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Fruticose lichens: structural diversity, taxonomic characteristics and evolution

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Summary: A morphological and taxonomical analysis of fruticose lichens has revealed the main characteristics of their structural diversity. The occurrence rate of the fruticose and similar growth forms in various taxa of the current lichen system has been identified. Various ways of origin have been investigated as well as the main directions of the fruticose growth form evolution.

Keywords: lichens, fruticose lichens, growth forms, evolution, biomorphology, morphogenesis, structural diversity

Lichens are morphologically more diverse than nonlichenized fungi (Zmitrovich 2010). Researchers became interested in lichen morphology and growth forms a long time ago (Krabbe 1883; Zahlbruckner 1896; Elenkin 1907; etc.). Many authors noted the importance and value of such research on various stages of lichenology (Nienburg 1926; Oxner 1974; Poelt 1986; Golubkova & Biazrov 1989; Golubkova 1993; Kotlov 1995; etc.). With the development of morphology new research on lichen morphogenesis (Hammer 1995, 1998a, b, 2000, 2001; Honegger 1991, 2006, 2008; Sanders & de los Ríos 2012; etc.) and ontogenesis has been conducted (Suetina 2001, 2007; Suetina & Glotov 2010; etc.). There is a growing interest in comparing lichens and plants based on their structure and evolution (Sanders 2001). Research on lichen genomes had a profound influence on the development of lichenology. Molecular data have changed our understanding of the phylogeny of many lichen groups (Ekman & Wedin 2000; Ekman 2001; Stenroos et al. 2002a, b; Wiklund & Wedin 2003; Anderson & Ekman 2005; Lumbsch et al. 2006; Schmitt et al. 2006; Tehler & Irestedt 2007; Thell et al. 2012; Arup et al. 2013; etc.). The current system of lichens comprises five classes of Ascomycota and one class of Basidiomycota (Nash III 2008; Kirk et al. 2008). Some morphologically very different lichens were placed within the same order and family. There are a lot of taxa placed in incertae sedis. A detailed research of the morphogenesis and evolution of growth forms as well as the comparison of such data with data of molecular phylogeny is of immediate interest (Stenroos et al. 2002a, b; Tehler & Irestedt 2007; Notov 2010a, b; etc.).

The fruticose growth form is of special importance in lichen evolution (Golubkova & Biazrov 1989; Kotlov 1995; Tehler & Irestedt 2007; etc.). The appearance of this form significantly increased the morphological and taxonomical diversity of lichens. In order to understand the evolutionary pathways of the fruticose growth form it is necessary to conduct structural and taxonomical analysis of the diversity of fruticose lichens. This is the main goal of the present study. Such research is important to identify the taxonomical value of the data about lichen growth forms and lichen morphogenesis.

Materials and methods

The morphology of various species was studied using the lichen herbarium of the V. L. Komarov Botanical Institute, Russian Academy of Sciences [LE]. Taxonomical reviews of various lichen groups were used (Dombrovskaya 1996; Ahti 2000; Ekman & Wedin 2000; Stenroos et al. 2002a, b; Wiklund & Wedin 2003; Lumbsch et al. 2006; Truong et al. 2011; Thell et al. 2012; etc.). Current works on lichen phylogeny were analyzed (Ekman & Wedin 2000; Ekman 2001; Stenroos et al. 2002a, b; Wiklund & Wedin 2003; Anderson & Ekman 2005; Lumbsch et al. 2006; Schmitt et al. 2006; Thell et al. 2012; Arup et al. 2013; Prieto et al. 2013; etc.). Floristic reports were studied to analyze the diversity of fruticose lichens on various continents and in tropical regions (Galloway 1991; McCune & Geiser 1997; Ahti 2000; Döring & Wedin 2000; Brodo et al. 2001; Lumbsch et al. 2006; Aptroot & Bungartz 2007; Aptroot 2008; Moberg 2011; Sharnoff 2014; etc.). Online photo collections of tropical lichens were studied (EOL 2007–2012; Enlichenment 2013; Pictures of tropical lichens 2014; Sharnoff photos 2014). We used the system cited in the 10th edition of the 'Dictionary of the Fungi' (Kirk et al. 2008). Taxa nomenclature is according to Index Fungorum (2014). Additional to the fruticose growth form, the author also analyzed similar growth forms in all groups of the current lichen system. In order to understand the possible modes and mechanisms of the formation of the fruticose form the author studied publications on lichen morphogenesis. Forms showing a tendency to create orthotropic and branched structures were also analyzed.

