
4 Pezizomycotina: Lecanoromycetes

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I. Introduction

Lecanoromycetes (formally named by Eriksson and Winka in 1997) constitutes one of the largest classes of Ascomycota with 14,199 known species (Kirk et al. 2008). The class mainly includes ascomycetes characterized by apothecial ascomata, amyloid asci with a two-layered wall and an apical thickening, and a hamathecium (interascal hyphae) formed with paraphyses or pseudoparaphyses. **This group comprises the largest number of lichen-forming ascomycetes, with approximately 90 % of all known lichen-forming fungi** (Miadlikowska et al. 2006). However, not all members of this class are lichenized; several nonlichenized species are nested within this lineage (Lutzoni et al. 2001, 2004; Schoch et al. 2009). Lecanoromycetes are well known for the broad range of secondary compounds, such as depsidones, terpenoids, and xanthenes (Huneck and Yoshimura 1996), that they exclusively produce, in some cases in large quantities out of proportion to the dry weight of their thalli.

In the past, ascoma structure or development and ascus types were used as the main characters in the classification of ascomycete fungi. Nannfeldt (1932) classified the euascomycetes according to their type of ascomatal development: Plectascales, Ascocolulares, and Aschohymeniales, where most Lecanoromycetes

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belonged. Luttrell (1951, 1955) in his classification system gave more importance to the ascus types and classified the euascomycetes as Bitunicatae (the Ascoloculares) and Unitunicatae (the Ascohymeniales and Plectascales). Unitunicatae were then subdivided according to their ascomata morphology: Plectomycetes, Pyrenomycetes, and Discomycetes, where most Lecanoromycetes belonged (Luttrell 1955). However, subsequent ultrastructural and ontogenetical studies showed that the complexity of these traits had been underestimated and that many taxa did not fit into these broad categories because of intermediate types (e.g., Bellemère and Letrouit-Galinou 1987; Henssen and Jahns 1974; Honegger 1982a). The reliability of these characters for higher-level classification was therefore doubted even before the beginning of the molecular era (e.g., Bellemère 1994; Poelt 1973; Reynolds 1989).

Molecular studies confirmed that classifications based on ascomatal characters often failed to capture monophyletic lineages within the ascomycetes (Berbee 1996; Lindemuth et al. 2001; Lumbsch and Huhndorf 2007a; Lutzoni et al. 2001; Liu and Hall 2004; Spatafora et al. 2006; Schoch et al. 2009). In particular, some groups within Lecanoromycetes (e.g., Ostropales, Caliciales) were shown to include a much larger diversity of ascoma and ascus types than expected (Grube et al. 2004; Schmitt et al. 2005; Wedin and Tibell 1997; Wedin et al. 2000a). **Molecular phylogenetic studies also cast doubts on the morphology-based delimitation of orders and families in Lecanoromycetes.** As a result, many families and genera were segregated from the large order Lecanorales, while several additional families were included in Ostropales, the second largest order in Lecanoromycetes (Grube et al. 2004; Hofstetter et al. 2007; Kauff and Lutzoni 2002; Lumbsch et al. 2004; Miadlikowska and Lutzoni 2004; Miadlikowska et al. 2006; Wedin et al. 2005). Lecanoromycetes currently includes 14 orders and 3 subclasses: Acarosporomycetidae, Lecanoromycetidae, and Ostropomycetidae (Gaya et al. 2012; Hodkinson and Lendemer

2011; Lumbsch and Huhndorf 2010; Schmutt et al. 2011).

II. Occurrence and Distribution

Lecanoromycetes have a broad distribution and can be found from the tropics to the poles. Their biomass is substantial in boreal to arctic climates, especially in the tundra, where species such as *Cladonia rangiferina* can constitute the main vegetation cover and are the main primary producer and food source for large herbivorous mammals (Brodo et al. 2001). In Antarctica, lichens (mostly from the class Lecanoromycetes) form the most species-diverse group within the vegetation cover, and some of them are found in the coldest and driest habitats of continental Antarctica (Green et al. 1999; Øvstedal and Lewis Smith 2001), where they are the basis of terrestrial life closest to a pole on Earth.

Lecanoromycetes are also very common and diverse in temperate regions, where they have been extensively studied (e.g., Brodo et al. 2001; Clauzade and Roux 1985; McCarthy 2003; Smith et al. 2009). In the tropics, they are thought to be as species diverse as in temperate regions, if not more so (Aptroot and Sipman 1997; Coppins and Wolseley 2002; Lücking 2008). A recent study in Papua New Guinea showed that a single *Elaeocarpus* tree could harbor up to 173 species of lichens, among which approximately 130 species were Lecanoromycetes (Aptroot 2001). Many tropical regions of the world are still mainly understudied, and many new species remain to be discovered (Sipman and Aptroot 2001).

Lecanoromycetes are found in a large number of natural terrestrial habitats, such as woodlands, heathlands, lowland and alpine grasslands, deserts, and arid shrublands. They are also commonly found in urban areas, wastelands, and other anthropogenous habitats (Gilbert 1990; Smith et al. 2010). Although most species occur in terrestrial environments, some species can grow on temporarily submerged substrates, in freshwater (Gilbert

1996; Gilbert and Giavarini 1997; Thüs and Schultz 2009), or in saltwater in the supralittoral zone (Brodo and Sloan 2004; Fletcher 1980).

III. Substrate Range and Ecology

A. Substrate Range

Lecanoromycetes grow predominantly on **tree bark** (corticolous species) and **rocks** (saxicolous species) but are also found on **leaves** (foliicolous species), **soil** (terricolous species), **wood** (lignicolous species), **mosses** (muscolous species), and **other lichens** (lichenicolous species). Most species tend to be specific to a particular type of substrate, although some can colonize several (e.g., *Parmelia sulcata*). In addition to a natural substrate, some Lecanoromycetes can grow on human-made materials, such as brick, concrete, asphalt, metal, plastic, glass, and rubber (Brodo et al. 2001; Gilbert 1990).

A few species even occur on the bones or shells of land tortoises (Brodo et al. 2001) and indeed on any material with a stable surface exposed for long enough. A few others, mainly from the genera *Aspicilia* s.l. and *Xanthoparmelia*, do not attach to a substrate and occur as an erratic or vagrant (e.g., Pérez 1997; Rosentreter 1993).

