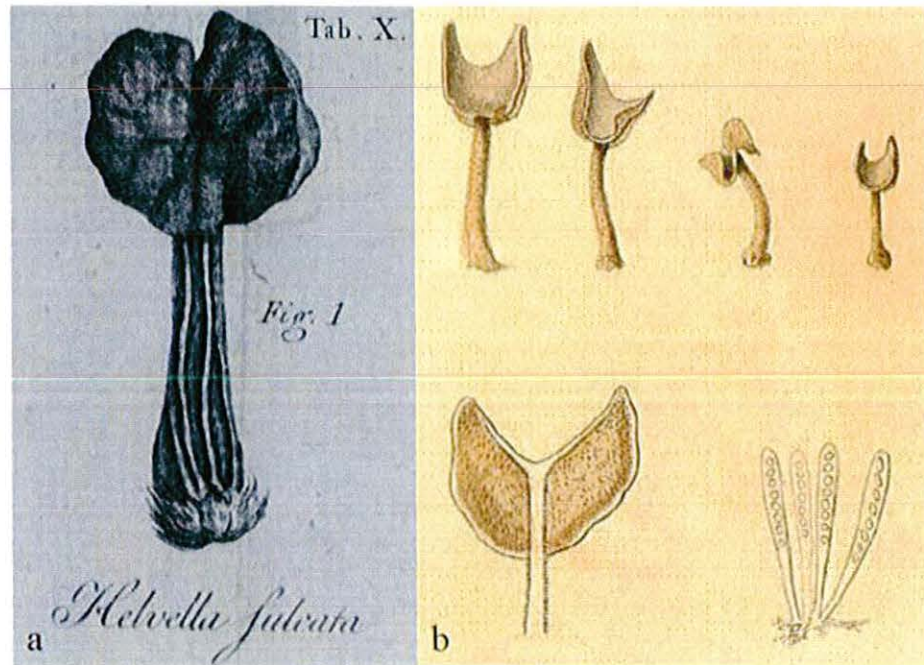


Fig. 8. a: Lectotype of *H. sulcata*, reproduced from Afzelius (1783), b: Lectotype of *H. ephippium*, reproduced of Lévillé (1841)

Species with undetermined infrageneric relationship

Helvella acetabulum (L.) Quél., Hyménomycètes (Alençon): 102, 1874.

Lectotype: Pl. 13, fig. 1, in Vaillant, Botanicon Parisienne, 1727.

Apothecium sterile surface with simple or branched ribs, anastomosed or not, ribs reaching from the half to the apothecium edge. **Stipe** costate or lacunose, ribs sharp-edged. **Asci** 230–350 x 14–18 μm . **Ascospores** 16.5–20 x 9.5–13 μm , smooth. **Paraphyses** 4–8 μm wide at the apex, thin-walled, light brown to yellowish, pigmented deposits in the wall, in the cytoplasm, and sometimes encrusted on the wall. **Medullary excipulum** hyaline. **Ectal excipulum** yellowish brown, pigmented deposits usually in the wall and sometimes in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** yellowish brown, pigmented deposits usually in the wall and sometimes in the cytoplasm. **Apothecial hyphal fascicles** 40–100 μm long, light brown, pigmented deposits in the wall and in the cytoplasm; **stipe hyphal fascicles** up to 50 μm long, pigmented deposits in the wall and in the cytoplasm. Pigments of all structures not visible under cotton blue. Medullary excipulum, basal cells of ectal excipulum, and stipe outer layer and inner layer slightly rr+ on Melzer's reagent.

Material examined: ESTONIA: Saaremaa, Kuivastu, Andruse, 21 May 2001, B. Kullman (TAA179637, TAAM). MEXICO: Michoacán, Municipality of Uruapan, 500 m before arriving to the

falls La Tzararacua, 3 November 1994, M.A. Hernández 164 (IBUG); Jalisco, Municipality of Tequila, km 11 trail from Tequila to microwave station, 25 September 2009, F. Landeros 3349 (IBUG).

Comments: *Helvella acetabulum* is characterized by its cup-shaped apothecium and ribbed or lacunose stipe, with ribs reaching to the half or to the apothecium edge. Sometimes it can be confused with *H. costifera*, *H. griseoalba*, and *H. verruculosa*, but all of these have ribs with blunt edge. Other features to separate them are: 1) in *H. verruculosa* the brown pigments of the paraphyses, ectal excipulum, and apothecial hyphal fascicles are visible under cotton blue (Landeros et al. 2012); 2) specimens of *H. costifera* are pubescent in the apothecium sterile surface and stipe (Landeros et al. 2012); and 3) *H. griseoalba* has the hymenium with greyish tones in contrast with the brown and cream tones of *H. acetabulum* (Weber 1972).

Helvella costifera Nannf., Fungi Exsicc. Suec., Fasc. (sched.): 37, 1953.

= *H. hyperborea* Harmaja, Karstenia 18(2): 57, 1978.

Lectotype: E.P. Fries s.n., as *Peziza costata*, Botanic Garden, Uppsala, Uppland, Sweden (UPS, lectotype, not seen; S, isoelectotype).

Material examined: FINLAND: Koillismaa, Kuusamo, Juuma, western part of the gorge Jäkälävuoma, alt. ca. 205 m, 27 August 1970, H. Harmaja (H, holotype of *H. hyperborea*); Lapland, Enontekiö, 6 August 1985, J. Vauras 1932 (H); Lapland, Kemi, 7 August 1998, U. Nummela-Salo and P. Salo 5318 (H); Northern Ostrobothnia, Kuusamo, 4 August 1994, T. Ulvinen (OULU, FO23453); Northern Savonia, Kuopio, 22 July 1984, J. Vauras 1638F (H); 23 August 1987, J. Vauras 2856 (H); Uusimaa, Lohja, 19 July 1998, U. Nummela-Salo and P. Salo 4924 (H); Varsinais-Suomen, 4 July 1996, J. Vauras 11192F (H). MEXICO: Hidalgo, Municipality of Epazoyucan, Peñas Largas, 3 August 1975, M. Medina and I. García 1104 (ENCB); Jalisco, Municipality of Atemajac de Brizuela, km 3 road of Puerto Nuevo-Club Ecole, 27 September 2009, F. Landeros 3358 (IBUG); Querétaro, Municipality of Cadereyta, El Doctor, 22 August 2004, F. Tapia 2301 (IBUG). NORWAY: Northern Norway, Finnmark, 19 August 1995, I. Kylövuori 95-744 (H); Northern Norway, Troms, 16 August 1992, I. Kytövuori 92-352 (H). SWEDEN: isoelectotype; Uppland, 22 June 1948, H. Smith (UPS); 7 July 1948, A. Melderis (UPS); 9 July 1948, Exsiccata J.A. Nannfeldt no. 9956 [K(M) 159848].

Comments: *Helvella costifera* has cup-shaped apothecium, costate stipe, with blunt-edged ribs, arriving from a quarter to the apothecium edge, and pubescent apothecium sterile surface and stipe. It can be confused with *H. acetabulum*, but the last one has sharp-edged ribs and its stipe can be costate or lacunose (Dissing 1966b; Landeros et al. 2012). See description and more comments in Landeros et al. (2012).

We studied the isoelectotype of *H. costifera* and some materials of the Scandinavian Peninsula, and we recorded ascospores of 16–20 x 10–13 μm , which is consistent with those reported by Dissing (1966b), while ascospores of Mexican specimens measured 13.5–17 (–18) x 8–11 μm . The specimens labeled in the phylogenetic trees (figs. 3 and 4) as *H. costifera* are from Scandinavian Peninsula (from where this species was described), while the Mexican specimens sequenced are labeled as *H. aff. costifera*, and they were collected in the neotropical region. Between the specimens of *H. costifera* and *H. aff. costifera* there are 7–9 different bases, while the specimens of *H. aff. costifera* have 5–6 different bases with *H. robusta* (appendix III). For this reason in the cladogram with only molecular data (fig. 3), the last species is between *H. costifera* and *H. aff. costifera*. However, using molecular and morphological data, the specimens of *H. costifera* and *H. aff. costifera* are grouped in a clade, although without support. On the other hand, Abbott and Currah (1997) reported *H. costifera* to

North America, and they mentioned ascospores with a wider range, 14.4–19.7 x 9.6–12.4 μm . So, it is necessary to sequence specimens of North America to diluciate if the American specimens labeled as *H. costifera* correspond to this species.

Helvella cupuliformis Dissing & Nannf., Svensk. bot. Tidskr. 60: 326, 1966.

Holotype: K.G. Ridelius, 30 July 1936, Uppsala, near Kåbo, in dense coniferous forest, on bare soil, under *Abies* sp., Uppland, Sweden (UPS, not seen).

Asci 250–330 x 14–18 μm , pleurorhynchous. **Ascospores** 17.5–21 x 11–13 μm , smooth or verrucose. **Paraphyses** 4–8 μm wide at the apex, thin-walled, hyaline to yellowish brown, pigmented deposits in the wall and in the cytoplasm. **Medullary excipulum** hyaline. **Ectal excipulum** yellowish brown, pigmented deposits in the wall and in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** yellowish brown, pigmented deposits in the wall and in the cytoplasm. **Apothecial hyphal fascicles** 30–150 μm long, yellowish brown in mass, pigmented deposits in the wall and sometimes in the cytoplasm; **stipe hyphal fascicles** 30–140 μm long, yellowish in mass, pigmented deposits in the wall and sometimes in the cytoplasm. Pigments of all structures not visible under cotton blue. All tissues rr–.

Material examined: SWEDEN: Uppland, Uppsala, Stadsskogen near Skogshall, 7 July 1948, J. Eriksson and R. Morander (F. Suec. Ups. Exs. 3265, K, paratype); 21 July 1948, J. Eriksson and R. Morander (UPS, paratype); Uppland, Uppsala, Stadsskogen, NV om Skogshall, På jord under gran I blandskog (I skogsbryn), 12 October 1951, S. Lundell (UPS).

Comments: *Helvella cupuliformis* for its cup-shaped apothecium and terete stipe can be confused with *H. macropus* and *H. fibrosa*. *Helvella macropus* is easy to distinguish, because it has fusoid to subfusoid ascospores. With respect to *H. fibrosa*, in fresh they can be identified for its hymenium color, *H. fibrosa* has grey, dark greyish-brown to dark brown or steel grey hymenium, while *H. cupuliformis* has pale brownish to yellowish-brown hymenium (Dissing 1966a, b), but in herbarium material this feature is not useful. In this case, stipe size is a good characteristic, *H. fibrosa* has stipe of 1–3 cm long and *H. cupuliformis* of 0.8–1.5 cm long (Dissing 1966a, b). The smaller stipe of *H. cupuliformis* makes it appears that the diameter of its cup is greater, but in reality both species have similar ranges. Weber (1972) mentioned the pigment location as an importante feature to separate both species, with pigment desposits in the wall in *H. fibrosa*, and in the cytoplasm in *H. cupuliformis*, but we observed similar distribution of the pigments in both species.

Helvella ephippium Lév., Annl. Sci. Nat., Bot., sér. 2, 16: 240, 1841.

Fig. 8b

Lectotype: Pl. 15, Figs. 7a–c, Annl. Sci. Nat., Bot., sér. 2, 16, 1841.

Asci 220–290 x 15–18 μm . **Ascospores** 17–20 x 10.5–12 μm , smooth or slightly verrucose. **Paraphyses** 4–7 μm wide at the apex, thin-walled, yellowish brown, pigmented deposits in the wall, in the cytoplasm, and sometimes encrusted on the wall. **Medullary excipulum** hyaline, with yellowish brown patches. **Ectal excipulum** yellowish brown, pigmented deposits in the wall and in the cytoplasm. **Stipe inner layer** hyaline, with yellowish brown patches. **Stipe outer layer** yellowish brown, pigmented deposits in the wall and in the cytoplasm. **Apothecial hyphal fascicles** 40–140 μm long, brown, pigmented deposits in the wall and in the cytoplasm; **stipe hyphal fascicles** 40–80 μm long, brown, pigmented deposits in the wall and in the cytoplasm. Only pigments in the wall of paraphyses, and apothecial and stipe hyphal fascicles visible under cotton blue. All tissues rr–.

Material examined: MEXICO: Jalisco, Municipality of San Sebastián del Oeste, road San Sebastián del Oeste to Santa Ana, 29 August 1994, O. Rodríguez 1022 (IBUG).

Comments: Here we select the figures of L veill  (1841) as the lectotype of *H. ephippium*, as it was suggested by Dissing (1966b) and Abbott and Currah (1997). *Helvella ephippium* is a very small species, with an apothecium less than 1.5 cm diam. Only *H. pocillum*, *H. rivularis* Dissing & Sivertsen, and *H. terrestris* can be as small, but all these species have a cup-shaped well defined apothecium, while *H. ephippium* has an involute, irregularly lobed to saddle-shaped apothecium. L veill  (1841) did not mention the measures of the ascospores, he only wrote “rondes et transparentes”. Masee (1895: 466) was the first to describe them, 16–18 x 10 μm ; more recently Dissing (1966b) mentioned ascospores 19–20.4–21.5 x 11–11.6–12 μm , while Weber (1972) described them 16.5–19 x 10.5–12 μm . Our measures are consistent with those of Abbott and Currah (1997), who cited 17–21 x 10.1–13 μm .

Helvella fibrosa (Wallr.) Korf, Mycotaxon 103: 311, 2008.

Lectotype: Tab. 19, Figs. B1–B6, in Hedwig, Micro-anal. musc., 1789.

Epitype: Lundell, Nannfeldt & Holm, Fungi exsiccate Suecici praesertim Upsaliensis # 3262, 1985 (UPS, not seen).

= *H. chinensis* (Velen.) Nannf. & L. Holm, in Lundell, Nannfeldt & Holm, Publications from the Herbarium, University of Uppsala, Sweden 18: 5, 1985.

= *H. pallidula* N.S. Weber, The Michigan Bot. 11(4): 171, 1972.

= *H. villosa* (Hedw.) Dissing & Nannf., Svensk bot. Tidskr. 60: 330, 1966.

Asci 210–280 x 14–18 μm . **Ascospores** 16–20 x 10–12 μm , smooth or slightly verrucose. **Paraphyses** 4–9 μm wide at the apex, hyaline to light brown, pigmented deposits in the wall and in the cytoplasm. **Medullary excipulum** hyaline. **Ectal excipulum** yellowish brown to light brown, pigmented deposits in the wall and in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** yellowish brown to light brown, pigmented deposits in the wall and in the cytoplasm. **Apothecial hyphal fascicles** 50–160 μm long, hyaline to yellowish, pigmented deposits in the wall and sometimes in the cytoplasm; **stipe hyphal fascicles** 50–120 μm long, hyaline to yellowish, pigmented deposits in the wall and sometimes in the cytoplasm. Pigments of all structures not visible under cotton blue. All tissues rr–.

Material examined: CHINA: Pai N'a, 28 August 1930, E. Licent 2398 (PRM 151669, holotype of *H. chinensis*); USA: Michigan, Montmorency Co., scattered on sandy soil in a deciduous woods, northwest corner, 24 July 1967, N.J. Smith 397 (MICH, holotype of *H. pallidula*).

Comments: Korf (2008) concluded that “*H. villosa* (Hedw. ex Kuntze) Dissing and Nannf.” is a later homonym, because Schaeffer (1774) proposed *H. villosa*, and following the priority principle was *Peziza fibrosa* Wallr. (an available name) the correct name, and not “*Macropodia chinensis* Velen.”, as was proposed by Nannfeldt and Holm (in Lundell et al., 1985). Also Korf (2008) indicated the Edwig’s figure as the lectotype of *H. fibrosa* and a exsiccate of Lundell, Nannfeldt and Holme as the epitype. On the other hand, Weber (1972) proposed *H. pallidula* as a new taxon based on “lacking any type of localized pigmentation in the tissues of the ascocarp.” We agree with H ffner (1987) and Abbott and Currah (1997) into consider *H. pallidula* as a synonym of *H. fibrosa*, because when we studied the holotype of this species we observed light brown pigments in the paraphyses, ectal excipulum and stipe outer layer, and yellowish pigments in the apothecial and stipe hyphal fascicles, as in *H. fibrosa*.

Helvella fibrosa can be confused with *H. cupuliformis*, *H. corium*, *H. macropus* and *H. rivularis*, for its cup-shaped apothecium and terete stipe, but *H. cupuliformis* has a smaller stipe (see

comments on *H. cupuliformis*), *H. corium* has a black apothecium, *H. macropus* has fusoid to subfusoid ascospores, and *H. rivularis* is a very small species (apothecium 3–8 mm diam.). Dissing (1966b) reported thinner paraphyses (5–6 µm wide at the apex) for *H. fibrosa*; our measures are consistent with those of Weber (1972) and Abbott and Currah (1997), who cited paraphyses 5–10 µm, and 5–7.5 µm, respectively.

Helvella griseoalba N.S. Weber, Michigan Bot. 11(4): 162, 1972.

Holotype: N.J. Smith 982, 10 June 1968, Douglas Lake, Univ. of Michigan Biol. Sta., Grapevine Point, Cheboygan Co., Michigan, USA (MICH, Barcode 14379).

Material studied: USA: holotype.

Comments: *Helvella griseoalba* is characterized by its cup-shaped apothecium, ribbed stipe, blunt-edged ribs, arriving from the half to a two-thirds of the apothecium sterile surface. In fresh conditions, *H. griseoalba* has a grey to grey-cinnamon apothecium, but in dry specimens is cream, light brown or greyish brown, causing confusion with *H. costifera*. Probably for this reason, Abbott and Currah (1997), following Häffner (1987), considered *H. griseoalba* as a synonym of *H. costifera*. Landeros et al. (2012) gave some reasons to keep both as separate taxa, and our phylogenetic data corroborate it. See description and more comments in Landeros et al. (2012).

Helvella macropus (Pers.) P. Karst., Bidr. Känn. Finl. Nat. Folk 19: 37, 1871

Type: Unknown.

= *H. brevis* (Peck) Harmaja, Karstenia 14: 104, 1974.

= *H. macropus* var. *brevis* Peck, Bull. Torrey Bot. Club 29: 74, 1902.

= ? *Peziza subclavipes* W. Phillips & Ellis, in Ellis and Everhart, North Amer. Fungi, n. 985, 1887.

Apothecium 5–50 mm diam., 3–20 mm high when cupulate, and 25–40 mm diam., 15–35 mm high when lobed. **Stipe** 5–75 x 2–10 mm, terete, even, sometimes with slight folds, but never with ribs, greyish brown to dark brown, pubescent. **Asci** 260–360 x 14–18 µm, aporhynchous. **Ascospores** 18–24 x 10–13.5 µm, fusoid to subfusoid, and smooth within ascus, subfusoid or slightly ellipsoid, and verrucose outside the asci, hyaline. **Paraphyses** 4–9 µm wide at the apex, thin-walled, yellowish brown to pale brown, pigmented deposits in the wall, in the cytoplasm, and sometimes encrusted on the wall. **Medullary excipulum** hyaline. **Ectal excipulum** yellowish brown to pale brown, pigmented deposits in the wall, and sometimes in the cytoplasm. **Stipe inner layer** hyaline. **Stipe outer layer** yellowish brown to pale brown, pigmented deposits in the wall, and sometimes in the cytoplasm. **Apothecial hyphal fascicles** 60–300 µm long, yellowish brown to pale brown, pigmented deposits in the wall, and sometimes in the cytoplasm; **stipe hyphal fascicles** 50–200 µm long, yellowish brown to pale brown, pigmented deposits in the wall, and sometimes in the cytoplasm. Pigments of all structures not visible under cotton blue, except the encrusted on the wall of the paraphyses and hyphal fascicles. All tissues rr–.