Structural diversity

The level of expression of the fruticose growth forms may vary. In addition to typical fruticose forms, covertly fruticose and dwarf-fruticose forms are usually identified. Detailed general classifications of lichen growth forms pay a lot of attention to the way the thallus is placed (endogenous or epigenous) (Golubkova 1983; Golubkova & Biazrov 1989; Nash III et al. 2002; Himelbrant & Kuznetsova 2014). Fruticose forms only exist among epigenous lichens. According to Elenkin (1907), the plagiotropic, the plagio-orthotropic and the orthotropic types can be identified based on their ability to grow orthotropically. A free-living type is considered separately. Fruticose lichens exist as a separate class among orthotropic and free-living forms. Only forms that are somewhat closer to fruticose ones, such as verruculose-fruticose, squamulose-fruticose and foliose-fruticose forms, are present in the plagio-orthotropic type. Spatial orientation and level of branching have been taken into account when identifying groups (Golubkova 1983; Golubkova & Biazrov 1989). However, fruticose forms and forms similar to them are very diverse in the general thallus structure and its elements.

When analyzing the structural diversity of fruticose and similar growth forms it is necessary to consider a number of different traits. Some of them are important for the identification of modules of lichen structural evolution (Notov 2010b). In addition to spatial orientation and attachment to substrate, traits that are connected with the structural differentiation of the thallus are also very important. When evaluating the complexity of the fruticose form's thallus structure, the existence or lack of horizontal and vertical subsystems must be taken into account. The structure of the elementary axis is also important, as well as the existence or lack of differentiation in growth length and functions.

A special type comprises thalli with two different structural and functional parts: a primary horizontal thallus and a system of orthotropic axes (Notov 2010b). Such thalli can be seen in

Cladoniaceae and Stereocaulaceae. The analysis of complex branched species of Cladoniaceae allows to note structural elements of various levels. Some of them are similar to elements that have been identified in vascular plants (Gatsuk 2008). For example, in some *Cladonia* an elementary axis, an elementary thallus, a single-axis (monopodial) thallus, a complex of the remaining single-axis thallus and a system of podetia can be identified in the orthotropic part of the thallus (Ivanova & Notov 2005; Notov 2010b).

Fruticose forms also have a large variety of lateral structures that are formed on the orthotropic axes like phylloclades, phylloclade shoots, fibrils and cephalodia (Oxner 1974; Dombrovskaya 1996; Ahti 2000; Plyusnin 2004; Honegger 2006).

The main traits characterizing the structural diversity of fruticose and similar growth forms are (possible types of structures are in brackets):

- expression of the fruticose forms (covertly fruticose, dwarf-fruticose, fruticose);
- thallus branching (weakly branching, highly branched);
- axes structure (radially-fruticose, explanately-fruticose, foliose-fruticose, with solid and hollow axes);
- separation into a vertical and horizontal subsystem (forms with a primary squamulose thallus and a system of podetia);
- existence of lateral structures and their type (phylloclade, phylloclade shoots, fibrils, cephalodia, etc.);
- spatial orientation (orthotropic, hanging, decumbent);
- attachment to substrate (attached, free-living).