B. Lifestyles

In Lecanoromycetes, most lichen-forming (mycobionts) fungi form **mutualistic associations** with one or two photosynthetic partners, either a green alga or a cyanobacterium (photobiont). Mycobionts obtain carbon from their photobiont, in the form of glucose when associated with cyanobacteria or in the form of polyhydric sugar alcohols (polyols) when associated with green algae (Palmqvist et al. 2008). Cyanobacteria found in lichens, such as *Nostoc*, can fix nitrogen and, therefore, can be a source of nitrogen for the mycobiont. The mycobiont protects the photobiont from UV light, temperature extremes, and, to some extent, desiccation (Nash 2008). The great majority of lichenized fungi in Lecanoromycetes are obligate mutualists, but a few species of *Stictis* can occur either as lichen symbionts or as

nonlichenized saprotrophs, depending on the substrate (Wedin et al. 2004). Some lichenized fungi can also be parasitic on other lichens, either throughout their life (Lawrey and Diederich 2003) or only in the first stage of their development (e.g., *Diploschistes muscorum*) (Friedl 1987). Finally, several lineages within Lecanoromycetes are always nonlichenized, most likely because of secondary losses of lichenization (Baloch et al. 2010; Gueidan et al. 2008; Lutzoni et al. 2001; Schoch et al. 2009). These nonlichenized lineages can have diverse lifestyles, **ranging from saprophytism to parasitism** (Lawrey and Diederich 2003; Sherwood 1977a, b; Sherwood-Pike 1987). They mostly occur on lichens (Lawrey and Diederich 2003) but are also found on diverse substrates such as bark or wood (e.g., Stictidaceae, Odontotremataceae).

C. Mycobiont–Photobiont Associations

Most Lecanoromycetes species associate with a single photobiont, a green alga (chlorobiont) or a cyanobacterium (cyanobiont). Some lichen-forming fungi are associated with both types of photobionts, forming tripartite thalli where the cyanobacterial photobiont is an accessory partner. The cyanobiont is then restricted to special organs of the thallus called cephalodia [although see exceptions in Henskens et al. (2012)], which can be internal or external outgrowths. Cyanobionts fix atmospheric nitrogen, transferring ammonia to the other partners. These tripartite associations are common in Lecanorales (e.g., *Stereocaulon*) and Peltigerales (e.g., *Lobaria*, *Nephroma*, *Peltigera*).

The majority of photobionts belong to Chlorophyta [approximately 90 % according to Tschermak-Woess (1988a); see also Ahmadjian (1967, 1993)]. The green algal genera *Trebouxia*, *Asterochloris* (Trebouxiophyceae), and *Trentepohlia* (Ulvophyceae) are the most common photobionts for Lecanoromycetes.

Other genera of photobionts associated with Lecanoromycetes include *Chlorella* (e.g., in *Pseudocyphellaria*) (Tschermak-Woess 1988b), *Chlorosarcinopsis* (in *Lecidea*) (Plessl 1963), *Coccomyxa* (e.g., in *Icmadophila*, *Peltigera*, *Solorina*) (Jaag 1933), *Dictyochloropsis* (e.g., in *Lobaria*, *Pseudocyphellaria*) (Tschermak-Woess 1984),

Elliptochloris (e.g., in *Baeomyces*) (Tschermak-Woess 1985), *Leptosira* (in *Vezdaea* and *Thrombium*) (Tschermak-Woess 1953; Tschermak-Woess and Poelt 1976), *Myrmecia* (e.g., in *Psora*) (Geitler 1963), and *Phycopeltis* (e.g., in Porinaceae) (Santesson 1952).

Cyanobacterial photobionts are associated with a relatively small number of lichen-forming fungal species (10 %, Tschermak-Woess 1988a; approximately 1,700 species, Rikkinen 2002) and, in Lecanoromycetes, are restricted to Arc-tomiaceae, Stereocaulaceae, Trapeliaceae, and Peltigerales. **The most common cyanobacterial (primary or accessory) lichen photobionts are *Nostoc* and *Rhizonema*** (Lücking et al. 2009b; Rambold et al. 1998; Tschermak-Woess 1988a). The cyanobacterial genus *Scytonema* was also listed in the past as one of the most common lichen photobionts, but a recent molecular study showed that all lichenized strains of *Scytonema* studied (including those from the Lecanoromycetes genera *Coccocarpia* and *Stereocaulon*) belonged to *Rhizonema*, a new strictly lichenized cyanobacterial lineage genetically distinct from *Scytonema* (Lücking et al. 2009b). The current status of the genus *Scytonema* as a lichen photobiont is therefore in need of determination using molecular data. *Stigonema* and *Gloeocapsa* are also often found in lichens but more often as accessory photobionts (Rambold et al. 1998).

Other cyanobacteria occasionally found as photobionts are *Anabaena* (in *Stereocaulon*) (DuVigneaud 1955), *Calothrix* (in *Coccotrema*, *Stereocaulon*) (Brodo 1973; Lamb 1977), *Dichothrix* (in *Placynthium nigrum*) (Geitler 1934), *Hyphomorpha* (in *Spilonema*) (Henssen 1981), and *Tolythrix* (in *Hertella*) (Henssen 1985).

Interestingly, patterns of mycobiont-photobiont associations have been observed at a high taxonomic level (Miadlikowska et al. 2006; Rambold et al. 1998). This is somewhat surprising for a symbiotic system that is believed to transmit its photobiont mostly horizontally across generations. However, the contribution of fungal sexual (horizontal transmission) versus asexual (vertical transmission) reproduction to the genetic composition of the mycobiont and photobiont populations has rarely been quantified. Dal Grande et al. (2012) estimated that more than

70 % of lichen thalli across worldwide populations of *Lobaria pulmonaria* were derived from asexual propagules. No recombination was detected for the photobiont, while it was detected in only 7.7 % of the mycobiont individuals. Therefore, vertical transmission of the photobiont through thallus fragments or differentiated asexual propagules might be more prominent than expected in shaping lichen populations and could explain in part the pattern of association observed at a high taxonomic level within Lecanoromycetes.

A population ecology study of the geographically widespread lichen *Cetraria aculeata* revealed that climate and codispersal are the most relevant factors shaping the genetic structure of the photobiont and that rare photobiont switches enabled the mycobiont to achieve a broad geographical distribution crossing bioclimatic zones (Fernandez-Mendoza et al. 2011).