Material examined: MEXICO: Edo. de Mexico, Nevado de Toluca, Cerro Prieto, 18 October 2003, L. Guzmán-Dávalos 8998 (IBUG); Jalisco, Municipality of Bolaños, Sierra de los Huicholes, km 30 Bolaños-Tuxpan de Bolaños, 29 August 2004, O. Rodríguez 2652 (IBUG); Municipality of Poncitlán, Mezcala, Cerro Colorado, 6 September 2009, K. Terríquez 239 (IBUG); Municipality of San Sebastián del Oeste, in the way of Real Alto to Bufa, 24 August 2008, O. Rodríguez 3409 (IBUG), 15 August 2009, O. Rodríguez 3627 (IBUG); Municipality of Tecolotlán, Sierra de Quila, Árbol de la Lira, 20 September 2008, F. Landeros 3271 (IBUG); Municipality of Tequila, volcán de Tequila, 25 September

2009, F. Landeros 3347 (IBUG), km 12.3 road to antennas, without date, J.M. Canseco 12 (IBUG); Querétaro, Municipality of San Joaquín, Santa Ana, 9 Octubre 2010, F. Landeros 3396a, 3396b, 3396c (IBUG). USA: New Jersey, Newfield, 6 June 1882, W. Phillips 3651 [(NY, *Peziza subclavipes*, lectotype); New Jersey, Newfield, Ellis's collections, 27 Sep 1882, November 1882, September 1899 (NY).

Comments: *Helvella macropus* can be easily identified because together with *H. terrestris* are the only species with fusoid to subfusoid ascospores within the asci, having *H. terrestris* 50–65 x 12–15 µm ascospores (Landvik et al., 1999). Peck (1902) proposed *H. macropus* var. *brevis*, based on specimens with smaller ascoma, with darker hymenium, and very short stipe. Later, Harmaja (1974) elevated it as *H. brevis*, considering the characteristics given for Weber (1972) for the variety (ascospores size and ecological features) enough to separate it as a different species. This was followed by Abbott and Currah (1988). However, Weber (1972) wrote “it is possible that the distinctions between the two varieties merely represent different responses to environmental conditions”; observation which we agree with, because all these features are very variable. In fact, later Abbott and Currah (1997) reconsidered their position and placed *H. brevis* as a synonymy of *H. macropus*.

On another hand, Dissing and Nannfeldt (1966) proposed *Peziza subclavipes* W. Phillips & Ellis [(= *Macropodia subclavipes* (W. Phillips & Ellis) Rehm, = *Paxina subclavipes* (W. Phillips & Ellis) Seaver)] as a synonym of *H. macropus*, and were followed by Dissing (1966b) and Abbott and Currah (1997). However, this species was described with ellipsoid ascospores (Phillips and Ellis 1887; Rehm 1904; Seaver 1942). Abbott and Currah (1997) mentioned that “[t]here are several specimens of *P. subclavipes* from Ellis collections, as well as several packets of Ellis labeled as North American Fungi Number 985 (NY). Of these, the specimen ‘Phillips, June 1882’ annotated by Ellis is the oldest collection from which the species was originally described. It is selected as a lectotype of *Peziza subclavipes*. Some specimens of *H. chinensis* (q.v.) were distributed as *Peziza subclavipes* in Ellis & Everhart Fungi Columbiani 1219.”, i.e., Ellis labeled some specimens as *P. subclavipes* which really correspond to *H. macropus* and others to *H. fibrosa* (= *H. chinensis*), and Abbott and Currah (1997) choose from them a specimen (Phillips, June 1882) as lectotype (which has fusoid to subfusoid ascospores). It is unlikely Phillips & Ellis used that specimen to describe *P. subclavipes*, because as we mentioned above, they described ellipsoid ascospores to their species. In conclusion, we think *P. subclavipes* cannot be considered as synonym of *H. macropus*, because Ellis mislabeled some specimens of *H. macropus* and *H. fibrosa* as *P. subclavipes*.

Helvella robusta S.P. Abbott, in Abbott & Currah, Mycotaxon 33: 242, 1988.

Holotype: R.M. Danielson 459, 30 August 1972, Nose Hill area, Calgary, Canada (DAOM, 143869).

Material examined: CANADA: holotype.

Comments: *Helvella robusta* is easy to recognize for its irregularly cupulate centrally depressed, to irregularly bi-lobed apothecium, which can cover the stipe. Abbott and Currah (1988) placed this species within Sect. *Acetabulum* Dissing, and later in their subgenus *Leucomelaenae* (Dissing) S.P. Abbott, mainly for its prominently ribbed stipe. However, in this work these suprageneric taxa were not supported. Besides its peculiar apothecium shape, the specimens of *H. robusta* are rr+ in the apothecial medullary excipulum and in the stipe inner layer, and moderately rr+ in the stipe outer layer, as some members of Sect. *Elasticae*, but it is probably due a convergence, because members of this section have lobed apothecium and terete well-defined stipe. See more on *H. robusta* in Landeros et al. (2012).

Helvella subglabra N.S. Weber, Michigan Bot. 11(4): 179, 1972.

Holotype: N.J. Smith 2145, 13 October 1968, Stinchfield Woods, near Dexter, Washtenaw Co., Michigan, USA (MICH, Barcode 14381).

Material examined: USA: holotype.

Comments: *Helvella subglabra* was proposed by Weber (1972) as a different species of *H. atra* based mainly on: 1) *H. subglabra* has hyphae projecting on the apothecium sterile surface when young, while *H. atra* “is truly glabrous”, 2) *H. subglabra* has “[h]ymenial surface dark gray to nearly black when young, gray to dark gray in age,” i.e., never black as in *H. atra*, and 3) dark gray to drab with whitish base stipe in *H. subglabra*, never black as in *H. atra*. Häffner (1987) considered such features as a result of the variation of *H. atra*, because he saw that other species such as *H. albella*, *H. lacunosa*, and *H. latispora* also show such intraspecific variation, for this reason he considered *H. subglabra* as a synonym of *H. atra*, and this was followed by Abbott and Currah (1997). Landeros et al. (2012) agree with the characteristics Weber (1972) gave to recognize *H. subglabra* from *H. atra*, and they provided two more reasons to keep both species as independent taxa: 1) tissues of the ascoma are negative under Melzer’s reagent in *H. atra*, while in *H. subglabra* the apothecial medullary excipulum is weakly reddish, and the stipe inner layer is strongly reddish; and 2) brown pigment in the cell wall of the paraphyses, ectal excipulum, and stipe outer layer is visible under cotton blue in *H. atra* while in *H. subglabra* is not visible. See description and more comments in Landeros et al. (2012).

Helvella ulvinenii Harmaja, Karstenia 19(2): 42, 1979

Holotype: H. Harmaja 25 Aug 1979, Kilpisjärvi, NE slope of W peak of fjeld Pikku-Malla, alt. ca. 650 m., par. Enontekiö, prv. Enontekiön Lappi, Finland (Holotype H).

Material examined: FINLAND: holotype.

Comments: *Helvella ulvinenii* is characterized by its cup-shaped apothecium, costate stipe, and ribs not reaching or only one quarter of the apothecium. Species with it might be confused are *H. solitaria* and *H. verruculosa*, because both have similar features. Landeros et al. (2012) mentioned the features which *H. ulvinenii* can be distinguish from *H. solitaria*: “1) a darker sterile surface in *H. ulvinenii* that is never grayish, 2) the stipe outer layer and hyphal fascicles are hyaline in *H. ulvinenii* and light brownish (on the walls) in *H. solitaria*, and 3) the apothecial hyphal fascicles pigments are deposited in the wall in *H. solitaria* and occur both in the cytoplasm and in the cell wall in *H. ulvinenii*.” Landeros et al. (2012) also mentioned the main features to recognize *H. ulvinenii* of *H. verruculosa*: 1) longer ascospores in *H. verruculosa*; 2) pigmented stipe hyphal fascicles in *H. verruculosa* and hyaline in *H. ulvinenii*. See description and more comments in Landeros et al. (2012).

Discussion

Infrageneric classification of *Helvella*

Any of the previous infrageneric classifications is completely supported in our analysis, only some sections. In our results the majority of the monophyletic clades are defined by more than one morphologic feature (except the clade representing Sect. *Leucomelaenae*, which is characterized only by its asci type). Figure 3 and 4 shows that the main features used by Dissing (1966b), Webber (1972), and Abbott and Currah (1997) to define suprageneric taxa (pubescence and apothecium shape) are present throughout the cladogram, and only the combination of them can be used as the diagnostic characteristics of the clades.

The analysis combining DNA sequences, morphological and chemical data generated trees with better supported clades, which demonstrates the importance of the incorporation of morphological data in phylogenetic analysis. We could recover four sections previously proposed based only on morphological data: 1) *Leucomelaenae* Dissing sensu N.S. Weber, with the following species: *H. crassitunicata*, *H. leucomelaena*, and *Helvella* sp. 1; 2) *Elasticae* Dissing sensu N.S. Weber, harboring to: *H. albella*, *H. compressa*, *H. elastica*, *H. latispora*, *H. leucopus*, and *H. stevensii* (= *H. connivens*), 3) *Helvella* with: *H. crispa*, *H. palustris*, and *H. maculata*, and 4) *Lacunosae* Dissing, enclosing: *H. fusca*, *H. lactea*, *H. lacunosa*, *H. palustris*, *H. philonotis*, *H. phlebophora*, *H. sulcata*, and *Helvella* sp. 2. In this study, it was not possible to determine the infrageneric relationships of the following species: *H. acetabulum*, *H. costifera*, *H. griseoalba*, *H. robusta*, and *H. ulvinenii* of Sect. *Acetabulum* Dissing sensu N.S. Weber; *H. atra*, *H. ephippium*, and *H. subglabra* of Sect. *Ephippium* Dissing sensu N.S. Weber, and *H. cupuliformis*, *H. fibrosa* (= *H. pallidula*), and *H. macropus* of Sect. *Macropodes* Dissing sensu N.S. Weber.

In both analyses, molecular and molecular-morphological (figs. 3–4), we obtained two supported clades, one clade of species with aporhynchous asci, and the other of species with pleurorhynchous asci. There is enough evidence to divided the genus *Helvella* into two subgenera, based on the ascus type: Subgen. *Helvella* (with pleurorhynchous asci), and Subgen. *Leucomelaenae* (with aporhynchous asci).

Helvella Subgen. *Helvella*

Mycobank:

≠ Subgenus *Helvella*, in Abbott & Currah, Mycotaxon 62: 54, 1997

Asci pleurorhynchous, i.e., ascus base forked, because a crozier is formed at the base.

Type species: *Helvella crispa* (Scop.) Fr., Syst. Myc. (Lundae) 2 (1): 14, 1822

Our Subgen. *Helvella* is different to the one proposed by Abbott and Currah (1997), because for them it is limited only to species with lobed apothecium and costate or lacunose stipe. Phylogenetically supported sections included in this subgenus are: 1) *Elasticae* Dissing emend. N.S. Weber, 2) *Helvella*, and 3) *Lacunosae* Dissing. From several species belonging to this subgenus its affinity could not be elucidated, they are: *H. acetabulum*, *H. atra*, *H. costifera*, *H. cupuliformis*, *H. ephippium*, *H. griseoalba*, *H. macropus*, *H. pallidula*, *H. robusta*, *H. subglabra*, and *H. ulvinenii*. It is necessary to use other DNA regions in order to solve their affinity. The morphological features that support the major monophyletic clades within Subgen. *Helvella* are described in the taxonomic part under each section.

Helvella Subgen. *Leucomelaenae* S.P. Abbott emend. Landeros & Guzm.-Dáv.

Mycobank:

Asci aporhynchous, i.e., ascus base simple, because no crozier is formed at the base.

Type species: *Helvella leucomelaena* (Pers.) Nannf., in Lundell & Nannfeldt, Fungi exsicc. upsal. 21: 952, 1941.

In our concept, Subgen. *Leucomelaenae* is characterized because its members have aporhynchous asci, while Abbott and Currah (1997) defined it for species with cup-shaped apothecium and costate stipe, no matter how the ascus base was; they considered this feature only to define the Sect. *Leucomelaenae*. We only recognize one section: *Leucomelaenae* Dissing sensu N.S. Weber.

Species diversity and new species in *Helvella*

Discussion on the relationships amongst species inferred from the molecular and morphological data are included under the commentaries of each species, in the taxonomic section.

Eliminating synonyms and species that have been transferred to other genera, and including those presented here, 36 species are recognized for Europe (Dissing 1966b; Häffner 1987; Calonge and Arroyo 1990; Dissing et al. 2000; Van Vooren 2010), 30 for North America (Weber 1972; Abbott and Currah 1997), 20 for Asia (Kaushal 1991; Zhuang 1995), three for South America (Dissing 1966b; Wright and Albertó 2006; Gamundi 2010) and for Africa (Dissing 1966b), and two species for Australia (Rifai 1968). The most widely distributed are *H. leucomelaena* which is the only species present on every continent, and *H. lacunosa* and *H. solitaria* located in four continents. On the other hand, species with restricted distribution are *H. dovrensis*, *H. fusca*, *H. latispora*, *H. paraphysitorquata*, *H. ulvinenii*, *Helvella* sp. 1 and *Helvella* sp. 2, only reported from Europe, *H. compressa*, *H. crassitunicata*, *H. griseoalba*, *H. maculata* and *H. robusta* exclusively known from America, *H. papuensis* just recorded from a tropical region of Papua New Guinea, and *H. aestivalis*, *H. dovrensis*, and *H. verruculosa* with an arctic and alpine distribution. It is necessary to examine the *Helvella* species that have been described from Asia, in order to determine their status.

Amount of variation.

We do not find an interval in the amount of variation in DNA sequences within individuals of the same species or between species, which could serve as a tool in their delimitation. In some cases, the intraspecific variation of the specimens of a species exceeded the interspecific variation of another species, this also was observed by Zhao et al. (2011), in fact, they mentioned that it “may lead to misidentifications”. Reviewing the matrix, we saw that although the number of different bases between individuals of the same species, and the variation of one species with respect to another may be similar, the type of variation, i.e., the relation transitions-transversions can be dissimilar. Between individuals of the same species usually the variation is due to transitions, while among species with few different bases, the transversions are more common. On the other hand, we also noted that among individuals of the same species the variation is in specific regions, as well as in closely related species, while in distant species such variation normally occurs in different regions. In conclusion, the criteria that we think are useful in the delimitation of the species, when DNA sequences are used are: 1) variation in number of bases, 2) the type of variation, and 3) where the variation is.

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Appendix I. Codification of morphological and chemical characters

- 1.- Apothecium shape when mature: (0) cup-shaped, (1) lobed, (2) auriculoid
- 2.- Apothecium margin: (0) free, (1) attached to the stipe
- 3.- Apothecium sterile surface: (0) glabrous to subpubescent, (1) pubescent
- 4.- Ribs on the apothecium sterile surface: (0) missing or reaching only up to $\frac{1}{4}$ of the surface, (1) reaching from $\frac{1}{4}$ to the apothecium edge
- 5.- Bifurcated ribs on the apothecium sterile surface: (0) absent, (1) present
- 6.- Stipe shape: (0) even, (1) ribbed
- 7.- Type of ribs on the stipe: (0) only longitudinal ribs, (1) with longitudinal and transversal ribs (forming cavities, lacunose)
- 8.- Edge of the ribs on the stipe: (0) sharp, (1) blunt
- 9.- Stipe surface: (0) glabrous to subpubescent, (1) subpubescent to pubescent
- 10.- Stipe color: (0) dark tones, (1) light tones
- 11.- Ascus type: (0) pleurorhynchous, (1) aporhynchous
- 12.- Reaction to Melzer's solution of apothecium medullary excipulum: (0) negative, (1) hemiamyloid
- 13.- Reaction to Melzer's solution of apothecium ectal excipulum: (0) negative, (1) hemiamyloid
- 14.- Reaction to Melzer's solution of stipe inner layer: (0) negative, (1) hemiamyloid
- 15.- Reaction to Melzer's solution of stipe outer layer: (0) negative, (1) hemiamyloid

Appendix II. Matrix of morphological and chemical data

	111111		111111
	123456789012345		123456789012345
<i>Wynnella silvicola</i> He328	000000000000000	<i>H. lacunosa</i> He323	210101101000000
<i>H. acetabulum</i> He191	101101110011110	<i>H. lacunosa</i> U42681	210101100010000
<i>H. acetabulum</i> AJ972414	101101110011110	<i>H. leucomelaena</i> He287	101000010100000
<i>H. albella</i> AJ972411	20001??00010000	<i>H. leucomelaena</i> He324	101000010100000
<i>H. atra</i> AJ972413	20?01???0????0	<i>H. macropus</i> He208	10101??11000001
<i>H. calyx</i> He286	101000010100000	<i>H. macropus</i> He321	20101??11000001
<i>H. compressa</i> He162	20101??10011100	<i>H. macropus</i> He322	20101??11000001
<i>H. connivens</i> He284	20101??10010100	<i>H. maculata</i> He165	201101110000000
<i>H. costifera</i> He292	101100010000000	<i>H. melaleuca</i> He273	101000010100000
<i>H. costifera</i> He301	101100010000000	<i>H. pallidula</i> He168	10101??10000000
<i>H. costifera</i> He302	101100010000000	<i>H. robusta</i> He163	101101110010110
<i>H. aff. costifera</i> He193	101100010000000	<i>H. stevensii</i> He281	20101??10010100
<i>H. aff. costifera</i> He226	101100010000000	<i>H. subglabra</i> He166	20001??01010100
<i>H. aff. costifera</i> He257	101100010000000	<i>H. sulcata</i> He274	210100101010000
<i>H. crispa</i> He177	201001110000000	<i>H. aff. sulcata</i> He224	210100100000000
<i>H. crispa</i> He230	201000110000000	<i>H. aff. sulcata</i> He320	210100101000000
<i>H. crispa</i> AY789399	201?0?1100????0	<i>H. ulvinenii</i> He248	101000010000000
<i>H. cupuliformis</i> He258	10101??10000000	<i>Helvella</i> sp. 1 He296	100000000100000
<i>H. elastica</i> He189	20001??00010100	<i>Helvella</i> sp. 1 He297	100000000100000
<i>H. ephippium</i> He221	20101??11000000	<i>Helvella</i> sp. 2 He289	200000000000100
<i>H. fusca</i> He270	210101100000000	<i>Helvella</i> sp. 2 He290	200000000000100
<i>H. griseoalba</i> He164	101100000000000	<i>Peziza subclavipes</i> He315	10101??11000001
<i>H. lacunosa</i> He244	210101100010000		

Appendix III. Variation, measured in bases, between specimens of the sequenced species of *Helvella*.