Many traits may be combined somewhat independently. For example, there are foliose-fruticose, hanging, free-living fruticose branched lichens (Golubkova & Biazrov 1989). The level of expression of the fruticose growth form correlates with the level of branching of different structural elements of the thallus and the level of axes differentiation. If forms with orthotropic, non-branched axes are considered as the first stage in the differentiation of covertly-fruticose forms, many of such lichens can be found among species of the endogenous group. For example, some calicioid lichens with orthotropic branching or forcipately-branched thallus have an endophloeodal thallus (Titov 2006).

When analyzing the diversity of morphogenesis of fruticose forms, the possibility of intercalary (diffuse) growth should be noted (Sanders & Ascaso 1995; Rolstad & Rolstada 2008; Sanders & de los Ríos 2012). This has also been described for nonlichenized fungi (Voisey 2010). In most species the mycobiont plays the leading role in morphogenesis (Oxner 1974; Honegger 2006, 2008). In gelatinous lichens the photobiont may be more profoundly active (Oxner 1974). However, the fruticose growth form is rather rare for them, whereas in the foliose-fruticose growth form the photobiont's level of morphogenetic activity declines and the one of the mycobiont grows.

Taxonomic characteristics

In the current system, lichens and allied fungi are grouped into five classes of Ascomycota and one class of Basidiomycota (Kirk et al. 2008; Nash III 2008). The tendency to create branching forms isn't obvious in all taxa of Ascomycota (Tab. 1). Fruticose forms are highly prevalent in Lecanoromycetes as well as Lecanorales and Teloschistales.

Table 1. Prevalence of fruticose and similar growth forms in lichen taxa. Genera and families in which fruticose growth forms are widely prevalent are semi-bold. * – taxa, in which there are covertly-fruticose, dwarflike-fruticose, foliose-fruticose growth forms and forms with vertical thalli, or with a trend to their appearance. Classes: ART – Arthoniomycetes; LIC – Lichinomycetes; LEC – Lecanoromycetes; EUR – Eurotiomycetes.