In Lecanoromycetes, the following **patterns of mycobiont-photobiont associations** have been observed (Miadlikowska et al. 2006; Rambold et al. 1998). Certain lineages, such as Parmeliaceae and Teloschistales, are mainly associated with *Trebouxia*, whereas Cladoniaceae, Stereocaulaceae, and Icmadophilaceae are mostly associated with *Asterochloris*. In Peltigerales, *Nostoc* is the main photobiont, and in Ostropales, *Trentepohlia* is the most common photobiont. Although some photobiont associations could potentially be used to classify higher taxa within Lecanoromycetes, current knowledge on the identity of lichen photobionts is still too sparse. They are notoriously difficult to identify when lichenized, or even when cultured, based on morphology only (Friedl and Büdel 2008), and molecular data are currently only available for a limited number of taxa.

IV. Mycobiont-Photobiont Cellular Contacts

The type of cellular contacts between symbionts ranges from appressoria to haustoria in Lecanoromycetes (Honegger 2008), and their structure depends on various factors. The taxonomic affiliation of photobionts plays

a large role, especially its morphology and cell wall composition (Honegger 2008). A correlation has been observed between thallus growth forms and types of cellular contact between symbionts, with simple crustose species tending to have less complex contact structures than do foliose or fruticose species (Honegger 2008). Environmental conditions can also be responsible for variation in the extent of penetration by the fungus (Ben-Shaul et al. 1969; Galun et al. 1970), as well as thallus age (Collins and Farrar 1978; Galun 1988; Geitler 1963). As a result, this character has not been used in the classification of lichen-forming fungi (Poelt 1973).

V. Morphological and Chemical Features

A. Thalli

The lichen thallus is a vegetative structure formed by the fungal hyphae and algal cells. In Lecanoromycetes, thallus structures range from simple to more complex organizations. The simplest thalli are found in leprose (powderlike, Fig. 4.1a) and byssoid (cottonlike) species, which lack differentiation into strata, and are formed of loosely intermingled fungal hyphae and algal cells (Ekman and Tønsberg 2002; Kantvilas 1996; Poelt 1987). The complex thalli (heteromerous) are differentiated into layers (Fig. 4.2): upper cortex, photobiont layer, medulla, and lower cortex.

Two main types of lichen thalli are recognized, mainly for convenience: microlichens and macrolichens. Microlichens can consist of powderlike or cottonlike thalli (**leprose and byssoid** thalli) or corticated granules (**granulose** thalli) or appear as crusts tightly appressed to the substrate and generally lacking rhizines and a lower cortex (**crustose** thalli) (Fig. 4.1b). Crustose thalli are quite diverse, ranging from continuous or slightly cracked crusts to crusts formed by areoles or small lobes often on a fungal hyphal mat (hypothallus). Crustose species generally grow above the substrate, but some have a thallus developing within the

superficial layer of the substrate, either in rock (endolithic species such as *Clauzadea immersa*) or in bark (endophloeic species such as *Caloplaca cerinella* or *Lecanora persimilis*).

The largest thalli are generally found in squamulose, foliose, and fruticose lichens (macrolichens). **Squamulose** lichens are composed of scattered or imbricated scalelike lobes. **Foliose** lichens have dorsiventral thalli formed by lobes mostly with a lower cortex, which are often only loosely attached to the substrate, most often by attachment structures such as rhizines (e.g., *Peltigera*) (Fig. 4.1c). Foliose thalli attached to the substrate with a single holdfast are called umbilicate and can be formed either by a single lobe or by several lobes (e.g., *Umbilicaria*) (Hestmark 1997). Lichens with long striplike or cordlike branches that are hanging or standing upward from their substrates are called **fruticose** (e.g., *Usnea*, *Ramalina*) (Fig. 4.1d). Some fruticose lichens (e.g., *Cladonia*) have a mixed thallus formed by a basal squamulose primary thallus and trumpetlike or spikelike structures (podetia) growing upward from the primary thallus and bearing fruiting bodies (secondary thallus).

Thallus growth forms were of prime importance in shaping the first classifications of lichens (Zahlbruckner 1926). With improved microscopical techniques, anatomical and ultrastructural characters became available, and ascomatal characters replaced thallus morphology as the main characters used in classification (e.g., Hafellner 1984; Henssen and Jahns 1974; Luttrell 1951, 1955; Nannfeldt 1932; Poelt 1973). Molecular data confirmed that thallus morphology could not be strictly used for classification purposes because most growth forms were shown to have evolved several times independently in Lecanoromycetes and in lichens in general [e.g., Grube and Arup 2001; Schmitt et al. 2001; Stenroos and DePriest 1998; see also the review in Grube and Hawksworth (2007)].

B. Ascomata

1. Ascoma Morphology

Ascomata (Fig. 4.3) are structures producing spore-bearing cells called asci. They generally consist of a hymenium enveloped by a pro-

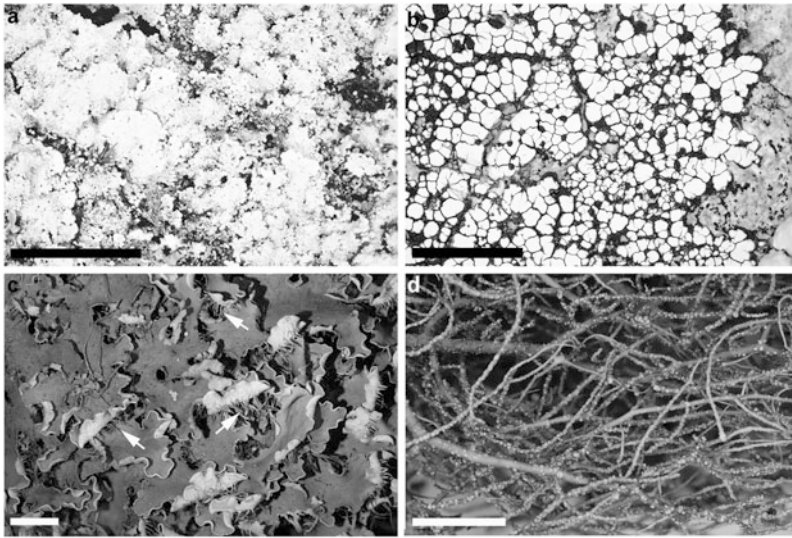


Fig. 4.1 Different types of thallus in Lecanoromycetes. (a) Powderlike leprose thallus of *Lepraria membranacea*. (b) Crustose areolate thallus of saxicolous species *Rhizocarpon macrosporum*. (c) Foliose thallus of *Peltigera rufescens*, with white rhizines visible on lower surface (white arrows). (d) Cordlike branches of fruticose thallus of *Usnea subfloridana*. Bars=5 mm

gera rufescens, with white rhizines visible on lower surface (white arrows). (d) Cordlike branches of fruticose thallus of *Usnea subfloridana*. Bars=5 mm