Species	<i>Wynnella silvicola</i> He328	<i>H. acetabulum</i> He191	<i>H. acetabulum</i> AJ972414	<i>H. albella</i> AJ972411	<i>H. atra</i> AJ972413	<i>H. calyx</i> He286	<i>H. compressa</i> He162	<i>H. connivens</i> He284	<i>H. costifera</i> He292	<i>H. costifera</i> He301	<i>H. costifera</i> He302	<i>H. aff. costifera</i> He193	<i>H. aff. costifera</i> He226	<i>H. aff. costifera</i> He257	<i>H. crispa</i> He177	<i>H. crispa</i> He230	<i>H. crispa</i> AY789399	<i>H. cupuliformis</i> He258	<i>H. elastica</i> He189	<i>H. ephippium</i> He221	<i>H. fusca</i> He270	<i>H. griseoalba</i> He164	<i>H. lacunosa</i> He244	<i>H. lacunosa</i> He323	<i>H. lacunosa</i> UA2881	<i>H. leucomelaena</i> He287	<i>H. leucomelaena</i> He324	<i>H. macropus</i> He208	<i>H. macropus</i> He321	<i>H. macropus</i> He322	<i>H. maculata</i> He165	<i>H. melaleuca</i> He273	<i>H. pallidula</i> He168	<i>H. robusta</i> He163	<i>H. stevensii</i> He281	<i>H. subglabra</i> He166	<i>H. sulcata</i> He274	<i>H. aff. sulcata</i> He224	<i>H. aff. sulcata</i> He320	<i>H. ubvnerii</i> He248	<i>Helvella</i> sp. 1 He296	<i>Helvella</i> sp. 1 He297	<i>Helvella</i> sp. 2 He289	<i>Helvella</i> sp. 2 He290	<i>Peziza subclavipes</i> He315
<i>Wynnella silvicola</i> He328	-	61	56	54	56	51	53	50	53	52	51	54	55	55	52	54	53	51	51	50	59	51	53	58	56	54	56	50	50	50	52	51	51	54	50	53	60	56	54	57	51	56	56	56	50
<i>H. acetabulum</i> He191	61	-	7	16	17	29	13	15	16	15	16	18	17	17	19	18	17	20	16	20	29	15	32	28	30	28	29	20	20	20	17	29	21	16	15	17	21	19	19	27	34	37	21	21	20
<i>H. acetabulum</i> AJ972414	56	7	-	17	15	25	14	14	14	13	12	15	13	13	18	18	17	17	15	17	27	11	28	24	27	26	25	17	17	17	15	25	18	12	14	15	18	18	16	24	30	32	16	16	17
<i>H. albella</i> AJ972411	54	16	17	-	17	31	9	7	12	11	12	16	15	15	21	22	21	14	4	14	24	13	29	25	27	32	30	14	14	14	19	31	15	14	7	16	17	16	16	20	30	33	15	15	14
<i>H. atra</i> AJ972413	56	17	15	17	-	30	14	15	12	11	12	16	17	17	23	24	23	17	16	18	27	13	25	27	25	27	28	16	16	16	22	30	18	16	15	12	24	21	19	27	29	32	21	21	16
<i>H. calyx</i> He286	51	29	25	31	30	-	29	27	28	27	26	28	27	27	33	32	31	28	29	15	39	25	40	40	40	10	8	30	30	30	33	0	29	26	27	25	35	32	30	37	22	27	33	33	30
<i>H. compressa</i> He162	53	13	14	9	14	29	-	5	11	10	11	14	14	14	16	17	16	15	7	13	26	11	27	25	27	30	31	15	15	20	29	16	13	5	16	20	17	17	21	28	31	16	16	15	
<i>H. connivens</i> He284	50	15	14	7	15	27	5	-	9	8	9	13	12	12	17	18	17	13	5	11	25	10	28	25	27	28	29	13	13	13	18	27	12	11	0	16	18	14	14	20	24	27	14	14	13
<i>H. costifera</i> He292	53	16	14	12	12	28	11	9	-	1	2	10	9	9	17	18	17	14	10	14	22	9	25	24	24	29	28	14	14	14	16	28	15	8	9	13	17	13	11	21	25	28	13	13	14
<i>H. costifera</i> He301	52	15	13	11	11	27	10	8	1	-	1	9	8	8	16	17	16	13	9	13	21	8	24	23	23	28	27	13	13	13	15	27	14	7	8	12	16	12	10	20	24	27	12	12	13
<i>H. costifera</i> He302	51	16	12	12	12	26	11	9	2	1	-	8	7	7	17	18	17	12	10	12	20	7	23	22	22	27	26	12	12	12	14	26	13	6	9	11	15	11	9	19	23	26	11	11	12
<i>H. aff. costifera</i> He193	54	18	15	16	16	28	14	13	10	9	8	-	1	1	20	19	18	14	14	13	23	5	27	26	27	29	30	12	12	12	15	28	15	6	13	17	21	16	14	21	27	30	17	17	12
<i>H. aff. costifera</i> He226	55	17	13	15	17	27	14	12	9	8	7	1	-	0	21	20	19	13	13	12	24	6	28	25	26	28	29	11	11	11	14	27	14	5	12	16	20	16	14	22	26	29	16	16	11
<i>H. aff. costifera</i> He257	55	17	13	15	17	27	14	12	9	8	7	1	0	-	21	20	19	13	13	12	24	6	28	25	26	28	29	11	11	11	14	27	14	5	12	16	20	16	14	22	26	29	16	16	11
<i>H. crispa</i> He177	52	19	18	21	23	33	16	17	17	16	17	20	21	21	-	3	2	25	19	19	27	18	31	30	30	36	36	25	25	25	12	33	24	20	17	25	23	22	20	28	34	37	21	21	25
<i>H. crispa</i> He230	54	18	18	22	24	32	17	18	18	17	18	19	20	20	3	-	1	26	20	20	28	17	34	33	33	35	35	26	26	26	13	32	27	20	18	27	24	23	21	29	35	38	22	22	26
<i>H. crispa</i> AY789399	53	17	17	21	23	31	16	17	17	16	17	18	19	19	2	1	-	25	19	19	27	16	33	32	32	34	34	25	25	25	12	31	26	19	17	26	23	22	20	28	34	37	21	21	25
<i>H. cupuliformis</i> He258	51	20	17	14	17	28	15	13	14	13	12	14	13	13	25	26	25	-	12	12	27	11	28	24	26	29	30	10	10	10	19	28	3	12	13	13	20	18	17	22	25	28	18	18	10
<i>H. elastica</i> He189	51	16	15	4	16	29	7	5	10	9	10	14	13	13	19	20	19	12	-	12	26	11	29	26	28	30	31	14	14	14	19	29	13	12	5	15	19	17	17	19	26	31	15	15	14
<i>H. ephippium</i> He221	50	20	17	14	18	25	13	11	14	13	12	13	12	12	19	20	19	12	12	-	25	11	29	26	26	33	34	12	12	17	15	11	12	11	17	22	19	19	23	29	32	18	18	12	

<i>H. fusca</i> He270	59	29	27	24	27	39	26	25	22	21	20	23	24	24	27	28	27	27	26	25	-	23	30	32	32	43	40	26	26	26	29	39	27	24	25	29	23	20	20	30	41	44	24	24	26
<i>H. griseoalba</i> He164	51	15	11	13	13	25	11	10	9	8	7	5	6	6	18	17	16	11	11	11	23	-	25	25	27	24	27	11	11	11	14	25	12	5	10	14	17	14	12	16	24	27	13	13	11
<i>H. lacunosa</i> He244	53	32	28	29	25	40	27	28	25	24	23	27	28	28	31	34	33	28	29	29	30	25	-	8	8	42	39	24	24	24	32	40	27	28	28	26	29	25	23	36	43	46	28	28	24
<i>H. lacunosa</i> He323	58	28	25	25	27	40	25	25	24	23	22	26	25	25	30	33	32	24	26	26	32	25	8	-	8	43	39	20	20	20	28	40	23	25	25	24	26	24	22	36	43	46	26	26	20
<i>H. lacunosa</i> U42681	56	30	27	27	25	40	27	27	24	23	22	27	26	26	30	33	32	26	28	26	32	27	8	8	-	43	39	22	22	22	28	40	25	27	27	24	26	26	24	38	43	46	28	28	22
<i>H. leucomelaena</i> He287	54	28	26	32	27	10	30	28	29	28	27	29	28	28	36	35	34	29	30	33	43	24	42	43	43	-	10	32	32	32	34	10	30	27	28	26	35	33	31	38	21	26	33	33	32
<i>H. leucomelaena</i> He324	56	29	25	30	28	8	31	29	28	27	26	30	29	29	36	35	34	30	31	34	40	27	39	39	39	10	-	33	33	33	33	8	31	28	29	23	34	32	30	37	26	31	32	32	33
<i>H. macropus</i> He208	50	20	17	14	16	30	15	13	14	13	12	12	11	11	25	26	25	10	14	12	26	11	24	20	22	32	33	-	0	0	19	30	11	12	13	15	21	19	17	25	28	31	19	19	0
<i>H. macropus</i> He321	50	20	17	14	16	30	15	13	14	13	12	12	11	11	25	26	25	10	14	12	26	11	24	20	22	32	33	0	-	0	19	30	11	12	13	15	21	19	17	25	28	31	19	19	0
<i>H. macropus</i> He322	50	20	17	14	16	30	15	13	14	13	12	12	11	11	25	26	25	10	14	12	26	11	24	20	22	32	33	0	0	-	19	30	11	12	13	15	21	19	17	25	28	31	19	19	0
<i>H. maculata</i> He165	52	17	15	19	22	33	20	18	16	15	14	15	14	14	12	13	12	19	19	17	29	14	32	28	28	34	33	19	19	19	-	33	14	13	18	19	21	20	18	28	33	36	19	19	19
<i>H. melaleuca</i> He273	51	29	25	31	30	0	29	27	28	27	26	28	27	27	33	32	31	28	29	15	39	25	40	40	40	10	8	30	30	30	33	-	29	26	27	25	35	32	30	37	22	27	33	33	30
<i>H. pallidula</i> He168	51	21	18	15	18	29	16	12	15	14	13	15	14	14	24	27	26	3	13	11	27	12	27	23	25	30	31	11	11	11	14	29	-	12	12	13	21	20	18	24	26	31	19	19	11
<i>H. robusta</i> He163	54	16	12	14	16	26	13	11	8	7	6	6	5	5	20	20	19	12	12	12	24	5	28	25	27	27	28	12	12	12	13	26	12	-	11	13	19	15	13	21	25	28	15	15	12
<i>H. stevensii</i> He281	50	15	14	7	15	27	5	0	9	8	9	13	12	12	17	18	17	13	5	11	25	10	28	25	27	28	29	13	13	13	18	27	12	11	-	16	18	14	14	20	24	27	14	14	13
<i>H. subglabra</i> He166	53	17	15	16	12	25	16	16	13	12	11	17	16	16	25	27	26	13	15	17	29	14	26	24	24	26	23	15	15	15	19	25	13	13	16	-	21	20	18	22	27	32	20	20	15
<i>H. sulcata</i> He274	60	21	18	17	24	35	20	18	17	16	15	21	20	20	23	24	23	20	19	22	23	17	29	26	26	35	34	21	21	21	21	35	21	19	18	21	-	12	11	26	35	38	4	4	21
<i>H. aff. sulcata</i> He224	56	19	18	16	21	32	17	14	13	12	11	16	16	16	22	23	22	18	17	19	20	14	25	24	26	33	32	19	19	19	20	32	20	15	14	20	12	-	2	21	32	35	12	12	19
<i>H. aff. sulcata</i> He320	54	19	16	16	19	30	17	14	11	10	9	14	14	14	20	21	20	17	17	19	20	12	23	22	24	31	30	17	17	17	18	30	18	13	14	18	11	2	-	23	30	33	11	11	17
<i>H. ulvinenii</i> He248	57	27	24	20	27	37	21	20	21	20	19	21	22	22	28	29	28	23	19	23	30	16	36	36	38	38	37	25	25	25	28	37	24	21	20	22	26	21	23	-	36	41	23	23	25
<i>Helvella</i> sp. 1 He296	51	34	30	30	29	22	28	24	25	24	23	27	26	26	34	35	34	25	26	29	41	24	43	43	43	21	26	28	28	28	33	22	26	25	24	27	35	32	30	36	-	5	31	31	28
<i>Helvella</i> sp. 1 He297	56	37	32	33	32	27	31	27	28	27	26	30	29	29	37	38	37	28	31	32	44	27	46	46	46	26	31	31	31	31	36	27	31	28	27	32	38	35	33	41	5	-	34	34	31
<i>Helvella</i> sp. 2 He289	26	21	16	15	21	33	16	14	13	12	11	17	16	16	21	22	21	18	15	18	24	13	28	26	28	33	32	19	19	19	19	33	19	15	14	20	4	12	11	23	31	34	-	0	19
<i>Helvella</i> sp. 2 He290	26	21	16	15	21	33	16	14	13	12	11	17	16	16	21	22	21	18	15	18	24	13	28	26	28	33	32	19	19	19	19	33	19	15	14	20	4	12	11	23	31	34	0	-	19
<i>Peziza subclavipes</i> He315	50	20	17	14	16	30	15	13	14	13	12	12	11	11	25	26	25	10	14	12	26	11	24	20	22	32	33	0	0	0	19	30	11	12	13	15	21	19	17	25	28	31	19	19	-

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Sinopsis del género *Helvella* (Ascomycota: Fungi) en México

Synopsis of the genus *Helvella* (Ascomycota: Fungi) in Mexico

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Resumen. Se hace una sinopsis taxonómica del género *Helvella* en México, con base en ejemplares depositados en los herbarios ENCB, FCME e IBUG, y algunos de XAL. En total se reconocen 18 especies de *Helvella* para México. Se reporta por primera vez para la micobiota mexicana a *H. compressa*. De *H. adhaerens*, *H. corium*, *H. kichneri*, *H. latispora*, *H. leucopus*, *H. leucopus* var. *populina*, *H. pityophila*, *H. queletiana*, *H. queletii*, *H. salvatierrae*, *H. sogarii* y *H. subglabra* especies previamente citadas para el país, no se encontró el ejemplar de referencia o éste estaba incorrectamente determinado, por lo que no se puede confirmar su presencia en México. Se incluyen comentarios taxonómicos para las especies que se reconoce prosperan en México, así como algunas observaciones para las que no se desarrollan en el país. Se presenta una clave dicotómica para las especies que crecen en México y algunas afines.

Palabras clave: registro nuevo, ejemplares tipo, descripciones originales

Abstract. A taxonomic synopsis of the genus *Helvella* in Mexico, based on specimens deposited in the herbaria ENCB, FCME, and IBUG, and some from XAL, is done. A total of 18 species of *Helvella* are known from Mexico. *Helvella compressa* is reported for the first time for Mexican mycobiota. Of the species previously cited for Mexico, *H. adhaerens*, *H. corium*, *H. kichneri*, *H. latispora*, *H. leucopus*, *H. leucopus* var. *populina*, *H. pityophila*, *H. queletiana*, *H. queletii*, *H. salvatierrae*, *H. sogarii*, *H. subglabra*, and *H. sulcata*, there was no reference specimen or it was incorrectly determined, so we cannot confirm its presence in Mexico. Taxonomic comments for species that thrive in Mexico are included, as well as some observations for some still not yet found in the country. A key to the species that grow in Mexico and some related is presented.

Key words: new record, type specimens, original descriptions

Introducción

El género *Helvella* L. tiene una distribución mundial, pero casi es exclusivo de regiones templadas del hemisferio norte (Dissing, 1966b; Abbott y Currah, 1997). La literatura sobre el género en el mundo es considerable (Nannfeldt 1937; Dissing, 1964, 1966a, 1966b; Dissing y Nannfeldt, 1966; Kempton 1970; Weber, 1972, 1975; Harmaja, 1974, 1977a, 1977b, 1978, 1979; Häffner, 1987; Abbott y Currah, 1988, 1997; Calonge y Arroyo 1990; Kaushal, 1991; Landeros et al., 2012). De acuerdo con el Diccionario de los Hongos se estima que existen aproximadamente 52 especies (Kirk et al., 2008).

En México el género ha sido motivo de varios estudios (Nieto-Roaro, 1941; Gómez y Herrera, 1965; Medel y Calonge, 2004; Vite-Garín et al., 2006). Medel y Calonge (2004) registraron 14 especies, mientras que Vite-Garín et al. (2006) estimaron la presencia de 20 especies para el país.

Se hizo una revisión de ejemplares depositados en los herbarios ENCB, FCME e IBUG y algunos de XAL, con el objetivo de contribuir al conocimiento de las especies que prosperan en México, y generar una clave dicotómica para su determinación.

Materiales y métodos

Con base en los trabajos, mencionados anteriormente, que se han publicado sobre *Helvella* en México, se hizo una selección de 107 especímenes de los herbarios ENCB, FCME, IBUG y XAL. Se revisaron siguiendo las técnicas descritas por Landeros et al. (2012), que consisten básicamente en hacer cortes a mano de los ascomas, colocarlos en alcohol al 70%, y posteriormente hidratarlos con agua, reactivo de Melzer o azul de algodón. La reacción rr+ o hemiamiloide es cuando la estructura cambia a color café-anaranjado con el reactivo de Melzer. Algunas especies fueron comparadas con el espécimen tipo (referido como material adicional estudiado), además se revisaron las descripciones originales de las especies en todos los casos para su correcta determinación.

La terminología aquí usada es la descrita por Landeros et al. (2012), excepto los términos que definió Weber (1972) para los tipos de asca: “aporhynchous” y “pleurorhynchous”, ya que sólo el término “aporhynchous” tiene una traducción en español que es “erostrado” (Berger, 1980). Pero tal palabra no existe en el diccionario de la Real Academia de la Lengua Española (RAE, 2012), por lo que se propone aquí para fines prácticos, una versión castellanizada de los mismos, quedando por lo tanto “aporhynchous” como “aporrincosa”, y “pleurorhynchous” como “pleurorrincosa”.

Resultados

Se determinaron 18 especies de *Helvella*: *H. acetabulum* (L.) Quél., *H. albella* Quél., *H. atra* J. König, *H. compressa* (Snyder) N.S. Weber, *H. costifera* Nannf., *H. crispa* (Scop.) Fr., *H. cupuliformis* Dissing & Nannf., *H. elastica* Bull., *H. ephippium* Lév., *H. fibrosa* (Wallr.) Korf, *H. lactea* Boud., *H. lacunosa* Afzel., *H. leucomelaena* (Pers.) Nannf., *H. macropus*, (Pers.) P. Karst., *H. pezizoides* Afzel., *H. solitaria* P. Karst., *H. stevensii* Peck., y *H. sulcata* Afzel. Las especies: *H. adhaerens* Peck, *H. corium* (O. Weberb.) Masee, *H. kichneri* Manzi, *H. latispora* Boud., *H. leucopus* Pers., *H. leucopus* var. *populina* I. Arroyo & Calonge, *H. pityophila* Boud., *H. queletiana* Sacc. & Traverso, *H. queletii* Bres., *H. salvatierrae* Manzi, *H. sogarii* Manzi, y *H. subglabra* N.S. Weber, que previamente habían sido citadas para México, se encuentran en alguno de los siguientes casos: 1) no se encontró el ejemplar de referencia, 2) estaba incorrectamente determinado, 3) es sinónimo de otra especie, 4) el nombre de la especie no se publicó en forma válida. *Gyromitra infula* (Schaeff.) Quél. que fue considerada por muchos autores del siglo pasado como *H. infula* Schaeff., no se considera en el presente trabajo por pertenecer a otro género.

Con el propósito de no repetir información, a continuación sólo se hacen comentarios sobre cómo reconocer a las especies de *Helvella* que se confirmó prosperan en México, lo anterior debido a que éstas ya han sido ampliamente descritas en otros trabajos (Dissing, 1966b; Weber, 1972; Abbott y Currah, 1997; Landeros et al., 2012). En las especies sólo se indican los sinónimos que han sido mencionados en la literatura mexicana. Además se discuten las especies que no se pudo confirmar su presencia y se incluye una clave dicotómica para la determinación de las que prosperan en México y de algunas cercanas con las cuales pudieran confundirse, pero que no se conocen para el país.