Class	Taxa
ART	ARTHONIALES Henssen ex D. Hawksw. & O. E. Erikss. __Roccellaceae__ Chevall.: ___Combea___ De Not.; *___Dendrographa___ Darb.; ___Dolichocarpus___ R. Sant; *_Hubbsia_ Weber; ___Ingaderia___ Darb.; ___Pentagenella___ Darb.; ___Roccella___ DC.; *___Roccellina___ Darb.; ___Simonyella___ J. Steiner
LIC	LICHINALES Henssen & Büdel Lichinaceae Nyl.: *___Ephebe___ Fr.; *_Jenmania_ W. Wächt.; *_Lichina_ C. Agardh; *_Peccania_ A. Massal. ex Arnold; *_Synalissa_ Fr.; *_Thermutis_ Fr.
LEC	BAEOMYCETALES Lumbsch, Huhndorf & Lutzoni Baeomycetaceae Dumort.: *_Baeomyces_ Pers. CANDELARIALES Miadl., Lutzoni & Lumbsch Candelariaceae Hakul.: *_Candelaria_ A. Massal. LECANORALES Nannf. __Cladoniaceae__ Zenker: ___Carassea___ S. Stenroos; ___Cladia___ Nyl.; *___Cladonia___ P. Browne; *_Notocladonia_ S. Hammer; *_Metus_ D. J. Galloway & P. James; *_Pilophorus_ Th. Fr.; *_Pycnothelia_ (Ach.) Dufour; *_Sphaerophoropsis_ Vain.; *_Thysanothecium_ Mont. & Berk. Calycidiaceae Elenkin: *_Calycidium_ Stirt. __Parmeliaceae__ Zenker: ___Alectoria___ Ach.; *_Allocetraria_ Kurok. & M. J. Lai; *_Anzia_ Stizenb.; ___Bryoria___ Brodo & D. Hawksw.; *_Arctoparmelia_ Hale; *_Brodoa_ Goward; *_Cavernularia_ Degel.; *___Cetraria___ Ach.; *___Coelocaulon___ Link; ___Cornicularia___ (Schreb.) Hoffm.; *_Dactylina_ Nyl.; _Davidgallowaya_ Aptroot; *___Evernia___ Ach.; *_Everniastrum_ Hale; *___Flavocetraria___ Kärnefelt & A. Thell; ___Gowardia___ Halonen, Myllys, Velmala & Hyvärinen; *_Hypogymnia_ (Nyl.) Nyl.; *___Kaernefeltia___ A. Thell & Goward; ___Letharia___ (Th. Fr.) Zahlbr.; ___Lethariella___ (Motyka) Krog; *_Neofuscelia_ Essl.; ___Oropogon___ Th. Fr.; *_Pannoparmelia_ (Müll. Arg.) Darb.; *_Platismatia_ W. L. Culb. & C. F. Culb.; *_Pseudephebe_ M. Choisy; *___Pseudevernia___ Zopf; *_Punctelia_ Krog; ___Sulcaria___ Bystrek; *_Tuckermanopsis_ Gyeln.; ___Usnea___ Dill. ex Adans.; *_Vulpicida_ J.-E. Mattsson & M. J. Lai; *_Xanthomaculina_ Hale; *_Xanthoparmelia_ (Vain.) Hale __Ramalinaceae__ C. Agardh: *_Krogia_ Timdal; *___Niebla___ Rundel & Bowler; *_Phyllopsora_ Müll. Arg.; *___Ramalina___ Ach.; *_Ramalinopsis_ (Zahlbr.) Follmann & Huneck __Sphaerophoraceae__ Fr.: ___Bunodophoron___ A. Massal.; *_Leifidium_ Wedin; ___Sphaerophorus___ Pers. __Stereocaulaceae__ Chevall.: ___Stereocaulon___ Hoffm. PELTIGERALES Walt. Watson Collemataceae Zenker: *_Leptogium_ (Ach.) Gray Lobariaceae Chevall.: *_Dendriscocaulon_ Nyl.; *_Lobaria_ Chevall.; *_Pseudocyphellaria_ Vain. Stictaceae Stizenb.: *_Sticta_ (Schreb.) Ach. Placynthiaceae Å. E. Dahl: *_Polychidium_ (Ach.) Gray PERTUSARIALES M. Choisy ex D. Hawksw. & O. E. Erikss. Icmadophilaceae Triebel: *_Siphula_ Fr.; *_Dibaeis_ Clem.; *_Thamnolia_ Ach. ex Schaer. Megasporaceae Lumbsch: *_Aspicilia_ A. Massal.; *_Circinaria_ Link Pertusariaceae Körb. ex Körb.: *_Loxosporopsis_ Henssen; *_Pertusaria_ DC. Ochrolechiaceae R. C. Harris ex Lumbsch & I. Schmitt: *_Ochrolechia_ A. Massal. TELOSCHISTALES D. Hawksw. & O. E. Erikss. Caliciaceae Chevall.: *_Calicium_ Pers. Physciaceae Zahlbr.: *_Acroscyphus_ Lév.; *_Anaptychia_ Körb.; *_Heterodermia_ Trevis., *___Santessonia___ Hale & Vobis; ___Tornabea___ Østh. Teloschistaceae Zahlbr.: *_Caloplaca_ Th. Fr.; *___Teloschistes___ Norman; *_Xanthodactylon_ P. A. Duvign.; *_Xanthoria_ (Fr.) Th. Fr. INCERTAE SEDIS Leprocaulaceae Lendemer & B. P. Hodk.: *_Leprocaulon_ Nyl. Coniocybaceae Reichenb.: *_Chaenotheca_ (Th. Fr.) Th. Fr.; *_Sclerophora_ Chevall.
EUR	MYCOCALICIALES Tibell & Wedin Mycocaliciaceae A. F. W. Schmidt: _Chaenothecopsis_ Vain.; *_Phaeocalicium_ A. F. W. Schmidt; *_Stenocybe_ Nyl. ex Körb.