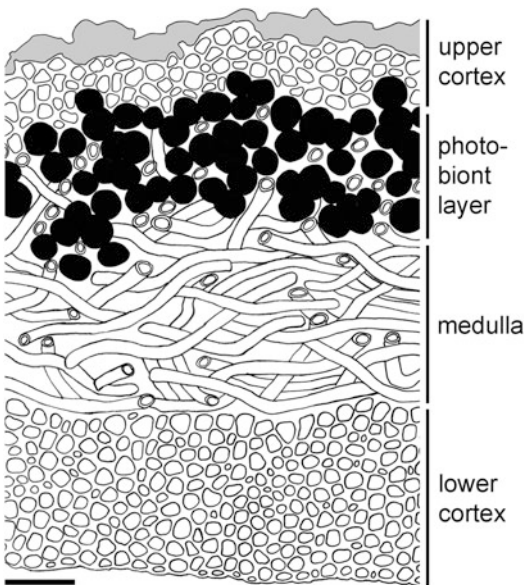


Fig. 4.2 Schematic representation of a cross section in thallus of *Xanthoria parietina*. The thallus is composed of four layers: upper cortex, photobiont layer, medulla, and lower cortex. Bar=20 μ m

tective structure called an excipulum. The hymenium comprises asci and sterile interascal hyphae. There are two main types of ascomata

in Lecanoromycetes. The most common type is the **disc-shaped apothecium**, where the **upper portion of the hymenium is mostly exposed** (Fig. 4.3a). When laterally elongated they are referred to as **lirellate apothecia** (Fig. 4.3b). In Lecanoromycetes, lirellate apothecia are restricted to Ostropales but can also be found in Arthoniomycetes, a distinct class within Leotiomyceta (Pezizomycotina), which also includes many lichen-forming fungi. The second type of fruiting body in Lecanoromycetes is the **flask-shaped perithecium** (Fig. 4.3c), where the **hymenium is exposed only through an ostiole**. The term perithecium was restricted in the past to species with an ascostromatic development (ascostromatic flask-shaped ascumata were called pseudothecia), but it is now used in a broad sense for all flask-shaped ascumata, regardless of their development type (Kirk et al. 2008). Perithecia are only found in a few lineages in Lecanoromycetes (e.g., Porinaceae, Protothelenellaceae, and Thelenellaceae). Some species have apothecia that can be confused with perithecia because they are immersed in the thallus and the hymenium is exposed only through a small aperture. Called perithecioid apothecia (Fig. 4.3d), these

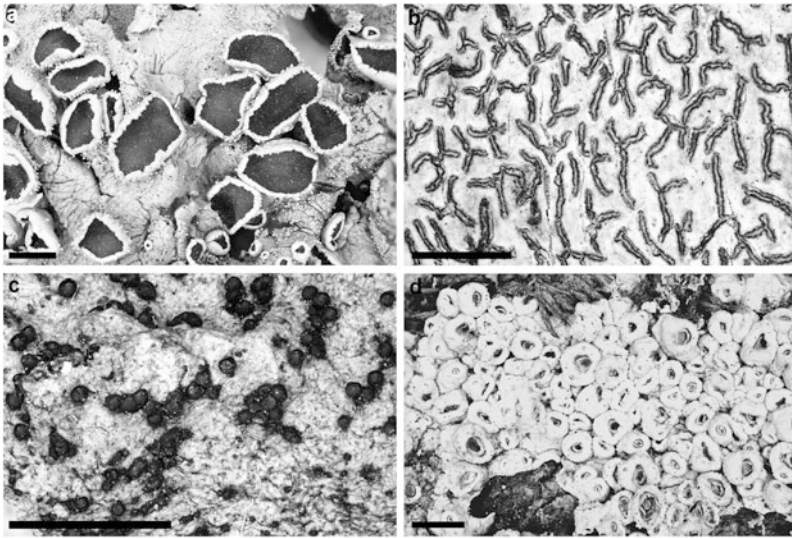


Fig. 4.3 Examples of fruiting bodies in Lecanoromycetes. (a) Disc-shaped fruiting bodies (apothecia) in *Xanthoparmelia tinctoria*. (b) Elongated fruiting bodies (lirellate apothecia) in *Graphis scripta*. (c) Flask-shaped

fruiting bodies (perithecia) in *Porina guentheri*. (d) Enclosed disc-shaped fruiting bodies (perithecioid apothecia) in *Thelotrema lepadinum*. Bars=2.5 mm

ascomata are frequently found in the subclass Ostropomycetidae.

In early classifications, ascoma morphology was used together with ascus characters to classify ascomycetes (e.g., Luttrell 1955; Nannfeldt 1932). However, molecular phylogenies demonstrated that **some types of ascomata evolved several times independently in Lecanoromycetes** [e.g., Grube et al. 2004; Schmitt et al. 2005, 2009; Wedin and Tibell 1997; see also the review in Grube and Hawksworth (2007)]. In particular, some groups with perithecioid ascomata (e.g., Porinaceae, Protothelenellaceae, and Thelenellaceae) were shown to be nested within the predominantly apothecial subclass Ostropomycetidae (Grube et al. 2004; Schmitt et al. 2005, 2009). In Lecanoromycetes, the convergent evolution of ascoma types also prevents the use of this character for defining orders and families, although some broad trends can be observed (e.g., predominantly lirellate apothecia in Graphidaceae).

In Ostropomycetidae, a correlation between ascoma type and ascoma development (Schmitt et al. 2009) suggested that angiocarpous development was a prerequisite adaptation in lineages in which perithecia

have evolved. These perithecioid fruiting ascomata may therefore have a neotenic origin (Grube et al. 2004; Schmitt et al. 2009).

