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APPROACHES TO A CLASSIFICATION OF THE FAMILY UMBILICARIACEAE (LICHENISED ASCOMYCOTA) BY ANATOMICAL AND MORPHOLOGICAL CHARACTERS

ПОДХОДЫ К КЛАССИФИКАЦИИ СЕМЕЙСТВА UMBILICARIACEAE (LICHENISED ASCOMYCOTA) С ИСПОЛЬЗОВАНИЕМ АНАТОМО-МОРФОЛОГИЧЕСКИХ ПРИЗНАКОВ

The paper provides a detailed historical survey of existing classificarion schemes of family Umbilicariaceae Chevall. focusing on basic anatomical and morphological characters used for intrafamilar taxa circumscription.

Since early 1990s, when analyses of PCR-amplified genes (White et al., 1990) became standart procedure for molecular phylogenetics, fungal taxonomy changed significantly (Hibbert at al., 2007). The result of the genophyletic (phylogenomic) methodology implementation into the taxonomical investigations was the reducion and re-evaluation of taxonomical significance of traditional (anatomical, morphological, and biochemical) characters. However, biologically important traditional characters still remain useful for taxonomists, because the molecular phylogenetic tree seems not the final result of the phylogenetic reconstructions, but a valuable material for interpretations, biological context of which should be understood using "phylogenetic thinking" (Pavlinov, 2007).

The aim of the present paper is to give the historical survey of classification schemes of the family Umbilicariaceae Chevall. focusing on main characters used for intrafamilar taxa circumscription. The knowledge of these characters and their implications in the history of Umbilicariaceae systematics helps to understand the biological sense of the molecular reconstruction of phylogeny of the family; such a study is in progress (Davydov et al., 2004, 2006).

The Umbilicariaceae Chevall. (Umbilicariales J.C. Wei et Q.M. Zhou) ia a distinctive family of lichenized Ascomycetes. The predominantly saxicolous members of the family are mainly distributed at high altitudes and latitudes around the world.

The classification of Umbilicariaceae has been rearranged several times. Koerber (1855) treated the family comprising two genera: *Gyrophora* Ach. (=*Umbilicaria*[1]) and *Umbilicaria* Hoffm. (=*Lasallia*). Elenkin et Savicz (1910) described the third genus, *Gyrophoropsis* Elenkin et Savicz. Frey (1931, 1933) and Imshaug (1957) treated *Umbilicariaceae* as a monotypic family with the genus *Umbilicaria* Hoffm. comprising three subgenera. Scholander (1934) and Llano (1950) segregated the family into four

[1]To improve comprehensibility of the following text, the current genus names *Lasallia* and *Umbilicaria* are given in brackets for outdated genus and section concepts.

and five genera, respectively. Savicz (1950) suggested a concept with the two genera, *Umbilicaria* (=*Lasallia*) and *Gyrophora* (=*Umbilicaria*). Poelt (1962, 1977), Wei (1966), and Wei & Jiang (1993) applied the same concept and assigned the legitimate names: *Umbilicaria* Hoffm. and *Lasallia* Mérat, which are currently accepted by most taxonomists.

Genera, subgenera, and sections in Umbilicariaceae were circumscribed based on the variety of morphological characters like apothecial structure (Table 1), number and types of ascospores (Table 2), and specific morphological structures of the thallus (e. g., pustules, rhizinomorphs). Usage of mentioned groups of characters in the classification systems is discussed below in detail. While apothecial structures, or ascospore wall structures and spore numbers per ascus were frequently used for delimitation of genera and subgenera within Umbilicariaceae, several authors combined these two approaches in their classifications as well.

Apothecial morphology. Apothecia of Umbilicariaceae belong to the lecideine type, with excipulum proprium, to the sublecanorine type (see Wei, Jiang, 1988) with pseudoexcipulum, mostly formed by the upper thallus cortex, or to the intermediate type, composed by the pseudoexcipulum in the basal and by an excipulum proprium in the upper part (Henssen, 1970). The sublecanorine type is corresponding to the superlecideoid type according to the terminology of Frey (1936). A characteristic feature of the apothecia in the family is the formation of sterile parts, which are used as distinctive feature among leiodisc, omphalodisc, gyrodisc, and actinodisc apothecial types (Scholander, 1934).