The most complex and the most branched thalli are prevalent in some families of Lecanorales (Tab. 1). Among them there are Cladoniaceae (*Cladonia* Hill. ex P. Browne), Stereocaulaceae (*Stereocaulon* Hoffm.), Parmeliaceae (*Bryoria* Brodo & D. Hawksw., *Usnea* Dill. ex Adans), Ramalinaceae (*Ramalina* Ach.). In Teloschistales typical fruticose forms exist within: *Anaptychia* Körb., *Heterodermia* Trevis. (Physciaceae), *Teloschistes* Norman (Teloschistaceae). Some dwarf-fruticose and covertly-fruticose forms exist in various groups of Pertusariales and Teloschistales (Tab. 1). In Arthoniomycetes and Lichinomycetes fruticose-like forms are significantly more rare. Species with fruticose, dwarflike-fruticose and covertly-fruticose thalli exist in *Roccella* DC., *Pentagenella* Darb., *Combea* De Not, *Ingaderia* Darb. (Arthoniomycetes), *Lichina* Moore, *Ephebe* M. Choisy and *Synalissa* Fr. (Lichinomycetes).

Nonlichenized fungi from Eurotiomycetes (Chaetothyriomycetes) that are traditionally treated together with lichens (Mycocalicales) form apothecia on stalks (podetia), which sometimes branch out (*Stenocybe* Körb.). This trait connects these forms with covert-fruticose and dwarf-fruticose forms. In Dothiodeomycetes only crustose forms are prevalent.

Evolution

Formation of fruticose forms is connected with an increase in the ability of branching and orthotropic growth (Elenkin 1907; Kotlov 1995; Zmitrovich 2010). The branching tendency of thallus elements can be seen in various biomorphological groups. Branched groups of hyphae are formed even in some crustose lichens with a leprose thallus (*Lepraria rigidula* (de Lesd.) Tønsberg). The apothecia in endophloeodal lichens (some species of *Opegrapha* Ach. and *Graphis* Adans.) are branched and can form complex branched systems.

Fruticose branching is characteristic of separate structures of the thallus. Examples include rhizines of *Peltigera* Willd., lobules of *Caloplaca* Th. Fr., isidia of some *Melanelia* Essl. s. 1. and soralia in some lichen groups. At the same time, the thallus itself has a foliose or sub-foliose form. In *Peltigera* a branched network of veins is formed on the lower surface of the thallus because various elements on the lower part of the thallus grow at different rates (Oxner 1974).

Many researchers highlighted the significant similarities in the development of the main groups of lichen growth forms. According to Elenkin (1926, 1929a, b, c), there was a shift from crustose to foliose and from foliose to fruticose forms in each of the five main phylogenetic groups of lichens. The possibility of the formation of a fruticose form on the base of a crustose and foliose form was noted by other authors as well (Golubkova & Biazrov 1989; Kotlov 1995).

It seems that the primary stages of the formation of dwarf-fruticose and covertly-fruticose forms on the basis of the crustose growth form are connected with the formation of orthotropic elements of the thallus. In the beginning they were barely separated and very short. Such wart-like, disc-like or funnelform structures exist in some species of *Aspicilia* A. Massal. Many species of this genus have a crustose or subfoliose thallus. Clearly marked vertical structures are formed in *A. transbaicalica* Oxner. *A. hispida* Mereschk. develops forms similar to dwarflike-fruticose ones. Such tendency is evident in some other systematic groups too (*Endocarpon pulvinatum* Th. Fr.).