2. Ascoma Development

Types of ascoma development have been used in the past to define higher divisions in filamentous ascomycetes. Originally, two main types of development were distinguished, **ascolocular and ascohymenial** (Nannfeldt 1932). In ascolocular ascomata, the asci develop in the cavity in a preformed stroma, whereas in ascohymenial ascomata, the asci develop in a hymenium not located in a preformed stroma (Kirk et al. 2008). In Lecanoromycetes, ontogenetic studies have helped describe in more detail the development of ascomata (e.g., Henssen 1976; Henssen and Jahns 1974; Letrouit-Galinou and Bellemère 1989). Henssen and Jahns (1974) recognized two main types of development in ascohymenial lichen-forming fungi, depending on the origin of the structure enveloping the ascogonia (or primordium), as well as other more specific types. These development types can lead to apothecia (angiocarps), perithecia (gymnocarps), or perithecioid apothecia (hemiangiocarps).

Letrouit-Galinou and Bellemère (1989) recognized two types of development depending on the differentiation of the excipulum (or parathecium, proper margin). Among the types without any differentiated excipulum are the *Pertusaria* and *Thelotrema* types for perithecioid apothecia and the *Graphis* and *Baeomyces* types for apothecia or lirellate apothecia. Among the types with a differentiated excipulum are the *Aspicilia* and *Gyalecta* types (excipulum reduced to a crown), the *Peltigera*, *Diploicia*, and *Xanthoria* types (typical excipulum), and *Cladonia* and *Parmelia* types (atypical excipulum).

Molecular studies showed that the classification in ascolocular and ascohymental fungi did not reflect monophyletic groupings (e.g., Berbee 1996; Lindemuth et al. 2001; Lumbsch and Huhndorf 2007a; Lutzoni et al. 2004). As a result, these characters are now rarely mentioned in classification work (e.g., Hibbett et al. 2007). Although the use of ascoma developmental types is inadequate for delimiting higher taxa of Ascomycota, their use at the ordinal and family levels may have some value since they can be characteristic of some groups of Lecanoromycetes (e.g., Parmeliaceae and Agyriaceae) (Henssen et al. 1981; Lumbsch et al. 2001a).

C. Asci

1. Ascus Walls

The first studies of asci with light microscopy (e.g., Chadefaud 1942; Luttrell 1951; Nannfeldt 1932) and electron microscopy resulted in the use of ascus characters in combination with ascomatal characters to establish higher-rank classification systems among filamentous ascomycetes (Barr 1983; Eriksson 1982; Luttrell 1951, 1955; Nannfeldt 1932). Thus, the structure of the ascus wall was one of the main ascus features used in higher classification. Currently, ascus walls are classified in three main types: a thin ascus wall formed of a single layer (**prototunicate ascus**), an ascus wall formed of two layers functioning as a single layer (**unitunicate ascus**), and an ascus wall formed of two layers functioning as two layers (**bitunicate ascus**). Most members of Lecanoromycetes have unitunicate asci (Honegger 1982a; Letrouit-Galinou 1973a).

Among unitunicate ascus types are the *Lecanora*, *Pertusaria*, and *Teloschistes* types from Honegger (1982a, b). Bellemère and Letrouit-Galinou (1987) grouped these three ascus types within the “archeacés” and distinguished the further *Lecidella*, *Catillaria*, *Psora*, *Lecidea*, *Cladonia*, and *Collema* types. Unitunicate asci are also found in *Anzina* (Scheidegger 1985), *Baeomyces* (Bellemère 1977; Honegger 1983), *Dactylospora* (Bellemère and Hafellner 1982), Gyalectaceae (Kauff and Büdel 2005), and *Trapeliopsis* (Bellemère and Letrouit-Galinou 1987).

Functionally bitunicate asci are less common in the Lecanoromycetes. They are found in Collemataceae, Peltigeraceae, and Rhizocarpaceae (Bellemère and Letrouit-Galinou 1987; Honegger 1982a). Prototunicate asci are rather rare in this fungal class and are only found in the families Caliciaceae and Sphaerophoraceae (Wedin and Tibell 1997; Wedin et al. 2000b), in which the released spores form a loose mass.

2. Ascus Apical Structure

With improving microscopy technologies, **the apical structure of asci was shown to be particularly variable within Lecanoromycetes** (e.g., Chadefaud 1973; Chadefaud et al. 1963; Honegger 1978, 1980; Letrouit-Galinou 1973a). Among the variations were the presence or absence of differentiated apical structures (apical thickening, ocular chamber, apical ring, apical nasse, subapical bourrelet) and their reaction to various stains such as iodine (e.g., Chadefaud 1973; Hafellner 1984; Letrouit-Galinou 1973a). Hafellner (1984) was the first to use these characters to systematically revise the classification within Lecanorales s.l. at the family and genus levels. He recircumscribed some species-rich families (e.g., Lecanoraceae and Lecideaceae) and described new families (e.g., Catillariaceae and Dactylosporaceae) based on the ascus apical structure (Bellemère and Hafellner 1982; Hafellner 1984). His classification system was broadly accepted (e.g., Eriksson and Hawksworth 1993; Hafellner 1994; Rambold and Triebel 1992), until **molecular data showed that these characters were not as conserved as initially thought and that similar apical structures have evolved several**

times independently in unrelated lineages [Ekman and Wedin 2000; Ekman et al. 2008; Lumbsch et al. 2001b, 2007c; Wedin et al. 2005, 2009; see also the review in Grube and Hawksworth (2007) and Printzen (2010)].

3. Dehiscence Mechanisms

The type of dehiscence (or the process leading to the liberation of ascospores from mature asci) varies greatly in Lecanoromycetes (Bellemère and Letrouit-Galinou 1987; Honegger 1982a). In most members of this class, dehiscence occurs by apical rupture of the ascus, combined with the ejection of the internal part of the ascus wall. When the ejection is not coupled with a sliding between the two layers of the ascus wall, this type of dehiscence is called a **rostrum type or Lecanora type** (Bellemère and Letrouit-Galinou 1987; Honegger 1978). It is the most common type of dehiscence in Lecanoromycetes (e.g., Lecanoraceae, Physciaceae, Parmeliaceae), and it has been suggested that it might be the ancestral dehiscence type in this class based on both anatomical data (“type archaeascé”) (Chadefaud et al. 1967) and molecular data (Miadlikowska et al. 2006; Wedin et al. 2005).

In *Rhizocarpon*, the internal layer of the ascus wall slides slightly along the external layer (*Rhizocarpon* type or hemifissitunicate type) (Bellemère 1994; Honegger 1980). In *Peltigera*, the sliding of the internal layer along the external layer is more important (*Peltigera* type, fissitunicate type or “Jack in the box”) (Bellemère and Letrouit-Galinou 1987; Honegger 1978).