Comentarios de las especies de *Helvella* que crecen en México

Helvella acetabulum (L.) Quél., Hyménomycètes (Alençon): 102, 1874
= *Paxina acetabulum* (L.) Kuntze, Revis. gen. pl. (Leipzig) 2: 864, 1891

Comentarios taxonómicos: Esta especie se caracteriza por presentar el apotecio en forma de copa, el estípote costillado, con las costillas llegando desde una cuarta parte hasta el borde de la superficie estéril del apotecio, con el borde de las costillas afilado, el estípote subpubescente (fascículos hifales hasta 50 μm de largo), y el tejido medio del estípote rr+. Se puede confundir con *H. costifera*, que presenta rasgos similares, pero se distingue por el borde de las costillas redondeado, el estípote pubescente (fascículos hifales de 20 a 80 μm de largo), y el tejido medio del estípote rr-. Es común en los bosques de coníferas de México y ha sido ampliamente citada (e.g., Pompa-González y Cifuentes, 1991; Esqueda-Valle et al., 1992; Medel y Calonge, 2004; Vite-Garín et al., 2006), algunas veces como *Paxina acetabulum* (e.g., Guzmán, 1977; Bautista et al., 1986; Guzmán-Dávalos et al., 2001). En el trabajo de Nieto-Roaro (1941) en la figura 4, el ascoma izquierdo, referido como *H. lacunosa*, se trata claramente de *H. acetabulum*.

Material revisado: GUANAJUATO: Sierra de Santa Rosa, Cañada de Llano Largo, 9 agosto 1995, Pérez, Valdovinos, Villanueva y Montañez 96 (FCME 7760). GUERRERO: Taxco, Parque cerro del Huizteco, 15 septiembre 1998, V. Patiño-Conde 15 (FCME 9804). JALISCO: Municipio de Tequila, volcán de Tequila, km 11 del camino del pueblo de Tequila a las antenas, 25 septiembre 2009, F. Landeros 3349 (IBUG). MICHOACÁN: Uruapan, 500 m antes de llegar a las cascadas La Tzararacua, 3 noviembre 1994, M.A. Hernández 164 (IBUG). OAXACA: desviación a Santiago Comaltepec, carretera Valle Nacional a Ixtlán de Juárez, 4 agosto 1976, G. Guzmán 16234 (ENCB). TLAXCALA: Tlaxco, km 4.5 del Rosario al parque recreativo El Rodeo, 17 julio 1992, A. Pompa-González 192 (FCME 4895).

Helvella albella Quélet, Compt. Rend. Assoc. Franç. Avancem. Sci. 24(2): 621, pl. 6, Fig. 16, 1896 (1895) (como “*Elvella*”)

Comentarios taxonómicos: Presenta el apotecio lobado, con la superficie estéril glabra, el himenio marrón oscuro a negro, el estípote liso, glabro, y normalmente sólido, y las ascosporas de 17.5–20 x 10.5–13 μm . Se puede confundir con *H. elastica* y *H. leucopus*, las siguientes características ayudan a reconocerlas: 1) *H. elastica* presenta el himenio de tonos marrón claro, y su estípote es hueco; 2) *H. leucopus* tiene ascosporas de 21–24 x 13–15 μm y el estípote también es hueco (Dissing, 1966b).

Helvella albella es una especie poco frecuente en los bosques de coníferas y mixtos con *Quercus* de México, se ha citado por varios autores para el país (Chacón y Medel, 1992; Vite-Garín et al., 2006). Chacón y Medel (1992) describieron para la especie ascosporas de (22.5–) 24.3–25.2 x 13.5–14.4 μm y paráfisis de 9.9–11.7 μm de ancho, más grandes en comparación a las reportadas por otros autores. Quélet (1895) la definió con ascosporas elipsoides de 18–20 μm (no mencionó el ancho, ni las medidas de las paráfisis); Dissing (1966b) registró ascosporas de 19–20.5–22 x 11–12.1–14 μm , y paráfisis de 6–8 μm de ancho; Weber (1972) reportó ascosporas de 20–22 (–23.5) x (12.5–) 13.5–14.5 μm , y paráfisis de 6–18 μm de ancho (en este caso seguramente un error y que en lugar de 18 μm son 8 μm , porque en el tamaño de las ascas mencionó de 18–20 μm de ancho, y en *Helvella* una paráfisis nunca llega a medir lo mismo que el ancho de una asca); Abbott y Currah (1997) describieron ascosporas de 18.6–23.3 x (10.3–) 11.8–13.9 μm , y paráfisis de 6–9.9 μm de ancho. Es probable que las medidas mayores dadas por Chacón y Medel (1992) se deban al método de hidratación, ya que los montajes los hicieron en KOH 5%, y como mencionó Weber (1972) el montaje en esta solución modifica la estructura de las ascosporas, y por lo tanto también modifican a las paráfisis, debido a que hincha el tejido.

Material revisado: ESTADO DE MÉXICO, Ocoyoacac, carretera México-Toluca, cerca de La Escondida, 13 agosto 1967, M. Frías 9 (ENCB). MICHOACÁN: Zitácuaro, Los Gallineros-El Cielito, 30 agosto 1998, Pellicer-González 63 (FCME, 15010).

Helvella atra J. König, Reisen ingien. Island, Append.: 20, 1770

Comentarios taxonómicos: Se caracteriza por presentar el apotecio lobado, con la superficie estéril glabra, negra o más clara que el himenio (gris oscuro), el himenio negro, y el estípite entero o a veces con surcos en la base, pero nunca costillado, negro o grisáceo y glabro a subpubescente. *Helvella atra* se puede confundir con *H. pezizoides* por la forma de su ascoma y coloraciones, pero esta última es subpubescente a pubescente en la superficie estéril del apotecio y estípite (Dissing, 1966b; Weber, 1972; Abbott y Currah, 1997). Otra especie con la que se puede confundir es *H. subglabra*; Weber (1972) y Landeros et al. (2012) indicaron varias características para separarlas: 1) color del himenio (gris oscuro a gris-marrón o pardo en *H. subglabra*), 2) color del estípite y superficie estéril del apotecio (pardo o gris en *H. subglabra*), 3) pigmento en las células hifales del excípulo ectal (pocas células con pigmento marrón en la pared en *H. subglabra* y células normalmente con pigmento marrón en la pared en *H. atra*), 4) textura de la superficie estéril del apotecio (subpubescente en *H. subglabra*), 5) tejidos del ascoma en reactivo de Melzer (en *H. atra* sólo el tejido medio del estípite puede ser ligeramente rr+, mientras que en *H. subglabra* el excípulo medular del apotecio es ligeramente rr+, y el tejido medio del estípite es fuertemente rr+), y 6) pigmento marrón en la pared de las paráfisis, y células del excípulo ectal y capa externa del estípite en azul de algodón (visible en *H. atra* y no visible en *H. subglabra*).

Helvella atra es una especie común en bosques de coníferas y mixtos, y se ha citado de México por varios autores (e.g., Nieto-Roaro, 1941; Gómez y Herrera 1965; Bautista et al., 1986; Esqueda-Valle et al., 1992; Guzmán-Dávalos et al., 2001; Medel y Calonge, 2004; Landeros et al., 2006; Vite-Garín et al., 2006). Los especímenes I. Álvarez 720, I. Arreaga 31 y F. Trujillo 589 (IBUG) fueron citados por Guzmán-Dávalos et al. (2001) como *H. subglabra*.

Material revisado: JALISCO: Municipio de Atemajac de Brizuela, Puerto Nuevo-Club Ecole, km 3 del camino a las cabañas, 27 septiembre 2009, F. Landeros 3357 (IBUG); Municipio de Tamazula de Gordiano, San Francisco, 31 julio 1985, I. Arreaga 31 (IBUG); Municipio de Tapalpa, km 7.5 de la brecha La Frontera-Juanacatlán, 15 octubre 1990, I. Álvarez 720 (IBUG); Municipio de Tapalpa, 15 septiembre 2009, F. Landeros 3342 (IBUG); Municipio de Tequila, volcán de Tequila, km 11 de la brecha del pueblo de Tequila a las antenas, 10 octubre 2009, F. Landeros 3365 (IBUG); Municipio de Zapotlán el Grande, 11 agosto 1984, F. Trujillo 589 (IBUG). MICHOACÁN: Anganguero, Laguna seca de Zirahuato, 27 agosto 1999, J.L. Villaruel-Ordaz y Sánchez-Espinosa 739 (FCME 17007).

Helvella costifera Nannf., Fungi Exsicc. Suec., Fasc. (sched.): 37, 1953

Comentarios taxonómicos: Se caracteriza por presentar el apotecio en forma de copa, con la superficie estéril pubescente, las costillas del estípite llegando a la mitad o hasta el borde del apotecio, y el estípite pubescente, costillado, con las costillas de borde redondeado.

Helvella costifera es común en los bosques mixtos de coníferas y *Quercus* de México.

Material revisado: ESTADO DE MÉXICO: Villa de Allende, Unidad de Experimentación y Monitoreo de la Biodiversidad San Cayetano, 12 agosto 1994, R. García-Sandoval & L. Pérez-Ramírez 1901

(FCME 06398). HIDALGO: Epazoyucan, Peñas Largas, 3 agosto 1975, M. Medina & I. García 1104 (ENCB); Parque Nacional el Chico, San Miguel El Cerezo, Llano Grande, 18 septiembre 1983, R.E. Santillán 471 (ENCB). JALISCO: Municipio de Atemajac de Brizuela, Puerto Nuevo-Club Ecole, km 3 camino de Puerto Nuevo-Club Ecole, 27 septiembre 2009, F. Landeros 3358 (IBUG). QUERÉTARO: Municipio de Amealco, Laguna de Servín, 2 octubre 2001, E. Rosique 42 (FCME 18427); Municipio de Cadereyta, El Doctor, 22 agosto 2004, F. Tapia 2301 (IBUG); Municipio de Landa de Matamoros, 3 km al SE del Lobo, camino a La Pila de agua, 28 julio 1984, R. Valenzuela 3594 (ENCB). TLAXCALA: Calpulalpan, ejido Mazapa, 27 septiembre 1983, González-Fuentes 632 (ENCB).

Material adicional estudiado: SUECIA: Uppland, Uppsala, Botanic Garden, E.P. Fries s.n., etiquetado como *Peziza costata* (S, **isolectotipo**).

Helvella compressa (Snyder) N.S. Weber, Beih. Nova Hedwigia 51: 35, 1975

Comentarios taxonómicos: Se distingue por su apotecio en forma lobada, con la superficie estéril pubescente (fascículos hifales de 50–320 µm de longitud), el himenio de color marrón grisáceo a marrón oscuro, el estípite entero, pubescente y de color crema a crema amarillento, las ascosporas de 17.5–21.5 x 11–13.5 µm, y el excípulo medular y las células basales del excípulo ectal, tejido medio del estípite y a veces los fascículos hifales del apotecio son rr+. Puede confundirse con *H. latispora* Boud. y *H. stevensii*, la primera tiene ascosporas de 18–21 x 13.5–18 µm (Boudier, 1907; Weber, 1972); *H. stevensii* tiene el himenio de color canela a marrón pálido (Weber, 1975), con pubescencia en la superficie estéril del apotecio de 30–120 µm de largo, sólo el excípulo medular y el tejido medio del estípite son rr+.

Abbott y Currah (1997) describieron a *H. compressa* como endémica de la costa Oeste de los Estados Unidos de América, aquí se registra por primera vez para México, de Baja California Norte y de Jalisco, de este último del bosque de Los Colomos, un parque con vegetación introducida. Los dos ejemplares citados aquí como *H. compressa* fueron publicados previamente como representantes de otros taxones. El espécimen I. Manjarrez 337 fue referido como *H. macropus* por Medel y Calonge (2004) y el ejemplar M. Lara s/n fue determinado como *H. queletii* por Guzmán-Dávalos et al. (2001).

Material revisado: BAJA CALIFORNIA NORTE: Tecate, Rancho la Cruz, carretera Ensenada-Tecate, desviación en San Antonio de las Minas, 2 marzo 1985, I. Manjarrez 337 (XAL). JALISCO: Municipio de Zapopan, bosque Los Colomos 1, 16 octubre 1993, M. Lara s/n (IBUG).

Material adicional revisado: E.U.A: Washington, Eaton, L.C. Snyder, 5 mayo 1934 (NY, **isotipo**).

Helvella crispa (Scop.) Fr., Syst. Mycol. (Lundae) 2 (1): 14, 1822

= *Helvella pityophila* Boud. Journ. de Bot. 1: 218-219, pl. 3, 1887

Comentarios taxonómicos: Presenta el apotecio lobado, libre, con la superficie estéril pubescente, el himenio de color crema, y el estípite costillado o lagunoso, pubescente y de color crema. Puede confundirse con *H. lactea*, *H. maculata* N.S. Weber y *H. papuensis* Dissing, se distingue de *H. lactea* porque el apotecio está unido al estípite en al menos dos puntos y su superficie estéril es glabra (Weber, 1975; Abbott y Currah, 1997). *Helvella maculata* tiene el himenio moteado, costillas del estípite grisáceas y el pigmento marrón de las células de la capa externa del estípite se conserva en azul de algodón, mientras que en *H. crispa* el color del himenio es uniforme, las costillas del estípite son

concoloras con el resto del estípote, y el pigmento de las células de la capa externa del estípote no son visibles en azul de algodón (Weber, 1975; Abbott y Currah, 1997; Landeros et al., 2012). Finalmente, *H. papuensis* tiene una distribución tropical, de hecho es la única especie tropical del género, mientras que *H. crispa* tiene una distribución templada (Dissing, 1979; Abbott y Currah, 1997).

Helvella crispa es una especie común en los bosques mixtos de coníferas y *Quercus*, y ha sido citada de México por numerosos autores (e.g., Nieto-Roaro, 1941; Gómez y Herrera, 1965; Guzmán, 1977; Manzi, 1978; Bautista et al., 1986; Guzmán-Dávalos et al., 2001; Medel y Calonge, 2004; García y Guevara, 2005; Landeros et al., 2006; Vite-Garín et al., 2006).

Garibay-Orijel et al. (2009) registraron a *H. pityophila* para Oaxaca, pero como su estudio es sobre disponibilidad de esporomas en los bosques de *Pinus-Quercus* de Ixtlán de Juárez y no taxonómico, no describen a la especie o citan el material estudiado. *Helvella pityophila* fue descrita por Boudier (1887), pero actualmente se considera un sinónimo de *H. crispa* (Dissing, 1966b).

Material revisado: GUERRERO: Mochitlán, cerro de Tepoxtepec, 16 km al SO de Mazatlán, 15 octubre 1978, Alarcón-Guevara 251 (ENCB). JALISCO: Municipio de Ahualulco, Piedras Bolas, 24 agosto 2008, L. Guzmán-Dávalos 10453 (IBUG); Municipio de Zapotlán el Grande, faldas del Nevado de Colima, El Floripondio, 7 septiembre 1996, M.R. Sánchez-Jácome 939 (IBUG), 18 diciembre 2007, I. Ruiz Prieto 19 (IBUG); Municipio de Mazamitla, faldas del cerro del Tigre, a 4 km de Mazamitla, 4 octubre 2009, V. Ramírez-Cruz 1115 (IBUG); Municipio de Tapalpa, al NE de la cabecera municipal, 14 agosto 1982, G. Nieves 37 (IBUG), 15 septiembre 2009, F. Landeros 3344 (IBUG); Municipio de Tecolotlán, Sierra de Quila, km 8 del camino de Quila al Árbol de la Lira, 26 septiembre 2009, F. Landeros 3355 (IBUG); Municipio de Tequila, volcán de Tequila, camino a la estación de microondas, 21 agosto 1990, O. Rodríguez 599 (IBUG); Municipio de Zapopan, 6 km al sur bosque de La Primavera, 3 septiembre 1992, O. Rodríguez s.n. (IBUG). MORELOS: Huitzilac, carretera a Chalma, ± 5 km delante de Huitzilac, 17 julio 1982, S. Chacón 231 (ENCB).

Helvella cupuliformis Dissing & Nannf., Svensk. bot. Tidskr. 60: 326, 1966

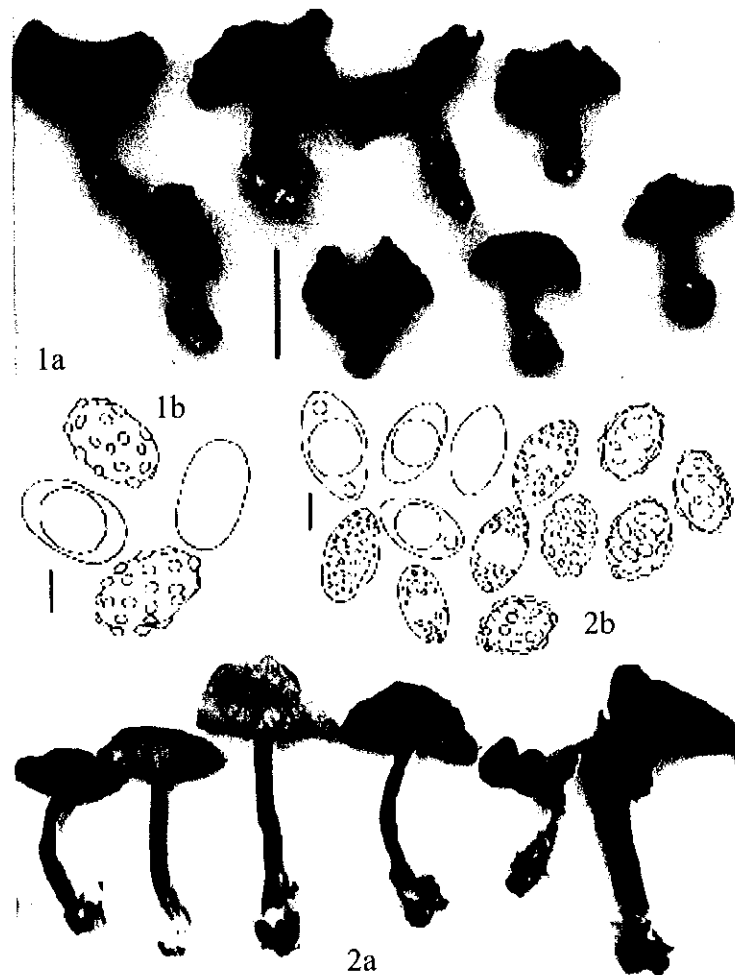
Fig. 1a-b

Comentarios taxonómicos: Las características que la distinguen son el apotecio en forma de copa y el estípote liso, en ocasiones con pliegues cortos que forman cavidades (especialmente en especímenes adultos) pero que nunca llegan a ser verdaderas costillas. Se puede confundir con *H. fibrosa*, *H. macropus* y *H. rivularis* Dissing & Sivertsen; en la primera el tamaño del estípote es mayor que el diámetro del apotecio, y el himenio es de tonos oscuros, grisáceos, gris-marrón oscuro a marrón oscuro, mientras que en los especímenes maduros de *H. cupuliformis* el diámetro del apotecio es mayor o igual que el tamaño del estípote, y el himenio es de tonos claros, marrón pálido a marrón amarillento (Dissing y Nannfeldt, 1966; Abbott y Currah, 1997). *Helvella macropus* tiene ascosporas fusoides a subfusoides, y en *H. cupuliformis* son elipsoides (Weber, 1975; Abbott y Currah, 1997; Landeros et al. 2011b).