The next stage in the development of the elements of a vertical thallus is connected with the formation of clearly separated orthotropic structures: podetia. They are unbranched or slightly branched in species with a weak divided thallus. In many cases they end with apothecia, which are exposed above the substrate. Such vertical podetia can be seen in various classes of lichen fungi and similar nonlichenized fungi (Arthoniomycetes, Lecanoromycetes, Chaetothyriomycetes) (Tab. 1). Unbranched and forcipate (rarely) podetia are formed in *Baeomyces* Pers. (Baeomycetaceae), *Dibaeis* Clem. (Icmadophilaceae), *Calicium* Pers. (Caliciaceae), *Chaenotheca* (Th. Fr.) Th. Fr., *Sclerophora* (Coniocybaceae), *Mycocalicium* Vain. ex Reinke, *Chaenothecopsis* Vain. (Mycocaliciaceae). More branched vertical axes occur in *Roccella* (Roccellaceae) and *Synalissa* Fr. (Lichinaceae). In addition to radial axes, they also form explanately-radial ones.

Markedly branched fruticose thalli and podetia are also formed in various taxa. A significant similarity in the evolution of growth forms (Golubkova & Biazrov 1989; Kotlov 1995) allows for the hypothesis that they have been formed on different structural bases. The similar vector of their development is connected with the increase in branching and axes differentiation. Axes can be different in growth period and functions. These changes could have happened on the basis of a thallus with solid cylindrical, hollow tubular, agaricaceous, scyphus-forming and reticulate axes (Notov 2010b). In some groups the morphogenesis of the fruticose form is connected with the formation of lacunes and osteols (Sanders 1989; Hammer 2001).

It is likely that in most taxa the formation of the fruticose growth form happened on the basis of the foliose form. For example, in Parmeliaceae, the formation of radially-fruticose forms occurred on the basis of foliose and explanately-fruticose forms (*Cetraria* Ach.). In some cases radially-fruticose thalli could have been formed as a result of foliose axes rolling into a tube and the subsequent cohesion of their edges. This is characteristic of *Flavocetraria cucullata* (Bellardi) Kärnefelt & A. Thell. The formation of explanately-fruticose and similar foliose forms occurred in various groups of Parmeliaceae with a foliose or subfoliose thallus. For example, in *Hypogymnia* (Nyl.) Nyl., *Pseudevernia* Zopf, *Xanthoparmelia* (Vain.) Hale there are species with a highly branched explanately-fruticose thallus (*Hypogymnia imshaugii* Krog, *H. duplicata* (Ach.) Rass., *Pseudevernia cladonia* (Tuck.) Hale & Culb., *Xanthoparmelia chlorochroa* (Tuck.) Hale). Foliose forms that are similar to explanately-fruticose forms can be seen in Lobariaceae and Teloschistaceae. Highly branched foliose forms that resemble explanately-fruticose forms occur in *Lobaria fendleri* (Tuck. ex Mont.) Lindau. In some cases dwarf-fruticose forms with radial or explanately-radial axes are formed on the basis of foliose forms (*Xanthoria candelaria* (L.) Th. Fr., *Teloschistes exilis* (Michaux) Vainio). More widely branched thalli are common in tropical species representing taxa in which foliose or dwarf-fruticose forms prevail.

Groups with prevailing fruticose growth forms may also display transitions from forms with radial axes to forms with explanate or flat axes. In Ramalinaceae with prevailing radially-fruticose forms (Keuck 1979), there are a lot of species with flat axes (for example, *Ramalina fraxinea* (L.) Ach.). But also reticulate axes formed on the basis of agaricaceous axes can be found (*R. menziesii* Taylor) (Larson 1983).

In Stereocaulaceae and Cladoniaceae fruticose forms emerged due to the differentiation of the thallus into vertical and horizontal systems. Externally the podetia of these groups are similar, but they are morphologically different (Dombrovskaya 1996). In Cladoniaceae they are a part of the askoma (outgrowths of exciple). In Stereocaulaceae the podetium is a descendant of the thallus. It has a central axis and and shows lengthening of all plectenchyma in the thallus. Vertical structures in species of *Stereocaulon* are often called pseudopodetia (Oxner 1974; Dombrovskaya 1996; Ahti 2000).