Dehiscence can also occur by apical rupture of the ascus without ejection of the internal part of the ascus wall (e.g., *Trapelia* and *Coccocarpia*) (Bellemère 1994). In *Teloschistes*, the apical pore forms after predehiscent elongation of the ascus wall (***Teloschistes* type or chimney type of dehiscence**) (Bellemère and Letrouit-Galinou 1987; Honegger 1978). In *Pertusaria*, a predehiscent elongation also occurs, but the ascospores are released after bursting or splitting of the ascus tip (Honegger 1982b). Finally, in Caliciaceae and Sphaerophoraceae, ascospores are passively

released after deliquescence of prototunicate asci (**evanescent type of dehiscence**) (Wedin and Tibell 1997). Although ascus dehiscence has been used in high-rank classifications (Luttrell 1955), the systematic value of this character has been questioned because dehiscence types more likely correspond to adaptations to various environmental conditions (Bellemère 1994).

D. Ascospores

Ascospore characters, such as septation, pigmentation, size, shape, and number per ascus, were originally used to delimit families or genera in many groups of Lecanoromycetes [e.g., in Graphidaceae (Müller 1880, 1882) or in Acarosporaceae (Zahlbruckner 1907)]. However, many authors have recognized subsequently that classification based on these characters might not reflect evolutionary history because of **convergent evolution in ascospores of lichenized and nonlichenized fungi** (e.g., Poelt 1973; Vainio 1890). Morphologically similar ascospores are indeed often found in distantly related groups, as confirmed by molecular data.

Molecular phylogenetic results have further thrown doubts on the use of ascospores as a main source of characters for classification at the generic level. Several Lecanoromycetes genera that were primarily circumscribed on ascospore characters were shown to be polyphyletic, and **characters such as ascospore septation and color were frequently shown to be homoplasious** (e.g., Ihlen and Ekman 2002; Rivas Plata and Lumbsch 2011; Staiger et al. 2006). Despite this conclusion, when combined with other features, ascospore characters provide important taxonomic information for most groups of lichenized fungi at the species and generic levels (e.g., within Thelotremaaceae) (Frisch et al. 2006). Ascospore characters can also, in some cases, be useful at higher taxonomic levels since some broad trends can be observed in some groups. For example, polarilocular ascospores are characteristic of the order Teloschistales and ascospores with

lens-shaped lumina, of the family Graphidaceae s.s. (Poelt 1973).

E. Interascal Filaments

Sterile filaments are usually present in fruiting bodies alongside asci. These interascal filaments constitute the **hamathecium** and are thought to protect the asci or promote their function (Poelt 1973). Historically, two broad categories of interascal filaments were described in ascomycetes depending on their origin in the development of the ascoma. Ascophymenial development leads to the formation of **paraphyses**, whereas ascolocular development forms **paraphysoids** or **pseudoparaphyses**. These two types of filament may look very similar in mature fruiting bodies and can be confused, so they have been applied only in more recent classification systems of Ascomycota (e.g., Barr 1983). At lower taxonomic levels, hamathecial characters (septation, anastomoses and branching, color, chemistry, and shape of the upper cell) have been used together with other characters to delimitate genera or families in Lecanoromycetes (e.g., Kärnefelt and Thell 1992; Staiger and Kalb 1999; Timdal 1992). The importance of some of these characters has been discussed in light of molecular data (e.g., Rivas Plata and Lumbsch 2011; Staiger et al. 2006). However, a comprehensive reevaluation of the evolution of hamathecial characters and their taxonomic value is still needed.

F. Pycnidia

In lichenized fungi, pycnidia (=conidiomata) are **minute flask-shaped structures located on the surface of, or embedded within, lichen thalli and producing small asexual spores called pycnidiospores** (also called conidiospores or conidia). The role of pycnidia has been insufficiently studied in lichens. Culture studies first suggested that conidiospores might act as asexual dispersal units (Möller 1888), but this possibility was questioned because more recent studies showed that, in Lecanoromycetes, conidiospores germinate only rarely

(Ahmadjian 1969; Bailey 1976; Vobis 1977). Microscopical observations revealed that conidiospores most probably act as spermatia since they have been found attached to trichogynes in several species (e.g., Honegger 1984a, b; Jahns 1970).

The systematic value of pycnidial characters was recognized early on (Choisy 1954; Steiner 1901; Zahlbruckner 1903–1907), but their use in systematic studies remains rather limited, mostly because they are difficult to observe. In the 1970s and 1980s, cytological and ontogenetical studies triggered a renewed interest in pycnidial characters, and several types of pycnidia and conidiophores were described in the Lecanoromycetes (e.g., Honegger 1984b; Janex-Favre 1977, 1982; Letrouit-Galinou 1972, 1973b; Letrouit-Galinou and Lallement 1977; Vobis 1980). However, data available on pycnidia remain sparse (Roux et al. 1986), and only relatively few studies have tried to assess their use for classification within Lecanoromycetes (e.g., Krog 1982; Matsumoto and Deguchi 1999; Thell et al. 2002).

G. Asexual Propagules

Lecanoromycetes can disperse asexually by thallus fragmentation aided by undifferentiated or specialized structures. **The two most common types of specialized dispersal structures are isidia** (corticated and more or less cylindrical thallus outgrowths) (Fig. 4.4a) **and soredia** (ecorticated thallus granules produced via openings in the cortex called soralia) (Fig. 4.4b). Such propagules facilitate successful codispersal of both lichen partners, in contrast to fungal dispersal through sexual ascospores, which requires finding appropriate photobionts to reestablish lichen thalli de novo. The taxonomic value of asexual propagules was first recognized by Du Rietz (1924). He described and classified them and introduced the concept of species pairs for species that differ only by their mode of reproduction, either primarily sexual or primarily vegetative. Poelt (1970, 1972) later developed this concept, and since then, it has been debated whether they correspond to conspecific individuals or separate