Con respecto a *H. rivularis*, tenemos dudas de que sea un taxon independiente de *H. cupuliformis*. Abbott y Currah (1997) usaron el criterio del tamaño del ascoma para separarlas; para *H. rivularis* describieron apotecios de menos de 9 mm de diámetro y estípote de menos de 1 cm de largo, y para *H. cupuliformis* apotecios de 9-35 mm de diámetro y estípote de 2-10 mm de alto, pero en las descripciones originales de ambas especies los tamaños de los ascomas son casi iguales; Dissing y Nannfeldt (1966) describieron para *H. cupuliformis* el apotecio de 5-20 mm de ancho y el estípote de 8-15 mm de alto, y para *H. rivularis*, Dissing y Sivertsen (1980) definieron el apotecio de 4-18 mm de ancho y el estípote de 2-15 mm de alto. Estos últimos autores no discutieron las características para distinguir su especie de *H. cupuliformis*. Con base en lo anterior, pensamos que es necesario hacer una

revisión del ejemplar tipo de *H. rivularis* (el cual no fue posible revisar en este estudio) para comprobar si se trata o no de taxones independientes.

Helvella cupuliformis es una especie rara en México, sólo ha sido citada por Sánchez-Jácome y Guzmán-Dávalos (2005); revisamos el espécimen (A.D. Zamarripa 134) que ellas citaron y se corroboró que corresponde a esta especie. El otro ejemplar (L. Guzmán-Dávalos 4388) que incluimos en el material examinado para esta especie fue citado por Sánchez-Jácome y Guzmán-Dávalos (2005) como *H. dissingii* Korf (que es un sinónimo de *H. fibrosa*). Vite-Garín (2005) y Vite-Garín et al. (2006) no citaron a *H. cupuliformis* del material depositado en el Herbario FCME que estudiaron, pero sí la incluyeron en la clave sinóptica, con estípites “lacunoso con costillas”, con paráfisis “no septadas” y “no ramificadas”, lo cual es impreciso, ya que como se mencionó anteriormente, en especímenes adultos pueden formarse pliegues, pero éstos nunca van a formar verdaderas costillas (como en *H. acetabulum*, *H. costifera* o *H. mexicana*), o ser lagunoso (como *H. fusca* Gillet, *H. lacunosa*, *H. lactea* o *H. maculata*), y todas las especies de *Helvella* presentan paráfisis septadas y ramificadas (excepto las paráfisis de pared gruesa de *H. crassitunicata* N.S. Weber). El espécimen R. Medel 258 (XAL) fue citado por Medel y Chacón (1997) como *H. macropus*, pero los ejemplares de esta especie, como ya se mencionó, tienen ascosporas fusoides a subfusoides, mientras que el ejemplar Galván-Mejía 9 (FCME 7761) fue citado por Vite-Garín 2005) como *H. chinensis*.



Figs. 1–2. 1: *Helvella cupuliformis*, a: ascomas de un paratipo (J. Eriksson & R. Morander 7 julio 1948, K), b: ascosporas. 2: *Helvella macropus* (F. Landeros 3396a, 3396b 3396c, IBUG), a: variación en sus ascomas, de forma de copa a lobado, b: variación en la ornamentación de sus ascosporas. Escala de las barras: 1a, 2a: 1 cm; 1b, 2b: 10 μ m.

Material revisado: GUANAJUATO: Municipio de Guanajuato, Cañada de Llano Largo, Sierra Santa Rosa, 30 septiembre 1995, Galván-Mejía (FCME 7761). JALISCO: Municipio de Autlán, 3 km al N de Autlán, Ayotita, 1 octubre 1988, A.D. Zamarripa 134 (IBUG); Municipio de Tecalitlán, Sierra del Halo, km 16 brecha Tecalitlán-Jilotlán, 28 agosto 1988, L. Guzmán-Dávalos 4388 (IBUG). VERACRUZ: Municipio de Coacoatzintla, carretera Jilotepec-Coacoatzintla, rancho Las Palmas, 12 octubre 1986, R. Medel 258 (XAL).

Material adicional revisado: SUECIA: Uppland, Uppsala, Stadsskogen near Skogshall, 7 julio 1948, J. Eriksson & R. Morander (F. Suec. Ups. Exs. 3265, K, **paratipo**); 21 julio 1948, J. Eriksson & R. Morander (UPS, **paratipo**).

Helvella elastica Bull., Herb. Fr., pl. 242, Figs. A, B, D–G, 1785; descripción en Hist. Champ. Fr. 1: 299–300, 1791.

Comentarios taxonómicos: Esta especie tiene el ascoma con apotecio lobado, con la superficie estéril glabra, el himenio de tono marrón, y el estípite liso, de tono claro (blanco a color crema, o marrón amarillento pálido), glabro y hueco. *Helvella elastica* puede confundirse con *H. albella*, *H. latispora* y *H. leucopus*, pero las siguientes características ayudan a distinguirla: 1) Color del himenio: *H. latispora* y *H. albella* presentan el himenio de color oscuro, marrón oscuro a negro, mientras que en *H. elastica* es claro (Dissing, 1966b; Abbott y Currah, 1997); y 2) tamaño de ascosporas: *H. latispora* tiene ascosporas de 18–21 x 13.5–18 µm, y en *H. elastica* son más angostas, de 18–21 x 11–13.5 µm (Boudier, 1907; Dissing 1966b). Abbott y Currah (1997) reportaron ascosporas de (16.5–) 18.6–19.9 (–20.8) x (10.9–) 11.4–12.4 µm para *H. latispora*, que no corresponden con la descripción original de la especie o con trabajos europeos en donde se han estudiado ejemplares de esa especie.

Helvella elastica es una especie común en los bosques mixtos de coníferas y *Quercus* de México, que ha sido citada por numerosos autores (e.g., Gómez y Herrera, 1965; Bautista et al., 1986; Guzmán-Dávalos et al., 2001; Medel y Calonge, 2004; García y Guevara, 2005; Landeros et al., 2006; Vite-Garín et al., 2006). Nieto-Roaro (1941) citó *H. elastica* del Valle de México, pero su figura 3 claramente representa el ascoma joven de *H. crispa*, debido a que presenta un estípite costillado-lagunoso y el apotecio irregularmente cupuliforme y libre.

Material revisado: ESTADO DE MÉXICO: Municipio de Naucalpan, Lerma, Las Rajas, km 29 carretera México-Toluca vía Naucalpan, 15 agosto 1968, E. González 78 (ENCB); Lerma, Salazar, carretera México-Toluca, 28 octubre 1969, G. Gómez-Murga 55-B (ENCB); Zinacantepec, Loma Alta, carretera Toluca-Temascaltepec, km 3 de la desviación al refugio del Nevado de Toluca, 19 septiembre 1982, L. Guzmán-Dávalos 526 (ENCB). DISTRITO FEDERAL: Cuajimalpa de Morelos, Puerto de las Cruces, S. Miller 191, 15 septiembre 1967 (ENCB). HIDALGO: Mineral del Chico, Parque Nacional El Chico, llano de Las Cebadas, 18 julio 1981, S. Acosta 641 (ENCB). JALISCO: Municipio de Zapotlán el Grande, faldas del Nevado de Colima, El Floripondio, 11 septiembre 1998, L. Guzmán-Dávalos 7554 (IBUG); Municipio de Zapopan, bosque La Primavera, km 1.5 de la caseta al autódromo, 8 octubre 2001, O. Rodríguez 2433 (IBUG).

Helvella ephippium Lév., Anns. Sci. Nat., Bot., sér. 2, 16: 240, 1841

Comentarios taxonómicos: Presenta el apotecio lobado, con la superficie estéril pubescente, el himenio de color sepia o marrón, y el estípite liso, pubescente y de tono ligeramente más claro que el himenio.

Puede confundirse con *H. pezizoides* y *H. stevensii*, pero el color del himenio y estípite, y la reacción de sus tejidos en solución de Melzer ayudan a reconocerla. En *H. pezizoides* el himenio y estípite son marrón oscuro a negro, y todos sus tejidos son rr⁻; *H. stevensii* presenta himenio de color canela, el estípite blanquecino a crema (Léveillé, 1841; Dissing, 1966b), y su excípulo ectal y tejido medio del estípite son rr⁺, mientras que en *H. ephippium* todos sus tejidos son rr⁻.

Helvella ephippium es relativamente común en los bosque mixtos de coníferas y *Quercus* de México. Pérez-Silva et al. (1996) la citaron por primera vez para México, posteriormente la registraron Guzmán-Dávalos et al. (2001), Medel y Calonge (2004), Medel et al. (2006) y Vite-Garín et al. (2006).

Material revisado: JALISCO: Municipio de San Sebastián del Oeste, camino de San Sebastián-Santa Ana, 29 agosto 1994, O. Rodríguez 1022 (IBUG), km 3.1 del camino Real Alto-La Bufa, 2 agosto 2009, O. Rodríguez 3590 (IBUG).

Helvella fibrosa (Wallr.) Korf, Mycotaxon 103: 311, 2008

= *Helvella chinensis* (Velen.) Nannf. & L. Holm, in Lundell, Nannfeldt & Holm, Publications from the Herbarium, University of Uppsala, Sweden 18: 5, 1985

= *Helvella dissingii* Korf, Mycotaxon 31(2): 381, 1988

= *Helvella pallidula* N.S. Weber, The Michigan Bot. 11(4): 171, 1972

= *Helvella villosa* (Hedw.) Dissing & Nannf., Svensk bot. Tidskr. 60: 330, 1966

Comentarios taxonómicos: Se caracteriza por presentar el apotecio en forma de copa, con la superficie estéril pubescente, el himenio de tonos oscuros, grisáceos, gris-marrón oscuro a marrón oscuro, y el estípite normalmente liso en especímenes jóvenes, que en ejemplares viejos puede llegar a formar pliegues, gris oscuro a marrón oscuro, hacia la base puede ser de tono más pálido a blanco-amarillento, pubescente. *Helvella fibrosa* puede confundirse con *H. cupuliformis* (ver la sección de comentarios taxonómicos de esta especie para conocer cómo distinguir las) y *H. macropus*. De esta última se distingue porque *H. fibrosa* tiene ascosporas elipsoides, mientras en *H. macropus* son fusoides a subfusoides (Abbott y Currah, 1997; Weber, 1972).

Es una especie común en los bosques mixtos de coníferas y *Quercus* de México, ha sido citada por varios autores como *H. chinensis* (Vite-Garín et al., 2006), o como *H. villosa* (Medel y Calonge, 2004; García y Guevara, 2005). Pompa-González y Cifuentes (1991) fueron los primeros en registrarla para México, pero en su descripción mencionaron “estípite ligeramente lacunoso” y además “pelos ausentes”, siendo que ésta presenta estípite liso y una de las características más distintivas de la especie, son sus pubescencias largas. Al revisar los ejemplares citados por Pompa-González y Cifuentes (1991) [Cid de León s.n. (FCME 1584) y S. Cappello 116 (FCME 1587)], observamos que ambos tienen estípite liso (a veces con ligeros pliegues, los cuales nunca forman verdaderas costillas, o llegando a ser lagunoso) y presentan pubescencias en la superficie estéril del apotecio y estípite; por lo que determinamos que el espécimen S. Cappello 116 si corresponde a *H. fibrosa*, mientras que el ejemplar Cid de León s.n. es *H. macropus* por tener ascosporas fusoides a subfusoides. Por otro lado, Sánchez-Jácome y Guzmán-Dávalos (2005) registraron esta especie como *H. dissingii* para Jalisco, que actualmente es considerada como un sinónimo de *H. fibrosa* (Korf, 2008). Revisamos el espécimen citado (L. Guzmán-Dávalos 4388) por Sánchez-Jácome y Guzmán-Dávalos (2005), pero determinamos que corresponde a *H. cupuliformis* (ver los comentarios taxonómicos de esta especie). Los especímenes V.M. Bandala 1670 (XAL) y L. Montoya 1461 (XAL) fueron citados por Chacón y Medel (1992) como *H. queletii* (ver discusión en *H. solitaria*).

Material revisado: GUERRERO: Municipio de Tlapa, km 128 carretera Chilpancingo-Tlapa, 7 agosto 1981, S. Capello 116 (FCME 1587). JALISCO: Municipio de Tapalpa, carretera Atemajac de Brizuela-La Frontera, 2 km antes de Juanacatlán, 28 julio 2002, L. Guzmán-Dávalos 8778 (IBUG); Municipio de Tecolotlán, La Ciénega, localidad Mesa del Cobre, M.P. Ramos-Suárez 12 (IBUG). VERACRUZ: Municipio Rafael Lucio, km 10 carretera Xalapa-La Hoya, granja Santa Bárbara, 10 octubre 1986, R. Medel 235 (XAL) ; 2 km al SO de Xalapa, cerca del río Coapexpan, 23 agosto 1989, V.M. Bandala 1670 (XAL); carretera Huatusco-Coscomatepec, camino a microondas, 26 agosto 1989, L. Montoya 1461 (XAL).

Material adicional revisado: CHINA: Pai N'a, 28 agosto 1930, E. Licent 2398 (PRM 151669, *H. chinensis*, **holotipo**). USA: Michigan, Montmorency Co., en un bosque de hoja caduca, esparcidos por el suelo arenoso, esquina noroeste, 24 julio 1967, N.J. Smith 397 (MICH, *H. pallidula*, **holotipo**).

Helvella lactea Boud., Hist. Class. Discom. Eur. (Paris): 36, 1907

Comentarios taxonómicos. Presenta el apotecio lobado unido al menos en dos puntos al estípite, con la superficie estéril glabra, el himenio blanquecino a color crema, y el estípite costillado o lagunoso, blanquecino y glabro. Puede confundirse con *H. crispa* (ver comentarios taxonómicos de esta especie para conocer cómo distinguirlas) y con *H. lacunosa*. De esta última se reconoce por el color del himenio, ya que *H. lacunosa* siempre va a presentar el himenio de tonos oscuros (grisáceos, marrón oscuro o negro) (Dissing, 1966b; Weber, 1972; Abbott y Currah, 1997).

Helvella lactea es una especie poco común en los bosques de coníferas de México. Medel y Calonge (2004) fueron los primeros en registrarla para México, y posteriormente por Vite-Garín et al. (2006). Revisamos uno de los ejemplares (Ayala 105) citado por Medel y Calonge (2004) y determinamos que se trata de *H. stevensii* (ver comentarios en esta especie). El espécimen Hernández Muñoz 163, citado por Vite-Garín et al. (2006), no se encontró cuando se hizo la revisión de los ejemplares de *Helvella* depositados en el Herbario FCME, pero la figura que presentan en su artículo (fig. 7), corresponde claramente con *H. lactea*.

Material revisado: GUERRERO: Tlapa, km 128 carretera Chilpancingo-Tlapa, 7 agosto 1981, E. Suárez (FCME). JALISCO: Sierra de Manantlán, 1 km al sur de la Estación Las Joyas, 12 septiembre 2002, G. Zarco 144 (IBUG); Municipio de Mazamitla, El Terrero, km 10 carretera Mazamitla-Tamazula, 9 septiembre 1998, O. Rodríguez 2003 (IBUG). MICHOACÁN: Coeneo, cerro El Salto, 2.5 km antes de San Marcos Matugeo, 30 agosto 1996, O. Rodríguez 1561 (IBUG). QUERÉTARO: Municipio de San Joaquín, Nuevo San Joaquín, 7 agosto 2004, J. Ramírez-López 98 (IBUG).

Helvella lacunosa Afzel., K. Vetensk-Acad. Handl. 4: 303, 1783

Comentarios taxonómicos: Se caracteriza por presentar el apotecio de forma lobada unido al estípite, con la superficie estéril glabra, el himenio de tonos oscuros (marrón oscuro, gris oscuro, marrón grisáceo o negro), y el estípite lagunoso, glabro y de tonos claros u oscuros (blanquecino, grisáceo o negro). *Helvella lacunosa* se puede confundir con *H. fusca* y *H. sulcata*; de *H. fusca* se distingue porque ésta tiene el himenio de color marrón pálido, sólo se conoce de Europa y está asociada con *Populus* spp., mientras que *H. lacunosa* presenta himenio de tonos oscuros, está distribuida por el todo el mundo y crece asociada a bosques de coníferas (Gillet, 1879; Landeros y Korf, 2012). *Helvella sulcata* tienen el estípite costillado, no lagunoso.

Helvella lacunosa es una de las especies del género más comunes que prosperan en los bosques de coníferas y mixtos con *Quercus* de México, por lo que ha sido citada ampliamente (e.g., Gómez y Herrera, 1965; Guzmán, 1977; Manzi, 1978; Bautista et al., 1986; Esqueda-Valle et al., 1992; Medel y Calonge, 2004; García y Guevara, 2005; Landeros et al., 2006; Vite-Garín et al., 2006). Nieto-Roaro (1941) incluyó en su trabajo varias figuras de ascomas de *H. lacunosa*; las figuras 1 y 2 corresponden claramente con esta especie, pero el ascoma izquierdo de la figura 4 es *H. acetabulum*.

Material revisado: ESTADO DE MÉXICO: Parque Nacional Nevado de Toluca, El Capulín, km 21 de la carretera a Sultepec, 25 septiembre 1983, R. Valenzuela 2598 (ENCB); Faldas del Nevado de Toluca, Cerro Prieto, 18 octubre 2003, L. Guzmán-Dávalos 9002 (IBUG). JALISCO: Municipio de Autlán, Sierra de Manantlán, 1 km al sur de la Estación Las Joyas, 12 septiembre 2002, G. Zarco 144 (IBUG); Municipio de Zapotlán el Grande, Nevado de Colima, 7 octubre 2010, A. Castro-Castro s.n. (IBUG); Municipio de Guadalajara, alrededores de la ciudad, J. Manzi 514 (IBUG); Municipio de Mazamitla, El Terrero, km 10 carretera Mazamitla-Tamazula, 9 septiembre 1998, O. Rodríguez 2003 (IBUG); Municipio de Tequila, volcán de Tequila, km 14-15 brecha a la estación de microondas, 21 septiembre 1986, M. Garza 257 (IBUG), km 3-6.5, 24 agosto 1986, O. Rodríguez 240 (IBUG), km 17, L. Guzmán-Dávalos 2505 (IBUG). MICHOACÁN: km 23 carretera Morelia-México, vía Mil Cumbres, agosto 1984, G. Guzmán 26013 (XAL); Coeneo, cerro El Salto, 1.5 km antes de San Marcos Matugeo, 30 agosto 1996, O. Rodríguez 1561 (IBUG); Uruapan, 500 m antes de llegar a las cascadas La Tzararacua, 3 noviembre 1995, M.A. Hernández 155 (IBUG). MORELOS: colonia Atlixac, 3 km al S de Tres Marías, antigua carretera a Cuernavaca, 11 octubre 1970, G. Guzmán 8944 (ENCB); carretera México-Cuernavaca, 6 km al sur de Tres Marías, 25 agosto 1967, P. Domínguez 80 (ENCB). PUEBLA: Paso de Cortés, entre el Popocatepetl e Iztaccihuatl, 17 octubre 1965, G. Guzmán 4953 (ENCB). QUERÉTARO: Municipio de Cadereyta, Chavarrías, 8 August 2004, F. Tapia 2229 (IBUG); Municipio de San Joaquín, Ranas, 20 septiembre 2004, F. Landeros 883 (IBUG). TAMAULIPAS: Miquihuana, sin fecha, G. Guevara 1061 (ITCV). TLAXCALA: carretera Apizaco a Chignahuapan, al N de Tlaxco, 19 septiembre 1974, R. Grada y R. Cerrato 33-T (ENCB). VERACRUZ: La Perla, 27 septiembre 1996, F. Tapia 1403 (XAL).