Some taxa have forms with an unusual axis structure. Highly branched forms with flat reticulate axes in *Ramalina menziesii* are similar to fruticose forms. This similarity can be seen in superfluous branching and axes differentiation. Hollow cylindrical and scyphus-forming reticulate axes are characteristic of *Cladonia fuliginosa* Filson. The podetia of the *Cladonia* are fruticose. In some South American species of *Cladonia* proliferate scyphus-forming podetia occur. At the same time many branched cylindrical or explanately-cylindrical fruticose axes are formed on the edges of scyphus-forming structures. Such podetia are characteristic of *Cladonia calycantha* Delise ex Nyl., *C. imperialis* Ahti & Marcelli, *C. penicillata* (Vain.) Ahti & Marcelli, *C. crinita* (Delise ex Pers.) Ahti (Ahti 2000).

In some taxa the formation of large vertical elements of the thallus was combined with the development of lateral structures. They are able to increase the area of the assimilating surface and the intensity of photosynthesis. Phyllocladia in *Cladonia* and *Stereocaulon*, short lateral axes, outgrowths, fibrils in *Usnea*, cephalodia in *Stereocaulon* can be considered as such structures. A higher stage of their development can usually be seen in forms with bigger thalli. A significant diversity of lateral structures emerged in some groups. In addition to phyllocladia, species of *Stereocaulon* have phyllocladioid stems. Their axes are similar to the anatomical structure of typical pseudopodetium axes (Dombrovskaya 1996). Phyllocladioid stems have numerous phyllocladia. Special lateral structures of *Stereocaulon* are cephalodia, containing cyanobacteria. External hyphae of pseudopodetia in some species of *Stereocaulon* form a tomentum (Plyusnin 2004). It is similar to the indumentum of higher plants. The dimension of the tomentum is correlated to solar insulation. Such a dependency demonstrates the universal nature of general tendencies of ecological evolution. In *Cladonia* with large phyllocladia one can often see their branching and the formation of lateral blades, which increase the area of the assimilating surface even more. The analysis of various ways of lateral element formation in lichens allows researchers to find some analogies with various modes of leaf formation in higher plants. The occurrence of the tomentum is similar to the formation of superfluous indumentums in xerophytic plants. All this supports the fact that comparative functional, evolutionary and morphologic studies in lichenology and botany are essential (Nienburg 1926; Sanders 2001, 2006).

Fruticose forms appeared repeatedly and at the same time in various family groups, which could be proven in Roccellaceae conclusively (Tehler & Irestedt 2007). Apparently, a similar situation can be seen in Parmeliaceae. This coincides with the results of the latest phylogenetic studies (Thell et al. 2012). A number of clades, in which the fruticose form emerged, can be identified. It seems that the parallelism in structural evolution became widely distributed in Cladoniaceae and Teloschistaceae as well (Ahti 1982, 2000; Stenroos et al. 2002a, b). Even though there is an external similarity of general morphology of cladoniamorphic lichens, they form a biomorphological and not a taxonomical group (Ahti 1982).

Conclusion

Thus, fruticose lichens and similar forms are characterized by a significant structural diversity. They differ in spatial orientation, level of attachment to substrate, peculiarities of structural differentiation of the thallus, the existence or lack of a horizontal and vertical substructure and the structure of elementary axes.

The tendency to form fruticose forms did not emerge in all taxa of Ascomycota. They became widely prevalent in Lecanorales and Teloschistales (Lecanoromycetes). Fruticose forms are also present in Arthoniales (Arthoniomycetes) and Lichinales (Lichinomycetes).

The formation of fruticose growth forms is connected with the tendency of branching and orthotropic growth. Fruticose forms could emerge on the basis of crustose and foliose forms. The formation of large vertical elements of the thallus was in some cases combined with the development of lateral structures. They increased the assimilation area and therefore photosynthesis.

In various groups fruticose forms emerged at the same time, but on different structural bases. A further analysis of fruticose lichens and similar forms will promote the development of functional and evolutionary lichen morphology. It will also provide additional information about their taxonomy and phylogeny. The results will aid in solving the problem of correlating molecular and morphological data.

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