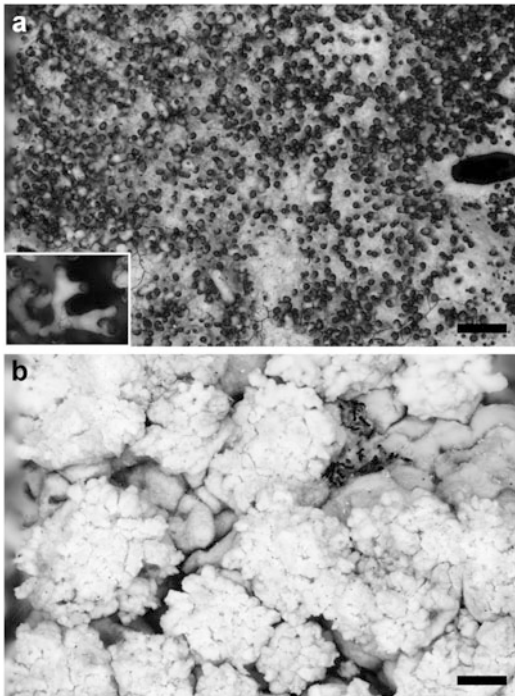


Fig. 4.4 Asexual propagules in Lecanoromycetes. (a) Upper surface of thallus of *Parmelina tiliacea* covered with small and easily detached, corticated outgrowths called isidia. In this species, isidia are simple to branched and brown at the tip (*inset*: detail of a long branched isidium). (b) Round openings (soralia) in the upper cortex of *Pertusaria flavicans* releasing eorticated granules called soredia. Bars=0.5 mm

sister species (e.g., Mattsson and Lumbsch 1989; Tehler 1982). Molecular studies on several species pairs have so far not confirmed them as separate species (e.g., Buschbom and Mueller 2006; Kroken and Taylor 2001; Myllys et al. 2001). The contribution of asexual reproduction to the ecology and evolution of lichens has rarely been addressed (e.g., Buschbom and Barker 2006; Dal Grande et al. 2012; Fedrowitz et al. 2011; Hestmark et al. 2011).

H. Secondary Compounds

Secondary compounds are **insoluble metabolites that are often deposited extracellularly by the fungal partner on the surface of hyphae**. These compounds are very diverse and numerous, with more than 700 described so far from

lichens (Elix and Stocker-Wörgötter 2008). Most of these compounds are found exclusively in lichens. They are derived from three main biosynthetic pathways (acetyl-polymalonyl, shikimic, and mevalonic acid pathways) and belong to different chemical groups such as anthraquinones, depsidones, triterpenes, pulvinic acids, and xanthenes (Asahina and Shibata 1954; Culberson and Elix 1989; Huneck 2001). Mostly present in the cortex and the medulla, they can help repel herbivores and microorganisms (Lawrey 1986, 1989) but in the cortex also act as light and UV screens (Armaleo et al. 2008; Millot et al. 2012; Solhaug et al. 2003). Armaleo et al. (2011) were the first to identify a gene cluster involved in the biosynthesis of a depside and a depsidone.

Approximately 5,000 lichen species have been investigated for their secondary compounds (Elix and Stocker-Wörgötter 2008). Methods of detection vary from simple spot tests to analysis of extracts with thin-layer chromatography and high-performance liquid chromatography (Huneck and Yoshimura 1996). The presence of secondary compounds has been used at all taxonomic levels, for both classification and species identification. **Most secondary compounds are found widely in Lecanoromycetes and only rarely form synapomorphies for single lineages.** However, the presence of some secondary compounds was shown to be informative at the genus and family levels (Lumbsch 1998a; Schmitt and Lumbsch 2004). The use of chemical characters for species delimitation has been controversial (Lumbsch 1998b). Recent molecular studies show that, depending on the group studied, chemotypes may correspond to separate species (e.g., Tehler and Källersjö 2001) or can represent infraspecific variability (e.g., Leavitt et al. 2011a, b; Nelsen and Gargas 2009; Velmala et al. 2009).

VI. Origin and Diversification

Dating the divergence time of fungi is not an easy task because of the relatively poor fossil record for these organisms and the variable rates of nucleotide substitution across this kingdom (Lumbsch et al. 2008a; Lutzoni and

Pagel 1997; Woolfit and Bromham 2003; Zoller and Lutzoni 2003). As a result, estimates of divergence times in fungi once varied considerably depending on the methods and calibrations used (Berbee and Taylor 1993, 2001; Heckman et al. 2001; Padovan et al. 2005; Taylor and Berbee 2006). With the reinterpretation of fossil data and the development of new phylogenetic methods allowing for rates to vary across lineages, **divergence estimates for the main fungal lineages have now reached a consensus** (Lücking et al. 2009a; Taylor and Berbee 2010), and divergences of more recent lineages have started to be investigated (Amo de Paz et al. 2011; Gueidan et al. 2011).

Soon after the divergence of Pezizomycotina, Leotiomyceta underwent a radiation during which the Lecanoromycetes lineage originated (Gazis et al. 2012; Schoch et al. 2009; Spatafora et al. 2006). So far, all ancestral state reconstruction studies agree that lichenization in Lecanoromycetes evolved at or prior to the onset of the evolution of this fungal class. This acquisition of lichenization has been placed at the base of a lineage including Lecanoromycetes, Eurotiomycetes, and Lichinomycetes (James et al. 2006; Lutzoni et al. 2001), at the base of a lineage including Lecanoromycetes and Lichinomycetes (Gueidan et al. 2008), or at the base of Lecanoromycetes (Schoch et al. 2009). According to Gueidan et al. (2011), Lecanoromycetes diverged from Eurotiomycetes during the late Devonian, around 371 million years ago (mya) (between 322 and 424 mya), and the diversification of extant Lecanoromycetes species (crown group) originated during the Carboniferous, approximately 322 mya (between 269 and 380 mya).

Within Lecanoromycetes, several well-interpreted fossils from amber are available to calibrate the molecular clock. A species of *Anzia* was described from European amber (35–40 mya) (Mägdefrau 1957), two species of *Parmelia* from Dominican amber (15–45 mya) (Poinar et al. 2000), and a species of *Alectoria* from Baltic amber (35–40 mya) (Rikkinen and Poinar 2002). A more recent discovery by Honegger et al. (2013) of exceptionally

well-preserved lichen thalli fragments in siltstone of the lower Devonian (415 mya) provided the oldest record of modern lichens.

One of the *Parmelia* fossils and the *Alectoria* fossil were used in a recent study to investigate the origin of Parmeliaceae, one of the largest families within Lecanoromycetes (Amo de Paz et al. 2011). Results show that this family radiated around the Cretaceous–Tertiary boundary (± 65 mya), just before a climatic period characterized by temperature and atmospheric CO₂ maxima. Most major parmelioid genera originated during the Eocene and early Oligocene and diversified during the cooler periods of late Oligocene to early Pliocene.