Helvella leucomelaena (Pers.) Nannf., in Lundell & Nannfeldt, Fungi exsicc. upsal. 21: 952, 1941
Fig. 3

Comentarios taxonómicos: Presenta el apotecio en forma de copa, con la superficie estéril pubescente, el estípite costillado y pubescente, y las ascas aporrincosas. Sólo reconocen dos especies con ascas aporrincosas: *H. crassitunicata* y *H. leucomelaena* (Weber, 1975; Abbott y Currah, 1997). *Helvella crassitunicata* es la única especie del género que presenta paráfisis de pared gruesa (Weber, 1975; Landeros et al., 2012).

Helvella leucomelaena es una especie poco frecuente en los bosques de *Pinus* de México. Medel y Calonge (2004) la citaron por primera vez para México, pero al revisar el ejemplar que mencionaron (Guzmán 29101), observamos que tiene ascas pleurorricosas, y por lo tanto dicho espécimen corresponde a *H. solitaria*. Posteriormente, Vite-Garín et al. (2006) no encontraron especímenes de esta especie depositados en el Herbario FCME, pero la incluyen en su clave sinóptica, pero con varias imprecisiones, ya que la describen con estípite “lacunoso con costillas” y esta especie sólo es costillada, con estípite “glabro”, pero es pubescente, paráfisis “no septadas” y “no ramificadas”, y son claramente septadas y ramificadas.

Material revisado: QUERÉTARO: Municipio de Pinal de Amoles, 5 km antes de Puerta del Cielo, 7 octubre 2011, F. Landeros 3404 (IBUG).

Helvella macropus (Pers.) P. Karst., Bidr. Känn. Finl. Nat. Folk 19: 37, 1871
= *Helvella brevis* (Peck) Harmaja, Karstenia 14: 104, 1974

Fig. 2a–b

Comentarios taxonómicos: Se caracteriza por el apotecio en forma de copa o lobado, con la superficie estéril pubescente, el estípite liso y pubescente, y las ascosporas fusoides o subfusoides. *Helvella macropus* junto con *H. terrestris* (Velen.) Landvik son las únicas especies conocidas que tienen ascosporas fusoides o subfusoides, pero las de esta última miden de 50–65 x 12–15 µm (Landvik et al., 1999), mientras que en *H. macropus* son de 18–24 x 10–13.5 µm (Dissing, 1966b).

Helvella macropus es una de las especies más comunes que prosperan en los bosques de coníferas y mixtos con *Quercus* de México, y ha sido citada ampliamente (e.g., Guzmán, 1977; Guzmán-Dávalos y Guzmán, 1979; Bautista et al., 1986; Pompa-González y Cifuentes 1991; Medel y Calonge, 2004; García y Guevara, 2005; Landeros et al., 2006; Vite-Garín et al., 2006).

Medel y Chacón (1997) registraron a *H. brevis* para el bosque mesófilo de Veracruz, que actualmente se considera un sinónimo de *H. macropus*, debido a que el tamaño de las ascosporas, que es la principal característica que usó Harmaja (1974) para proponerla como un taxón diferente, es muy variable entre los especímenes de *H. macropus* (Weber, 1972; Abbott y Currah, 1997). Medel y Chacón (1997) indicaron para sus especímenes (R. Medel 202, 211, 234, 258, XAL) ascosporas “elíptico filiformes con el ápice ensanchado”, y efectivamente su figura 1 representa eso, pero *H. macropus* se caracteriza por presentar ascosporas fusoides a subfusoides. Desafortunadamente sólo pudimos estudiar los especímenes R. Medel 211 y R. Medel 258, y determinamos que el primero, debido a que el ejemplar no presenta apotecio (sólo consta de dos estípites), no puede identificarse, mientras que el otro corresponde a *H. cupuliformis*, por presentar ascosporas elipsoidales. Los especímenes G. Guzmán 8288 y L. Montoya 972 (XAL) fueron citados por Chacón y Medel (1992) como *H. corium*, al igual que el espécimen Corona y L. Pérez-Ramírez 736 (FCME 14047) por Pompa-González y Cifuentes (1991), Vite-Garín (2005), y Vite-Garín et al. (2006), mientras que el ejemplar Cid de León s.n. (FCME 1584) fue registrado como *H. villosa* por Pompa-González y Cifuentes (1991) y como *H. chinensis* por Vite-Garín et al (2006), y el espécimen R. Medel (684) como *H. villosa* por Medel y Calonge (2004).

Material revisado: ESTADO DE MEXICO: carretera Toluca-Temascaltepec, Puerto de la Mapa, cerca de la desviación al Nevado de Toluca, 23 septiembre 1970, G. Guzmán 8288 (XAL); Nevado de Toluca, cerro Prieto, 18 octubre 2003, L. Guzmán-Dávalos 8998 (IBUG). GUERRERO: Municipio de Atlixac, km 76 carretera Chilpancingo-Tlapa, 21 septiembre 1981, Cid de León s.n. (FCME 1584). JALISCO: Municipio de Autlán, Sierra de Manantlán, Yerbabuena, C. Téllez 274 (IBUG); Municipio de Bolaños, Sierra de los Huicholes, km 30 Bolaños-Tuxpan de Bolaños, 29 agosto 2004, O. Rodríguez 2652 (IBUG); Municipio de Mezquitic, Sierra de los Huicholes, 2.3 km antes de Bajío de los Amoles, 30 agosto 2004, O. Rodríguez 2669 (IBUG); Municipio de Poncitlán, Mezcala, cerro El Colorado, 6 septiembre 2009, K. Terríquez 239 (IBUG); Municipio de San Sebastián del Oeste, en el camino de Real Alto-Bufa, 24 agosto 2008, O. Rodríguez 3409 (IBUG), 31 julio 2009, O. Rodríguez 3551 (IBUG), 15 agosto 2009, O. Rodríguez 3627 (IBUG); Municipio de Tapalpa, carretera Atemajac de Brizuela-Tapalpa, 2 km antes de Juanacatlán, 4 septiembre 2004, A. Pichardo-Jiménez 15 (IBUG), L.F. García 4 (IBUG); Municipio de Tecolotlán, Sierra de Quila, Árbol de la Lira, 20 septiembre 2008, F. Landeros 3271 (IBUG), km 8 del camino de Quila al Árbol de la Lira, 26 septiembre 2009, F. Landeros 3352 (IBUG); Municipio de Tequila, volcán de Tequila, 25 septiembre 2009, F. Landeros 3347

(IBUG); km 12.3 de la brecha del pueblo de Tequila a las antenas, J.M. Canseco 12 (IBUG). MICHOACÁN: Municipio de Zinapécuaro, km 5.5 carretera San Pedro-Jacuaro-Los Azufres, 15 agosto 1987, Corona y L. Pérez-Ramírez 736 (FCME 14047). PUEBLA: terracería que va de Hidalgo al albergue Pico de Orizaba, 31 octubre 1998, R. Medel 684 (XAL). QUERÉTARO: Municipio de San Joaquín, Santa Ana, 9 octubre 2010, F. Landeros 3396a, 3396b, 3396c (IBUG). VERACRUZ: Municipio de Villa, Cruz Blanca, km 39 carretera nacional Xalapa-Perote, 21 octubre 1986, L. Montoya 972 (XAL).

Helvella pezizoides Afzel., K. svenska Vetensk-Akad. Handl.: 308, 1783

Comentarios taxonómicos: Esta especie presenta el apotecio de forma lobada en estado maduro, con la superficie estéril subpubescente a pubescente, el himenio de color marrón oscuro a negro, y el estípite liso, subpubescente a pubescente. Se puede confundir con *H. atra* y *H. ephippium* (ver los comentarios taxonómicos de éstas).

Helvella pezizoides es común en los bosques de *Quercus* de México, y ha sido citada por varios autores (Bautista et al., 1986; Pérez-Silva et al., 1996; Guzmán-Dávalos et al., 2001; Medel y Calonge, 2004). El espécimen A. Pompa-González 254 fue determinado por Vite-Garín et al. (2006) como *H. ephippium*, pero en esa especie el ascoma es de tonos claros. El ejemplar V. Bandala 1313 (XAL) fue determinado como *H. leucopus* (ver comentarios en esta especie) por Medel y Calonge (2004), y el espécimen L. Guzmán-Dávalos 2970 como *H. subglabra* (ver comentarios en esta especie) por Guzmán-Dávalos et al. (2001).

Material revisado: JALISCO: Municipio de Autlán, Sierra de Manantlán, Predio Las Joyas, 15 octubre 1985, L. Guzmán-Dávalos 2970 (IBUG); Municipio de Tequila, volcán de Tequila, km 12 del camino del pueblo de Tequila a las antenas, 10 septiembre 2005, L. Guzmán-Dávalos 9770 (IBUG). TLAXCALA: Taxco, km 4.5 de El Rosario, parque recreativo El Rodeo, 5 septiembre 1992, A. Pompa-González 254 (FCME). VERACRUZ: Perote, Cruz Blanca, km 39 por la carretera nacional Xalapa-Perote, sin fecha, V. Bandala 1313 (XAL).

Helvella solitaria P. Karst., Bidr. Känn. Finl. Nat. Folk 19: 37, 1871
= *Helvella queletii* Bres., Fungi trident. 1(3): 39, 1883

Fig. 4

Comentarios taxonómicos: Esta especie se distingue por el apotecio en forma de copa, con la superficie estéril pubescente y sin costillas, y el estípite costillado y pubescente. Puede confundirse con *H. leucomelaena*, *H. ulvinenii* Harmaja y *H. verruculosa* (Sacc.) Harmaja; *H. leucomelaena* tiene ascas aporrincosas, mientras que en *H. solitaria* son pleurorricosas (Weber, 1972; Abbott y Currah, 1997; Landeros et al., 2012). *Helvella ulvinenii* presenta la superficie estéril del apotecio de color marrón, sepia a negro, y el pigmento marrón de los fascículos hifales del apotecio son visibles en azul de algodón; en *H. solitaria* la superficie estéril es marrón grisáceo pálido a blanquecino hacia el estípite, y marrón grisáceo oscuro hacia el borde, y el pigmento marrón de sus fascículos hifales del apotecio no es visible en azul de algodón. Landeros et al. (2012) mencionaron que posiblemente *H. ulvinenii* se trate de una variedad de *H. solitaria*, debido a las pocas características morfológicas que las separan, y a que ambas son especies descritas del norte de Europa. Finalmente, en *H. verruculosa* el pigmento citoplasmático de las células del excípulo ectal y fascículos hifales del apotecio es visible en azul de algodón, y tiene una distribución ártica y alpina, mientras que en *H. solitaria* tanto el pigmento citoplasmático de las células del excípulo ectal, como el de los fascículos hifales del apotecio no es

visible en azul de algodón, y tiene una distribución boreal-templada (Abbott y Currah, 1997; Landeros et al., 2012).

Helvella solitaria es una especie escasa en bosques mixtos de coníferas y *Quercus* en México. Chacón y Medel (1992) la citaron por primera vez para México, y posteriormente la registraron Guzmán-Dávalos et al. (2001), en ambos casos como *H. queletii*, la cual es considerada actualmente un sinónimo (Harmaja 1977a; Abbott y Currah, 1997; Landeros et al., 2012). Chacón y Medel (1992) describieron a los especímenes que estudiaron (V.M. Bandala 1670 y L. Montoya 1461, XAL) de estípite “con depresiones redondeadas”, y el dibujo que presentan (fig. 14) así lo muestra, pero *H. solitaria* presenta costillas bien definidas. Al estudiar tales ejemplares determinamos que corresponden a *H. fibrosa*; las “depresiones” que presenta el estípite son también comunes en ejemplares adultos de otras especies de *Helvella*, como en *H. atra*, *H. elastica*, *H. macropus* y *H. pezizoides*, pero tales pliegues son irregulares y cortos, y nunca llegan a formar costillas verdaderas, que es una de las características que definen a *H. solitaria*. Por otro lado, Guzmán-Dávalos et al. (2001) mencionaron sólo un ejemplar (M. Lara s.n.), que se estudió y se determinó como *H. compressa* (ver los comentarios taxonómicos de esta especie).

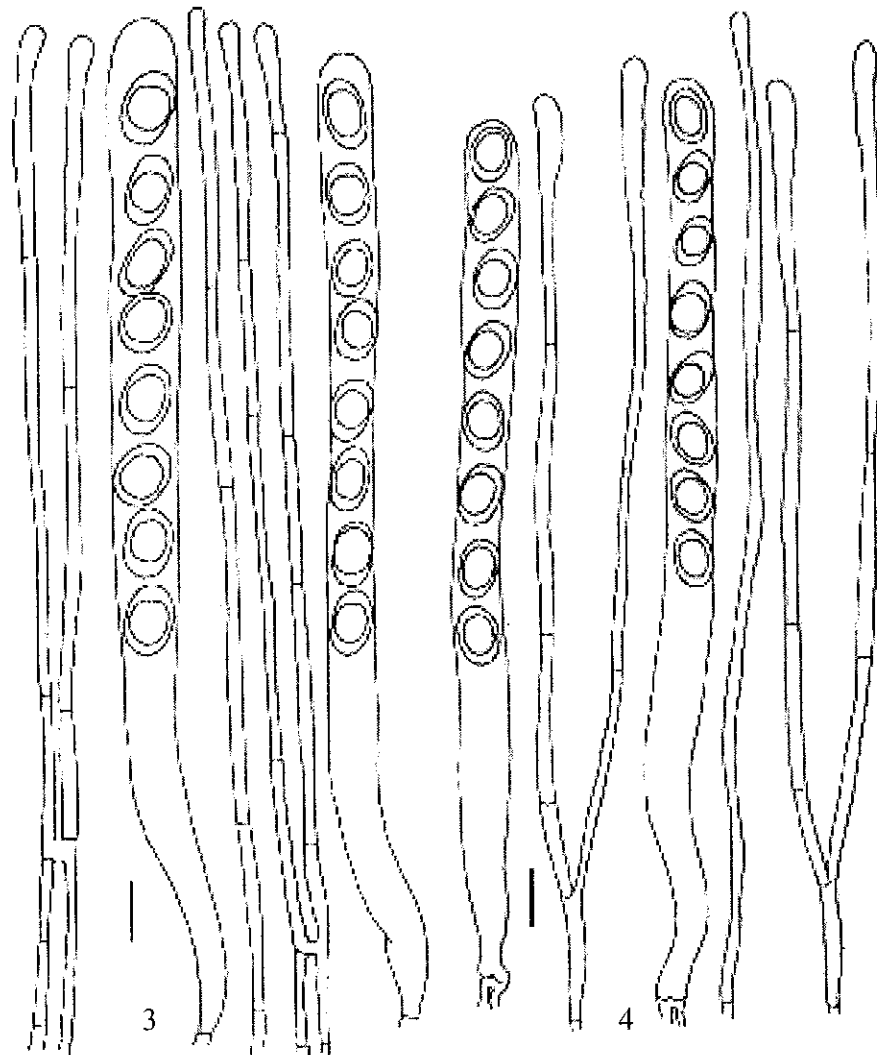


Fig. 3–4. 3: *Helvella leucomelaena* (F. Landeros 3404, IBUG), ascas pleuorrincosas y paráfisis. 4: *Helvella solitaria* (G. Guzmán 29101, XAL), ascas aporrincosas. Escala de las barras: 3, 4: 10 μ m.

Helvella solitaria fue además citada por Vite-Garín et al. (2006), desafortunadamente no se localizó el ejemplar depositado en el Herbario FCME (T. Vite-Garín 61, FCME 21284). Como se mencionó anteriormente, la característica que distingue a *H. solitaria* de *H. leucomelaena* es el tipo de asca, y Vite-Garín et al. (2006) no refieren qué tipo de asca presenta el ejemplar que revisaron. El ejemplar que aquí indicamos fue anteriormente referido como *H. leucomelaena* por Medel y Calonge (2004).

Material revisado: JALISCO: Municipio de Autlán, Sierra de Manantlán, predio Las Joyas, entre el Zarzamoro y puerto de San Campus, 14 octubre 1984, G. Guzmán 29101 (XAL).

Material adicional revisado: FINLANDIA: Mustiala, in horto, ad marg. rivula, 21 septiembre 1866, P. Karsten PAK 3288 (H, *H. solitaria*, **holotipo**). ITALIA: Bosee di lance sopra Terzolaj, mayo 1882, J. Bresadola (S, *H. queletii*, **holotipo**).

Helvella stevensii Peck, Bull. Torrey bot. Club 31: 182, 1904

Comentarios taxonómicos: Se caracteriza por presentar el apotecio en forma lobada, con la superficie estéril pubescente, el himenio de color canela a marrón pálido, y el estípite liso, de color crema a crema amarillento y pubescente. Puede confundirse con *H. compressa* (ver los comentarios taxonómicos bajo esta especie) y *H. elastica*, pero esta última es glabra, mientras que *H. stevensii* es pubescente (Dissing, 1966b). Abbott y Currah (1997) consideraron a *H. stevensii* como un sinónimo de *H. latispora*; pero seguramente se trata de taxones diferentes, debido a que el tamaño de las ascosporas es diferente, en *H. latispora* son de 18–21 x 13.5–18 µm y en *H. stevensii* de 17–20 x 10–12.5 µm.

Helvella stevensii es poco frecuente en los bosques de coníferas de México. Bautista et al. (1986) la registraron por primera vez para el país, pero mencionaron el estípite de “color café oscuro” como la característica que la diferenciaba de *H. elastica*, que tiene “pie blanquecino”, lo cual es una imprecisión, ya que ambas especies presentan estípite de tonos claros. Desafortunadamente no se pudo estudiar el espécimen que citaron (Montiel 169, Herbario Micológico de la Universidad Autónoma de Morelos), motivo por el cual no podemos corroborar su determinación.

Material revisado: BAJA CALIFORNIA NORTE: km 15 al NO de Ensenada, El Junco, marzo 1983, N. Ayala 105 (XAL). ESTADO DE MÉXICO: Villa del Carbón, Presa Plan Presidencial Benito Juárez, 23 agosto 1984, A. Estrada-Torres 1109 (ENCB). QUERÉTARO: Municipio de San Joaquín, Santa Ana, sin fecha, Alatorre 75 (IBUG).

Helvella sulcata Afzel., K. Vetensk-Akad. Handl. 4: 305, 1783, Tab. 10, Fig. 1

Comentarios taxonómicos: *Helvella sulcata* se caracteriza por presentar el apotecio lobado unido en dos puntos al estípite, la superficie estéril del apotecio estéril y sin costillas, el himenio de tonos oscuros (marrón oscuro a negro), y el estípite costillado, blanquecino, de color crema o grisáceo oscuro, puede confundirse con *H. lacunosa*, pero ésta presenta el estípite lagunoso y costillas en la superficie estéril del apotecio (Afzelius, 1783; Weber, 1972). Otras especies afines son *H. palustris* Peck, y *H. phlebophora* Pat. & Doass., pero ambas especies tienen el apotecio libre (Peck, 1880; Dissing, 1966b). *Helvella sulcata* crece en bosque de *Quercus* y coníferas, y seguramente es una especie común, que está etiquetada en muchos herbarios del país como *H. lacunosa*.