The apothecial morphology has been used to classify the family from the beginning of the investigations by Acharius (1803), who circumscribed *Gyrophora* by the presence of striated (gyrose) apothecial discs and assigned five species to this genus. Furthermore, he placed two species with plane discs (now *Lasallia pennsylvanica* (Hoffm.) Llano and *L. pustulata* (L.) Mérat) into the genus *Lecidea*. Subsequently, scientists also employed apothecial morphology in their diagnoses (Table 1).

Scholander (1934) proposed four genera (Table 1), according to the four different apothecial types (leiodisc, omphalodisc, gyrodisc, and actinodisc), which are distinguishable by the characteristic formation of sterile parts in the apothecia.

Llano (1950) improved and modified the system, and assigned the legitimate names. The author considered *Gyrophora* Ach. as a synonym of *Umbilicaria* Hoffm., and reinstalled *Lasallia* Mérat instead. Supporting Scholander's view on apothecial types as being basic characters at genus level in this family, he improved and modified the system, by dividing the heterogenous genus *Umbilicaria* Hoffm. into the more natural units *Lasallia* Mérat and *Agyrophora* Nyl., and assigned the legitimate name *Umbilicaria* Hoffm. to Scholander's taxon *Gyrophora* Ach. Schade (1955) reduced all genera to subgeneric rank.

Wei (1966) and Wei & Jiang (1993) used the apothecial type as major diagnostic character for segregating *Lasallia* and *Umbilicaria* and to distinguish two subgenera within the first and four subgenera within the latter genus. These authors suggested to use primarily apothecial morphology for the delimitation of subgenera, but used ascospore

Table 1

Apothecial morphology as a character for the classification of the family Umbilicariaceae

Type of apothecium	Scholander (1934)	Llano (1950)	Schade (1955)	Wei (1966)
	Gen. *Umbilicaria*		Gen. *Umbilicaria*	
				Gen. *Lasallia*
Leiodisc	*Umbilicaria,* sect. *Lasalliae*	Gen. *Lasallia*	subg. *Umbilicaria*	subg. *Lasallia*
Gyrodisc				*Lasallia,* subg. *Pleiogyra*
				Gen. *Umbilicaria*
Leiodisc	*Umbilicaria,* sect. *Anthracinae*	Gen. *Agyrophora*	subg. *Agyrophora*	subg. *Agyrophora*
Omphalodisc	Gen. *Omphalodiscus*	Gen. *Omphalodiscus*	subg. *Omphalodiscus*	subg. *Omphalodiscus*
Gyrodisc	Gen. *Gyrophora*	Gen. *Umbilicaria*	subg. *Gyrophora*	subg. *Umbilicaria*
Actinodisc	Gen. *Actinogyra*	Gen. *Actinogyra*	subg. *Actinogyra*	subg. *Actinogyra*

types for segregating the subgenera into sections.

Scholander (1934) suggested an evolution of apothecial structure from leiodisc through omphalodisc to gyrodisc and actinodisc. However, Motyka (1964) and Oxner (1968) stated out the derived status of the leiodisc type with reference to *Lasallia*, which could be demonstrated by correlation with other assumed derived character states within *Lasallia*, like bicellular large mural spores. Members of subgenus (resp. genus) *Agyrophora* (= sect. *Anthracinae*) were pointed out by the same authors to represent the most basal representatives of Umbilicariaceae due to their unicellular ascospores and the lacking rhizinomorphs. Frey (1936) was the first to assume that leiodisc, omphalodisc and gyrodisc types may reflect only successional steps of apothecial ontogeny and should not be applied for classification. Henssen (1970) provided support of this suggestion by detailed ontogenetic studies. Imshaug (1957) emphasized that gyrodisc apothecia evolved more than once in the family. In the scheme of relationships within the Umbilicariaceae, he described section *Velleae* which he regarded as most ancient in the family, because it includes *Umbilicaria lambii*, assumed to be the most primitive taxon. Starting from there, he suggested four main evolutionary lineages: 1) to *Glabrae*, 2) to *Actinogira*, 3) through *Agyrophora* to *Lasallia*, 4) through *Agyrophora* and *Omphalodiscus* to sect. *Polymorphae*. Thus, gyrodisc apothecia of *Velleae* and *Polymorphae* represent two different lineages of development.