García-Romero et al. (1970) mencionaron que *H. sulcata* fue citada por Lloyd 1898-1926 de México, sin localidad precisa. Revisamos los escritos de Lloyd (Mycological writing, vol. 1-5, 1898-1926) y no encontramos ninguna referencia de esta especie. Además revisamos el trabajo de Stevenson (1933), que es un índice general de las especies mencionadas en los trabajos de Lloyd, y tampoco hace referencia a *H. sulcata*. Posteriormente esta especie fue citada por Guzmán-Dávalos et al. (2001) del estado de Jalisco.

Material revisado: JALISCO: Municipio de Bolaños, Sierra de los Huicholes, km 30 Bolaños-Tuxpan de Bolaños, 24 agosto 2004, I. Álvarez 2195 (IBUG); Municipio de Guadalajara, sin fecha, J. Manzi 514 (IBUG); Municipio de Tecolotlán, Sierra de Quila, 2 km al N de La Ciénega, 26 septiembre 2009, F. Landeros 3353 (IBUG); Municipio de Tequila, volcán de Tequila, 29 agosto 1985, L. Guzmán-Dávalos 2506-B (IBUG), 10 octubre 2009, F. Landeros 3360 (IBUG), 14 septiembre 1986, O. Rodríguez 347 (IBUG), 21 septiembre 1986, O. Rodríguez 361 (IBUG), 12 octubre 1986, O. Rodríguez 525 (IBUG). MORELOS: Hueyapan, 1980, De Ávila 13B (ENCB). QUERÉTARO: Municipio de San Joaquín, Nuevo San Joaquín, 7 agosto 2004, F. Landeros 1848 (IBUG, **holotipo**); Municipio de San Joaquín, Ranas, 15 septiembre 2004, F. Landeros 883 (IBUG).

Comentarios de las especies dudosas

En este apartado se incluyen las especies de las que no se pudo confirmar su presencia en México, o que son sinónimas de otras.

Helvella adhaerens Peck, Annual Report on the New York State Museum of Natural History 54: 956, pl. 50, Figs. 11-15, 1902

Comentarios taxonómicos: Esta especie fue citada por Nieto-Roaro (1941) para México, sin indicar material estudiado. La describió “con el margen [del apotecio] adherido al estípote, blanquecino o amarillento” y el “[e]stípote... igual color al del píleo, liso”. Desafortunadamente ninguna de las especies descritas hasta el momento tienen el apotecio adherido al estípote y el estípote liso; las que tienen el apotecio adherido al estípote presentan estípote lagunoso (*H. lacunosa*, *H. fusca* y *H. lactea*). Por otro lado, Dissing (1966b) describió a *H. adhaerens* como un sinónimo de *H. elastica*. Nieto-Roaro (1941) también citó en su trabajo a *H. elastica* (pp. 564-565), pero su descripción y fotografía (fig. 3) claramente pertenecen a *H. crispa*. Con base en lo anterior no podemos definir a qué especie corresponde lo que Nieto-Roaro (1941) determinó como *H. adhaerens*.

Helvella corium (O. Weberb.) Masee, Brit. Fung.-Fl. 4: 463, 1895

Comentarios taxonómicos: Fue citada para México por Manzi (1978), Chacón y Medel (1992), Pompa-González y Cifuentes (1991), Vite-Garín (2005), y Vite-Garín et al. (2006). La descripción que hizo Manzi (1978) en su clave sinóptica no contribuye para reconocerla, debido a que esa misma descripción aplica para *H. macropus*. De hecho Guzmán-Dávalos y Trujillo (1984) mencionaron que “*H. corium* [de Manzi] es *Macropodia macropus* [= *H. macropus*]”, desafortunadamente Manzi (1978) no citó material estudiado para corroborar esto. Por otro lado, la descripción de Chacón y Medel (1992) coincide con el concepto de *H. corium* dado por Masee (1895); sin embargo, al revisar el material (G. Guzmán 8288 y L. Montoya 972, XAL) que estudiaron, determinamos ambos especímenes corresponde a *H. macropus*, por presentar ascoporas fusoides a subfusoides. Pompa-González y

Cifuentes (1991), Vite-Garín (2005), y Vite-Garín et al. (2006) estudiaron el mismo espécimen (Corona y L. Pérez-Ramírez 736, FCME 14047), el cual determinaron como *H. corium*. La fig. 6A' de este espécimen que mostró Vite-Garín (2005) no corresponde con *H. corium*, debido a que el himenio y estípites son de color marrón, no negro, y las ascosporas son subfusoides, no elipsoides, y al estudiarlo, determinamos que se trata de *H. macropus*.

***Helvella kichneri* Manzi nom. nud.**, Boletín del Instituto de Botánica 8: 29, 1978

Comentarios taxonómicos: Fue propuesta por Manzi (1978) pero debido a que no cumple con las disposiciones del Código de Viena (McNeill et al 2006), ya que la publicación no incluye descripción, diagnóstico o alguna referencia a una descripción o diagnóstico (art. 50B.1), es un *nomen nudum*. Guzmán-Dávalos y Trujillo (1984) también la refieren como *nomen nudum*, al igual que a *H. salvatierrae*, *H. sierrae* y *H. sogarii*, también propuestas en el mismo trabajo. La descripción que Manzi (1978) hizo de esta especie se reduce a las características que se incluyen en la clave dicotómica, las cuales son demasiado ambiguas para saber con certeza si efectivamente se trata de un taxón distinto. Desafortunadamente no citó material estudiado y en el Herbario IBUG no existe material etiquetado bajo este nombre.

***Helvella latispora* Boud.**, Bull. Soc. mycol. Fr. 14: 16, 1898

Comentarios taxonómicos: Fue registrada para México por Vite-Garín (2005) y Vite-Garín et al. (2006). De acuerdo con Vite-Garín (2005) el concepto de *H. latispora* que siguió es el de Abbott y Currah (1997), el cual, como se discutirá a continuación, no corresponde a esta especie. *Helvella latispora* fue descrita con ascosporas de 18–20 x 15–17 μm por Boudier (1907, p. 16, lám. III, fig. IIe), similares a las que indicó Dissing (1966b), de 18–19.4–21 x 13.5–14.8–18 μm . Sin embargo, Abbott y Currah (1997) mencionaron ascosporas de (16.5–) 18.6–19.9 (–20.8) x (10.9–) 11.4–12.4 μm , pero tales medidas corresponden a *H. stevensii*. Debido a este error es que Abbott y Currah (1997) consideraron a *H. stevensii* como un sinónimo de *H. latispora*. El ejemplar de Vite-Garín (2005) pudiera corresponder a *H. stevensii*, ya que las ascosporas que reportó son de (15.45–) 16.48–17.51 (–18.54) x 10.3–11.33 μm , pero las coloraciones que presenta el material en seco no parecen corresponder con *H. stevensii*, debido a que esta especie aún en seco presenta coloraciones claras. Desafortunadamente no se localizó este espécimen en el Herbario FCME.

***Helvella leucopus* Pers.**, Mycol. eur. (Erlanga) 1: 213, 1822

Comentarios taxonómicos: Fue citada de México por Medel y Calonge (2004), escribiendo que esta especie es “[f]ácil de reconocer por su píleo ondulado, negro, con estípites blanco y liso”, además se distingue por el tamaño de las ascosporas (21–24 x 13–15 μm) (Dissing, 1966b). Se revisó el material (V. Bandala 1313, XAL) que citaron Medel y Calonge (2004) y no corresponde con *H. leucopus* por las siguientes características: 1) Pubescencias (*H. leucopus* es glabra en la superficie estéril del apotecio y estípites, mientras que el espécimen tiene fascículos hifales de 30–80 μm en la superficie estéril del apotecio y de 30–90 μm en el estípites); y 2) tamaño de las ascosporas (en *H. leucopus* son de 21–24 x 13–15 μm , y en el espécimen estudiado son de 17–20 x 10.5–12 μm). Con base en las características anteriormente mencionadas consideramos que el espécimen V. Bandala 1313 corresponde a *H.*

pezizoides. Vite-Garín (2005) y Vite-Garín et al. (2006) también la mencionaron para México en su clave sinóptica, pero no la describieron ni indicaron material estudiado.

Helvella leucopus* var. *populina I. Arroyo & Calonge, en Calonge, Bol. Soc. Micol. Madrid 25: 302, 2000

Comentarios taxonómicos: Esta variedad fue citada para México por Medel y Calonge (2004). Después de revisar el ejemplar tipo de esta especie y el espécimen citado (S. Chacón 3184, XAL) por Medel y Calonge (2004), podemos asegurar que el ejemplar de México no corresponde con ese taxón. Las características que las distinguen son: 1) pubescencias en la superficie estéril del apotecio y estípite (en el ejemplar mexicano las pubescencias de la superficie estéril del apotecio miden de 30–100 µm de largo y las del estípite de 60–180 µm de largo, mientras que el ejemplar tipo de *H. leucopus* var. *populina* es totalmente glabro); 2) reacción hemiamiloide (todos los tejidos del ejemplar mexicano son rr–, mientras que en el tipo de *H. leucopus* var. *populina* el tejido medio del estípite es rr+); 3) forma de las ascosporas (el espécimen mexicano tiene ascosporas fusoides a subfusoides, mientras que el tipo de *H. leucopus* var. *populina* tiene ascosporas elipsoides); y 4) color del himenio (el espécimen mexicano tiene himenio de color marrón claro, mientras que el tipo de *H. leucopus* var. *populina* lo tiene de color marrón oscuro a negro). Es interesante la forma de ascosporas del material mexicano; como se mencionó anteriormente sólo *H. macropus* y *H. terrestris* tienen ascosporas fusoides a subfusoides, y aunque algunos especímenes de *H. macropus* puede tener apotecios lobados, las coloraciones de este ejemplar no corresponden con *H. macropus* y posiblemente se trate de un taxón nuevo.

Material adicional revisado: ESPAÑA: Guadalajara, Sigüenza, 8 mayo 1988, M.J. Rodríguez 888 (MA Fungus 22870, **holotipo**).

Helvella queletiana Sacc. & Traverso, *nom. ambig.*, Syll. fung. (Abellini) 19: 850, 1910

Comentarios taxonómicos: Fue citada para México por Nieto-Roaro (1941), con “[p]ileo: Bilobado, comprimido y luego doblado, festoneado, con una venas características que bajan hacia el estípite, reticulado, de color gris claro” y “[e]stípite: Corto, grueso, lagunoso, acanalado, pruinoso, grisáceo”, pero su figura 4 representa el ascoma de *H. solitaria*; desafortunadamente no citó material estudiado. Vite-Garín et al. (2006) no encontraron ejemplares de esta especie, pero en su clave sinóptica la incluyeron.

Helvella queletiana es una especie que se ha malinterpretado, posiblemente por los cambios que ha tenido de nombre, lo que hizo que la información de la descripción original se abandonara. Fue originalmente descrita como *H. venosa* por Quélet (1880), pero Fries (1823) ya había usado este nombre para otra especie, por lo que posteriormente se describió como *H. phlebophora* por Saccardo (1889), pero este nombre también ya había sido usado para otra especie por Patouillard & Doassans (en Patouillard, 1886), para terminar finalmente con el nombre *H. queletiana* por Saccardo y Traverso (in Saccardo, 1910). En la obra de Quélet (1880) hay una figura (lámina VIII, fig. 15) que representa lo que el autor definió como *H. venosa*, y coincide con la descripción, con el apotecio bilobulado y glabro. Posteriormente Saccardo (1889) dio las mismas características, desafortunadamente Anderson e Ickis (1921) hicieron una malinterpretación, describiendo a la especie con apotecio de forma convexa, aclarando que sólo en los estadios jóvenes puede ser en forma de silla de montar (lo común dentro del género es que los especímenes jóvenes de algunas especies sean en forma de copa y los adultos de forma lobada), pero además mencionaron que el margen del apotecio normalmente es libre (en la figura de Quélet se observa que el apotecio está adherido al estípite), y que sus ascomas son glabros. Las

figuras de Anderson e Ickis (1921, figs. 6-7) son muy diferentes a la figura de Quélet (1880). Dissing (1966b) se basó en parte en la descripción de Anderson e Ickis (1921) y definió a esta especie con apotecio de forma convexa, pero pubescente. Éste es el concepto que actualmente se maneja para la especie, de hecho Calonge y Arroyo (1990) en su clave para determinar las especies de *Helvella* de España mencionaron a ésta como pubescente. Con base en lo anterior, pensamos es necesario hacer una revisión más extensa sobre el concepto y delimitación de *H. queletiana*, por lo cual por ahora la consideramos como “*nomen ambiguum*”.

***Helvella salvatierrae* Manzi, nom. nud., Boletín Instituto de Botánica 8: 29, 1978**

Comentarios taxonómicos: Fue propuesta por Manzi (1978), pero al igual que *H. kirchneri*, no cumple con las disposiciones del Código de Viena (McNeill et al 2006, art. 50B.1). Guzmán-Dávalos y Trujillo (1984) refieren que *H. salvatierrae* corresponde a *H. crispa*, pero Manzi (1978) también mencionó a esa especie en su estudio; sin embargo las características que utilizó para separarlas son demasiado ambiguas. Además, Manzi (1978) no citó material estudiado y en el Herbario IBUG no existe ningún espécimen etiquetado con este nombre.

***Helvella sierrae* Manzi, nom. nud., Boletín Instituto de Botánica 8: 29, 1978**

Comentarios taxonómicos: Fue propuesta por Manzi (1978), pero al igual que *H. kirchneri* y *H. salvatierrae* no cumple con las disposiciones del Código de Viena (McNeill et al 2006, art. 50B.1). Guzmán-Dávalos y Trujillo (1984) no mencionaron a qué especie posiblemente corresponde y Manzi (1978) no dio elementos suficientes para definir si se trata de un taxón distinto o si corresponde a uno ya descrito. No existe material etiquetado como *H. sierrae* en el Herbario IBUG.

***Helvella sogarii* Manzi, nom. nud., Boletín Instituto de Botánica 8: 29, 1978**

Comentarios taxonómicos: Fue propuesta por Manzi (1978), y está en el mismo caso que las otras tres especies que designó, ya que no cumple con las disposiciones del Código de Viena (McNeill et al 2006, art. 50B.1). Guzmán-Dávalos y Trujillo (1984) refieren que *H. sogarii* seguramente corresponde a *H. lacunosa*, pero Manzi (1978) también mencionó a esa especie en su estudio. Las características que utilizó Manzi (1978) son demasiado ambiguas y no pueden atribuirse a un taxón en específico y desafortunadamente no citó material estudiado y en el Herbario IBUG no existen especímenes bajo este nombre.

***Helvella subglabra* N.S. Weber, Michigan Bot. 11(4): 179, 1972**

Comentarios taxonómicos: Guzmán-Dávalos et al. (2001) citaron a *H. subglabra* para Jalisco. Revisamos el ejemplar tipo de *H. subglabra* y los especímenes (F. Trujillo 589, G. Guzmán 29046, I. Álvarez 720, I. Arriaga 31, L. Guzmán-Dávalos 1697, 2376, 2970, todos en IBUG, y algunos con duplicado en XAL) citados por Guzmán-Dávalos et al. (2001), y concluimos que algunos corresponden a *H. atra* y a *H. pezizoides*, otros debido a su estado de inmadurez o deterioro, no se pudieron determinar.

Material adicional estudiado: E.U.A.: Michigan, Washtenaw Co., Stinchfield Woods, cerca de Dexter, 13 octubre. 1968, N.J. Smith 2145 (MICH, Barcode 14381, **holotipo**).

Clave taxonómica para las especies de *Helvella* que crecen en México y relacionadas

- 1.- Ascas aporrincosas *H. leucomelaena*
- 1.- Ascas pleurorricosas 2
- 2.- Ascosporas fusoides o subfusoides *H. macropus*
- 2.- Ascosporas elipsoides 3
- 3.- Estípite liso, algunas veces con pliegues, pero nunca con verdaderas costillas 4
- 3.- Estípite costillado o lagunoso 15
- 4.- Apotecio irregularmente lobado o en forma de silla de montar 5
- 4.- Apotecio en forma de copa bien definida 14
- 5.- Estípite de color crema o blanquecino 6
- 5.- Estipe grisáceo o negro 11
- 6.- Superficie estéril del apotecio glabra o subglabra 7
- 6.- Superficie estéril del apotecio pubescente 10
- 7.- Himenio marrón oscuro o negro 8
- 7.- Himenio blanquecino o marrón pálido 9
- 8.- Ascosporas de 21–24 x 13–15 μm *H. leucopus**
- 8.- Ascosporas de 17.5–21 x 10.5–12 μm *H. albella*
- 9.- Margen del apotecio no se recurva hacia el himenio cuando joven; estípite hueco; ascosporas de 18–22 x 11–13.5 μm *H. elastica*
- 9.- Margen del apotecio recurvado hacia el himenio cuando joven; estípite sólido; ascosporas 18–22 x 14–18 μm *H. latispora**
- 10.- Himenio de color marrón o marrón grisáceo; células basales del excípulo ectal y excípulo medular hemiamiloides *H. compressa*
- 10.- Himenio de color canela o marrón claro; excípulo ectal no hemiamiloide, excípulo medular ligeramente hemiamiloide *H. stevensii*
- 11.- Superficie estéril del apotecio glabra o subpubescente 12
- 11.- Superficie estéril del apotecio pubescente 13
- 12.- Himenio grisáceo o marrón grisáceo, nunca negro; superficie estéril del apotecio subglabra; excípulo medular y tejido medio del estípite hemiamiloide *H. subglabra**
- 12.- Himenio gris oscuro a negro, superficie estéril del apotecio glabra; excípulo medular no hemiamiloide, tejido medio del estípite hemiamiloide *H. atra*
- 13.- Ascomas relativamente pequeños (apotecio hasta 15 mm de diám. y estípite hasta 25 x 3 mm); himenio de color sepia o marrón *H. ephippium*
- 13.- Ascomas relativamente grandes (apotecio de 15–55 mm de diám. y estípite de 20–60 x 3–15 mm); himenio de color marrón oscuro a negro *H. pezizoides*
- 14.- Apotecios maduros con diámetro igual o más grande que la longitud del estípite *H. cupuliformis*
- 14.- Apotecios maduros con diámetro menor que la longitud del estípite *H. fibrosa*
- 15.- Apotecio maduro en forma de copa 16
- 15.- Apotecio maduro lobado, irregularmente lobado o en forma de silla de montar 18
- 16.- Costillas de borde agudo o afilado *H. acetabulum*
- 16.- Costillas de borde redondeado 17
- 17.- Costillas presentes en la superficie estéril del apotecio *H. costifera*

- 17.- Costillas ausentes en la superficie estéril del apotecio, o sólo llegan a la parte basal *H. solitaria*
- 18.- Superficie estéril del apotecio glabra o subpubescente 19
- 18.- Superficie estéril del apotecio pubescente 21
- 19.- Estípite principalmente costillado *H. sulcata*
- 19.- Estípite principalmente lagunoso 20
- 20.- Himenio blanquecino a crema *H. lactea*
- 20.- Himenio negro, grisáceo o marrón oscuro *H. lacunosa*
- 21.- Himenio de color crema pálido, no moteado; fascículos hifales del apotecio de 50–130 μm longitud; pigmentos de la células de la capa externa del estípite no son visibles en azul de algodón *H. crispa*
- 21.- Himenio moteado, zonas de tonos marrón grisáceo sobre un fondo crema; fascículos hifales del apotecio de 100-200 μm longitud; pigmentos de las células de la capa externa del estípite son visibles en azul de algodón *H. maculata**

* Especies que no se reconoce que estén distribuidas en México

Discusión

Después de la revisión de especímenes de *Helvella* depositados en los herbarios ENCB, FCME e IBUG y de comparaciones con especímenes tipo, de las 28 especies previamente citadas para México, en este trabajo sólo se reconocen las siguientes 16 especies para el país: *H. acetabulum*, *H. albella*, *H. atra*, *H. costifera*, *H. crispa*, *H. cupuliformis*, *H. elastica*, *H. ephippium*, *H. fibrosa*, *H. lactea*, *H. lacunosa*, *H. leucomelaena*, *H. macropus*, *H. pezizoides*, *H. solitaria*, *H. stevensii* y *H. sulcata*, además se reporta a *H. compressa* como un registro nuevo para el país.

Vite-Garín et al. (2006) en su trabajo sobre *Helvella* en México incluyeron en su clave sinóptica varias especies de *Helvella* con paráfisis sin septos y no ramificadas. Nannfeldt (1937) en la delimitación que hizo del género no mencionó nada al respecto de estas características para las paráfisis, lo mismo que Weber (1972, 1975) y Abbott y Currah (1988, 1997), mientras que Anderson e Ickis (1921), Eckblad (1968) y Rifai (1968) describieron al género con paráfisis septadas, excepto para las paráfisis de pared gruesa presentes en *H. crassitunicata*, que son no septadas. Coincidimos con los autores que definen al género con paráfisis de pared delgada con septos, y no sabemos si por el método de montaje de las preparaciones que usaron Vite-Garín et al. (2006) no observaron los septos para varias especies. Respecto a las paráfisis ramificadas, Anderson e Ickis (1921) las describieron como algunas veces ramificadas, ya que éstas pueden ser simples o ramificadas, es decir, en un mismo espécimen de cualquier especie de *Helvella* se pueden encontrar paráfisis ramificadas y sin ramificar.

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Capítulo VI. Discusión general y conclusiones

DISCUSIÓN GENERAL

ESTUDIO CON CARACTERES MORFOLÓGICOS

Revisión de ejemplares tipo

Con el fin de tener un concepto claro de las especies del género, se realizó una revisión de 28 ejemplares tipo, correspondientes a 26 taxones (Cuadro 1).

Cuadro 1. Especímenes tipo que se estudiaron

Espece	Tipo	Herbario
<i>Acetabula calyx</i> Sacc.	Isotipo	K
<i>H. chinensis</i> (Velen.) Nannf.	Holotipo	PRM
<i>H. compressa</i> (Snyder) N.S. Weber	Holotipo	WTU
	Isotipo	NY
<i>H. confusa</i> Harmaja	Holotipo	H
<i>H. connivens</i> Dissing & M. Lange	Holotipo	MICH
<i>H. costifera</i> Nannf.	Isolectotipo	S
<i>H. crassitunicata</i> N.S. Weber	Holotipo	MICH
<i>H. cupuliformis</i> Dissing & Nannf.	Paratipo	UPS
<i>H. dryadophila</i> Harmaja	Holotipo	O
<i>H. fusca</i> Gillet	Epitipo	S
<i>H. griseoalba</i> N.S. Weber	Holotipo	MICH
<i>H. hyperborea</i> Harmaja	Holotipo	H
<i>H. leucopus</i> var. <i>populina</i> I. Arroyo & Calonge	Holotipo	MA
<i>H. maculata</i> N.S. Weber	Holotipo	MICH
<i>H. melaleuca</i> Rifai	Holotipo	K
<i>H. pallidula</i> N.S. Weber	Holotipo	MICH
<i>H. paraphysitorquata</i> I. Arroyo & Calonge	Holotipo	MA
<i>H. pocillum</i> Harmaja	Holotipo	UPS
<i>H. queletii</i> Bres.	Holotipo	S
<i>H. robusta</i> S.P. Abbott	Holotipo	DAOM
<i>H. solitaria</i> P. Karst.	Holotipo	H
<i>H. subglabra</i> N.S. Weber	Holotipo	MICH
<i>H. ulvinenii</i> Harmaja	Holotipo	H
<i>H. verruculosa</i> (Sacc.) Harmaja	Holotipo	K
	Isotipo	FH
<i>Peziza debeauxii</i> Roum.	Isotipo	K
<i>P. subclavipes</i> W. Phillips & Ellis	Lectotipo	NY

El estudio de los especímenes tipo sirvió para completar y corregir descripciones originales de todas las especies, y delimitar especies problemáticas.

Con respecto a las correcciones, la más común fue la ornamentación de las ascosporas. Por ejemplo, Arroyo y Calonge (1990) definieron a *H. leucopus* var. *populina* y *H. paraphysitorquata* con ascosporas lisas. Sin embargo, sus especímenes maduros claramente tienen esporas verrugosas;

probablemente el tipo de rehidratación que hicieron (KOH al 2% o NH₃ al 10%) provocó que la ornamentación se perdiera.

A su vez, al corregir y/o completar las descripciones originales de las especies, se pudo sinonimizar o delimitar de mejor manera especies problemáticas. Ejemplo de sinónimos que se describieron en este estudio son: *H. queletii* de *H. solitaria*, *H. dryadophila* de *H. verruculosa*, *H. pallidula* de *H. fibrosa*. A continuación se describen brevemente ambos casos. *Helvella queletii* fue descrita por Bresadola (1882), pero la descripción carece de medidas de ascosporas, lo cual generó confusión. De acuerdo a nuestras mediciones, el espécimen tipo tiene ascosporas de 17.5–21.5 × 10.5–12.5 µm, lisas. Por otro lado, Karsten (1871) describió a *H. solitaria* con ascosporas de 14–16 × 10 µm, pero sin mencionar su ornamentación. Al revisar el espécimen tipo se observó que presenta ascosporas verrugosas, de 15–17.5 × 9.5–11.5 µm, y ascosporas lisas de 18–20 × 9.5–12 µm. Este es un ejemplo de descripción de especies con base en diferentes estados de maduración de las ascosporas, siendo las ascosporas jóvenes más grandes y lisas, y las adultas más pequeñas y verrugosas. Por tal motivo, se apoya la propuesta de Harmaja (1977a) de considerarlas sinónimos, siendo *H. solitaria* el nombre que tiene prioridad.

Por otro lado, Abbott y Currah (1997) propuso que *H. dryadophila* sea un sinónimo de *H. verruculosa*, al igual que *H. pallidula* de *H. fibrosa*, con lo cual coincidimos, ya que en ningún caso existen características que permitan su separación, Además se propone un nuevo sinónimo, *H. hyperborea* de *H. costifera*, debido a que las características que había propuesto Harmaja (1978, 1979) para separarlas, entre las que destaca las costillas en la superficie estéril del apotecio, se tratan de características continuas, y no discretas, es decir son producto de la variación de la especie.

Ejemplo en donde se hizo delimitación de especies problemáticas son *H. subglabra* vs *H. atra*, *H. compressa* y *H. fusca*. Weber (1972) propuso a *H. subglabra* como un taxón diferente a *H. atra*. El color del ascoma, el pigmento en las células del excípulo ectal, y superficie estéril del apotecio finamente pruinosa (subpubescente) fueron utilizadas para su separación. Sin embargo, Häffner (1987) y Abbott & Currah (1997) consideraron a ambas especies como sinónimos, debido a que para ellos las características mencionadas por Weber (1972) no eran suficientes para separarlas, y eran producto de la variación de la especie. Los datos aquí analizados apoyan la propuesta de Weber (1972) por lo tanto, *H. subglabra* es un taxón independiente. En *H. subglabra* el tejido del excípulo medular del apotecio y el tejido medio del estípite son fuertemente rojizos en reactivo de Melzer, mientras que todos los tejidos del ascoma de *H. atra* son negativos, que quiere decir que se trata de taxones independientes; Más aún, el pigmento marrón en la pared celular de las paráfisis, excípulo ectal y tejido externo del estípite son visibles en azul de algodón en *H. atra*, y no visibles en *H. subglabra*.

Snyder (1936) describió a *Paxina compressa* (= *H. compressa*) con ascosporas de 23–25 × 13–19 µm. Sin embargo, Weber (1975) registró ascosporas de 19.5–21 × 12–14 µm, Abbott y Currah (1997) de 19.7–23.8 × 11.4–14.8 µm, y en este estudio se registran de 17.5–21.5 × 11–13.5 µm. Es posible que la variación se deba al método de hidratación que usó Snyder (1936), pero que desafortunadamente no indicó.

Helvella fusca fue descrita por Gillet (1879) con ascosporas esféricas a subesféricas, sin ninguna otra característica microscópica útil. Dissing (1966) consideró a esta especie como pubescente en la superficie estéril del apotecio y estípite, y por lo tanto cercana a *H. crispa*, pero al revisar el epitipo se observó que el espécimen presenta una superficie estéril del apotecio y estípite glabro a

subpubescente (es decir, tiene fascículos hifales hasta 50 μm de largo), lo cual la relaciona más a *H. lacunosa*, y ésto fue corroborado con el análisis filogenético.

Revisión del género *Helvella* en México

En México han sido registradas 30 especies y una variedad de *Helvella*. La revisión del material depositado en IBUG, ENCB, FCME y XAL, permitió seleccionar material de *Helvella* citado en trabajos previos para México (Manzi 1978, Bautista et al. 1986, Chacón y Medel 1992, Medel y Chacón 1997, Guzmán-Dávalos et al. 2003, Medel y Calonge 2004, Vite-Garín et al. 2006). No todos los especímenes citados se pudieron encontrar, por lo cual, en esos casos, se revisó a minuciosamente el artículo donde hicieron la descripción o la mención de la especie para determinar si correspondía con el taxón en cuestión.

Algunas de las especies de *Helvella* citadas para México (*H. adhaerens*, *H. corium*, *H. kichmeri*, *H. latispora*, *H. leucopus*, *H. leucopus* var. *populina*, *H. pityophila*, *H. queletiana*, *H. queletii*, *H. salvatierrae*, *H. sogarii* y *H. subglabra*) están incorrectamente determinadas o bien no hay ejemplar de referencia que permita su corroboración. Por tal motivo, sólo se pueden reconocer 18 especies del género para el país. Destaca *H. compressa*, que representan un nuevo registro para México (Landeros y Guzmán-Dávalos 2012).

Aporte de características nuevas en la taxonomía del género

Existe un conjunto de características que ayudan a reconocer a especies del género *Helvella* (Dissing 1966, Weber 1972 y Abbot & Currah 1997), a continuación se desglosan y comentan las características macroscópicas usadas en la taxonomía del género. La forma del apotecio es la característica más usada, y se evalúa si el espécimene es lobado o en forma de copa. El estípite es también considerado de importancia, y para este se describe si es liso, costillado (sulcado) o lagunoso. La coloración del ascoma (himenio, superficie estéril del apotecio y estípite), actualmente se le ha dado más peso, inclusive Weber (1972) lo utiliza para su clasificación infragenérica. La forma del borde de las costillas (redondeado o agudo) del estípite es importante para reconocer a *H. costifera* (costillas de borde redondeado) de *H. acetabulum* (costillas de borde afilado). También las costillas en la superficie estéril del apotecio (llegando a una cuarta parte, la mitad, tres cuartas partes, o hasta el borde, simples o bifurcadas, y/o anastomosadas) fueron consideradas por Harmaja (1977a, 1977b, 1978, 1979) de gran importancia, aunque actualmente sólo se considera importante la presencia o ausencia.

Por otro lado, las características microscópicas y microquímicas de importancia en la taxonomía del género se comentan a continuación. El tipo de ascas (aporrincosas o pleurorincosas) propuesto por Weber (1972) es la característica menos valorada, pero que los estudio filogenéticos aquí presentados, muestran que tal característica es de importancia para dividir al género en dos subgéneros. El tamaño y forma de las ascosporas (elipsoides, fusoides o subfusoides), sólo se ha visto que tiene importancia a nivel de especie, contrario a lo que pensaban Abbott & Currah (1997), quienes proponían que las esporas fusoides a subfusoides eran una característica exclusiva de la sección Macropodes. La pubescencias, es decir, el tamaño de los pelos o fascículos hifales son importantes, ya que hay secciones que comprenden exclusivamente especies glabras o pubescentes, es importante señalar que se recomienda usar la siguiente terminología: a) glabro (fascículos hifales ausentes), b) subpubescente (fascículos hifales menores de 50 μm de longitud), y c) pubescente (fascículos hifales mayores de 50 μm de longitud). El color de las células del excípulo ectal y las células de la capa externa del estípite es constante en los ascomas de la misma especie, por lo tanto, no es útil, sin embargo, en *H. ulvinenii* las

células del excípulo ectal presentan pigmento de color marrón dentro y en la pared la célula, mientras que las células de la capa externa del estípote son hialinas. La visibilidad del pigmento del hongo en azul de algodón es importante. es decir, además de describir el color del pigmento presente en las estructuras y su localización, también hay que evaluar si tal pigmento es visible en azul de algodón. Normalmente, el tamaño de las células del excípulo ectal y la capa externa del estípote son constantes, la excepción está en *Helvella* sp. 1, que se reconoce por presentar células excepcionalmente grandes. Por último, algunos tejidos se tornan de color rojizo en reactivo de Melzer, la respuesta se conoce como reacción hemiamoide (rr+), esta reacción tiene importancia desde el punto de vista taxonómico y filogenético.

ESTUDIO CON BASE EN SECUENCIAS DE ADN

El resultado del análisis filogenético utilizando secuencias de la región LSU del ADN_r mostró dos grandes clados. En el primero están agrupadas las especies de ascas aporrincosas (*H. leucomelaena* y *Helvella* sp. 1), y en el segundo las especies de ascas pleurorincosas (el resto de las especies). Aunque no pudieron resolverse las relaciones infragenéricas, hay dos clados con soporte, la sección *Leucomelaenae*, que alberga a *H. leucomelaena* y *Helvella* sp. 1, y la sección *Helvella*, formada por *H. maculata* y *H. crispa*.

ESTUDIO COMBINANDO CARACTERÍSTICAS MORFOLÓGICAS Y SECUENCIAS DE ADN

El análisis combinado con datos morfológicos y secuencias de ADN incrementó el número de caracteres parsimoniosamente informativos. También aumentó la resolución y apoyo de los diferentes clados. Por ejemplo el clado “b” (fig. 4, Landeros et al. 2012b), que corresponde a la sección *Lacunosae*, no tenía soporte cuando sólo se usaron datos moleculares (fig. 3, landeros et al. 2012b) y con la combinación de los datos presentó un soporte de BS-ML = 60%, BS-MP = 67%, PP = 100%; y el clado “2” (subgénero *Helvella*), y el subclado “a” (sección *Helvella*) (figs. 3 y 4, Landeros et al. 2012b) incrementaron el soporte en BS-ML = 71%, BS-MP = 88%, PP = 99%, y BS-ML = 94%, BS-MP = 87%, PP = 100%, respectivamente.

Los resultados apoyan que *Helvella* sección *Leucomelaenae*, *Helvella* sección *elasticae*, *Helvella* sección *Helvella* y *Helvella* sección *Lacunosae* son grupos naturales. En la primera se agrupan *H. leucomelaena* y *Helvella* sp. 1. A la sección *Elasticae* pertenecen *H. albella*, *H. compressa*, *H. elastica* y *H. stevensii*. La sección *Helvella* está conformada por *H. crispa* y *H. maculata*. Por último, a la sección *Lacunosae* la integran *H. fusca*, *H. lacunosa*, *H. sulcata* y *Helvella* sp. 2. Sin embargo, las relaciones filogenéticas entre *H. acetabulum*, *H. atra*, *H. costifera*, *H. cupuliformis*, *H. ephippium*, *H. griseoalba*, *H. macropus*, *H. pallidula*, *H. robusta*, *H. subglabra* y *H. ulvinenii*, continúan sin resolverse.

Nuevas especies para la ciencia

Se descubrieron 2 especies nuevas de *Helvella* para la ciencia, que están en proceso de ser publicadas. *Helvella* sp. 1 está relacionada con *H. leucomelaena*, por el tipo de asca, aunque las células del tejido del excípulo ectal y el tejido externo del apotecio son diferentes, Mientras que *Helvella* sp. 2, con base en su ascoma grabro a subpubescente y estípote sulcado, están asociadas a *H. sulcata*.

PERSPECTIVAS PARA ESTUDIOS FUTUROS EN EL GÉNERO

Revisión y secuenciación de las especies de *Helvella* faltantes (con espécimen tipo designado)

Desafortunadamente, no se consultaron los especímenes tipo de *H. asteri* (holotipo, PC), *H. lactea* (lectotipo, PC), *H. latispora* (holotipo, PC), *H. leucomelaena* (lectotipo, L), *H. leucopus* (lectotipo, L), *H. macropus* var. *brevis* (holotipo, NYS), *H. oblongispora* (holotipo, C), *H. palustris* (holotipo, NYS), *H. philonotis* (holotipo, C), *H. rivularis* (isotipo, C), *H. stevensii* (holotipo, NYS), *H. unicolor* (neotipo, PC), y *H. zhongtiaoensis* (holotipo, MHSU). Las razones son varias. No había curador designado (herbario NYS), el curador estaba dedicado a otras labores (herbario C), el herbario cerró por remodelación (herbario PC), el espécimen sólo se puede consultar en sus instalaciones (herbario L), o nunca respondieron a la solicitud de material (herbario MHSU). Se deberán intensificar esfuerzos por contactar a los curadores de los herbario mencionados anteriormente, para el estudio de tales especímenes.

Revisión y secuenciación de ejemplares de otras partes del mundo

Helvella es un género con distribución casi exclusiva del hemisferio norte. Aún es necesario estudiar y secuenciar material que se ha registrado del continente asiático, específicamente de Corea, China e India (Kaushal, 1991, Zhuang 2004, Han et al. 2010). La comparación entre estas y el material aquí estudiado, es necesario para el descubrimiento de especies crípticas.

CONCLUSIONES

El género *Helvella* comprende aproximadamente 52 especies, y está representado en México por 18 de ellas. Se ejecutó un análisis filonético con secuencias de 44 especímenes, que corresponden a 27 especies, utilizando características morfológicas y secuencias de ADN. Los resultados muestran que el análisis, combinado de características morfológicas y secuencias de ADN mejoran el soporte a los clados. Los resultados fueron mejores en comparación con la utilización de ambos tipos de datos por separado. De acuerdo con el análisis, filogenético el género *Helvella* debe ser dividido en dos subgéneros *Helvella* y *Leucomelaena* S.P. Abbott emend. Landeros & Guzm.-Dáv. El único carácter congruente con esta propuesta es el tipo de asca (pleurorricosa o aporrincosa).

Es posible reconocer las siguientes secciones en el subgénero *Helvella*, sección *Elasticae* Dissing emend. Weber, sección *Helvella*, y sección *Lacunosae* Dissing. Mientras que el subgénero *Leucomelaena* sólo presenta una sección (*Leucomelaena* Dissing emend. Weber). Es importante señalar que la delimitación de las secciones sólo es posible mediante la conjunción de varias características.

La reacción hemiamiloide en los tejidos ascomas es una característica de importancia taxonómica y filogenética en el género *Helvella*, situación que no había sido considerada en trabajos previos.

Finalmente, se encontraron dos nuevas especies de *Helvella*, ambas de Europa, las cuales están en proceso de ser publicadas.

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