Types of ascospores and numbers per ascus . Species of the Umbilicariaceae exhibit a wide range of ascospore types. The majority of *Umbilicaria* spp. are characterized by octosporic asci with hyaline, simple, often immature spores. A few species such as *U. cylindrica* (L.) Delise ex Duby, *U. proboscidea* (L.) Schrad., *U. dendrophora* (Poelt) Hestmark, and, according to Frey (1933), *U. polyphylla* (L.) Baumg., occasionally have bicellular hyaline or brownish ascospores. Several species show asci with submuriform, i. e., oligocellular muriform spores (e. g. *U. cine-*

reorufescens (Schaer.) Frey, *U. crustulosa* (Ach.) Frey, *U. spodochroa* Hoffm., *U. koidzumii* Yasuda ex Satô), which, during development, may become brown. Members of *Lasallia* were characterized by one to two brown muriform spores per ascus.

Ascospore type-based classifications were applied very soon after light microscopical investigation became possible. First, Massalongo (1852) proposed the new genus *Macrodictya* for species with muriform, dark pigmented spores (subsequently, he used the prior generic name *Lasallia* Mérat for these species). Koerber (1855) divided Umbilicariaceae into two genera: *Gyrophora* (with small, unicellular, hyaline spores, 8 per ascus) and *Umbilicaria* (with large, multicellular, dark spores, 1–2 per ascus) and thus established the two-generic system of Umbilicariaceae as it is still accepted today (Table 2).

Elenkin & Savicz (1910) based on ascospore characters suggested a system including three genera (Table 2). Those authors proposed the new genus, *Gyrophoropsis* Elenkin et Savicz for *Umbilicaria caroliniana* Tuck., exhibiting octosporic asci with muriform spores.

Frey (1931, 1933, 1936) treated Umbilicariaceae as a monotypic family. He (Frey, 1931, 1933, 1949) created the system based on the complex of morphological characters of the thallus and on the ascospore types, while the role of apothecial morphology as a diagnostic character has been rejected. The genera proposed by Elenkin and Savicz (1910) were reduced to subgeneric rank (Table 2), and their circumscription was modified (Frey, 1931). In particular, the limits of the subgenus *Gyrophoropsis* were considerably expanded by including all the octosporic species with muriform spores being present in the upper part of the ascus, at least.

Savicz (1950) published a new concept with two genera applying Koerber's names "*Umbilicaria* Elenkin" (= *Lasallia* Mérat) and "*Gyrophora* Ach. em. Savicz" (= *Umbilicaria* Hoffm.) and transferred *Gyrophoropsis* to *Gyrophora* which was

Table 2

Ascospore type and number as a character for the classification of the family Umbilicariaceae

Ascospore types and numbers	**Koerber, 1855**	**Elenkin, Savicz, 1910**	**Frey, 1931**	**Savicz, 1950**	**Poelt, 1962; Wei, 1966**
			Gen. *Umbilicaria*		
Simple, hyaline, 8 per ascus	Gen. *Gyrophora*	Gen. *Gyrophora* s. Koerber	subg. *Gyrophora*		
Simple, hyaline to bicellular or muriform brownish, 8 per ascus				Gen. *Gyrophora* incl. 5 subg.	Gen. *Umbilicaria*
Muriform, brownish (mature), 8 per ascus		Gen. *Gyrophoropsis*	subg. *Gyrophoropsis*	*Gyrophora,* subg. *Gyrophoropsis*	
Muriform, brownish (mature), 1–2 per ascus	Gen. *Umbilicaria*	Gen. *Umbilicaria* s. Koerber	subg. *Lasallia*	Gen. *Umbilicaria* s. Koerber	Gen. *Lasallia*

thus extended by the addition of species with muriform ascospores. Poelt (1962, 1977), Wei (1966), and Wei & Jiang (1993) also applied a classification based on two genera with the currently accepted legitimate names *Umbilicaria* Hoffm. and *Lasallia* Mérat.

In Llano's system (Llano, 1950), the taxa belonging to *Gyrophoropsis* sensu Frey were assigned to the section *Spodochroa* Schol. ex Llano of the genus *Omphalodiscus* and the section *Muriformes* Llano of *Umbilicaria* (not shown in Table 2). Thus, species with muriform spores were assigned to two genera, delineated mainly on the base of apothecial morphology (see above).

Wei (1966) and Wei & Jiang (1993) suggested to use primarily apothecial morphology (see above) for the delimitation of subgenera, but used ascospore types for segregating the subgenera into sections. For species with muriform spores they applied two sections in different subgenera with the same delimitation as Llano (1950), but the name *Gyrophoropsis* (Elenkin et Savicz) A. Zahlbr. was restored for a section with the same delimitation as section *Muriformes* Llano of the genus *Umbilicaria*.

Thallus characters. While ascospores or apothecial type were in focus of systematics, Minks (1900) did not consider these characters as being relevant for the classification of this family and split the Umbilicariaceae into five units ("Artkreis") – "*U. pustulata", "U. tessellata", "U. hyperborea", "U. vellerea"*, and "*U. muehlenbergii"* – based on morphological traits of the thallus.

The systematical significance of the thalline pustules development was discussed several times. Frey (1931) showed that *U.* [*Lasallia*] *glauca* may also exhibit weakly developed pustulae, while *U. deusta, U. hyperborea, U. erosa*, and *U. corrugata* are occasionally pustulate. This was regarded as support for the hypothesis of a monophyletic origin of the Umbilicariaceae (ibid.). However, species which combine such characters as pustulate thallus, leiodisc apothecia, and muriform ascospores, were segregated by Savicz (1950) and Llano (1950) to the separate genus (*Lasallia* Mérat).

Frey (1933, 1949) suggested the division of the subgenus *Gyrophora* into four sections, i. e., *Vellea* Frey, *Polymorphae* Frey, *Glabrae* Frey, and *Anthracinae* Frey, mainly based on thalline characters, including characteristics of the upper and lower surface structure, color, and the presence of rhizinomorphs. In recent years, various authors mentioned groups of related species which particularly correspond to Frey's sections, like the "*U. vellea*-group" (Poelt, 1977; Poelt, Nash, 1993) and the "*U. cylindrica*-group" (Hestmark, 1993). Llano (1950) used the color of the lower surface to distinguish between two sections of *Lasallia*: *Pallidae* Llano (with light to dark, but never black surface) and *Obscurae* Llano (with wholly black surface).

Thus, authors of mentioned systems used different approaches to a classification of the family Umbilicariaceae to make the system natural. However, new data on molecular phylogeny (Davydov et al., 2004, 2006) suggest modifying the system, because obtained monophyletic groups are not in congruence with any of the traditional classifications.

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РЕЗЮМЕ

В статье дается детальный анализ классификационных схем семейства Umbilicariaceae с акцентом на используемые авторами систем анатомо-морфологические признаки. Существует две основные группы признаков, применяемых для выделения родов и подродов в семействе Umbilicariaceae: морфология апотеция либо структура и количество аскоспор. В качестве дополнительных признаков используются детали морфологического строения таллома (наличие либо отсутствие пустул, ризиноморф и др.). В настоящее время общепризнанной считается система из двух родов: *Umbilicaria* (8 спор в сумках, все типы апотециев, как правило, отсутствие пустул) и *Lasallia* (1–2 споры в сумке, как правило, гладкий диск апотеция, наличие пустул).

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