VII. Orders and Classification

A. Acarosporales

Acarosporales (Acarosporomycetidae) (Fig. 4.5) is a small order with a single family, Acarosporaceae, 11 genera, and 183 species (Kirk et al. 2008). They are mostly crustose species with apothecial ascomata, poorly to moderately branched and anastomosed paraphyses, unitunicate polysporous asci, and small hyaline simple ascospores (Hibbett et al. 2007). They occur worldwide and mostly colonize rocks. Traditionally, Acarosporaceae had been placed in the order Lecanorales based on ascus characters (Kirk et al. 2001). However, molecular studies showed that they did not belong to this order but represent instead the **earliest diverging lineage in Lecanoromycetes** (Lumbsch et al. 2007b; Miadlikowska et al. 2006; Reeb et al. 2004; but see Hofstetter et al. 2007). The order Acarosporales was therefore formally described for this family (Hibbett et al. 2007).

Although polyspory is not uncommon in nonlichenized and lichenized ascomycetes, the family Acarosporaceae was originally characterized by its true polyspory (polyspory resulting from a meiosis followed by several mitoses generating more than 100 ascospores, as opposed to polyspory resulting from budding or fragmenting ascospores). However, in Lecanoromycetes, true polyspory is not restricted to the Acarosporaceae. As a result, the circumscription of this family has been variable, with

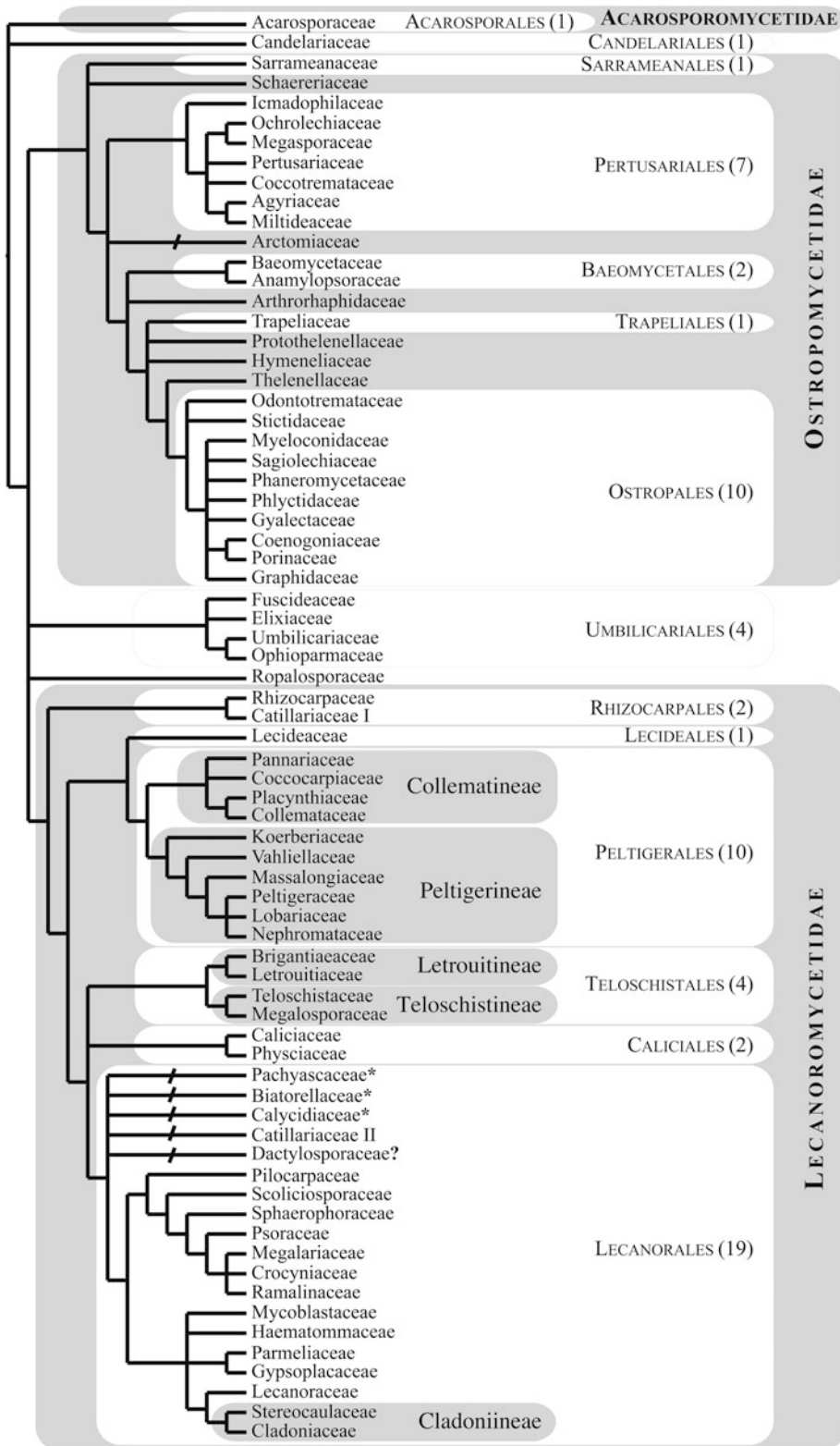


Fig. 4.5 Schematic representation of phylogeny and classification of Lecanoromycetes based on selected published sources (Andersen and Ekman 2005; Arup

et al. 2007; Baloch et al. 2010; Bylin et al. 2007; Ekman et al. 2008; Gaya et al. 2012; Hodkinson and Lendemer 2011; Hofstetter et al. 2007; Kirk et al. 2008; Lumbsch

many polysporous genera (e.g., *Maronea*, *Pleopsidium*, and *Thelocarpon*) being successively excluded from, or included in, the family depending on the system adopted for their classification [Golubkova 1988; Hafellner 1995; Magnusson 1936; Zahlbruckner 1907; see the detailed review in Reeb et al. (2004)].

Molecular data have helped resolve the circumscription of Acarosporaceae (Reeb et al. 2004; Wedin et al. 2005), and the genera *Acarospora*, *Glypholecia*, *Pleopsidium*, *Polysporina*, *Sarcogyne*, *Thelocarpella*, and *Timdalia* were confirmed as part of this family, whereas the genera *Biatoridium*, *Maronea*, *Sporastatia*, *Strangospora*, and *Thelocarpon* were excluded. Molecular studies also confirmed the **multiple independent origins of true polyspory in Lecanoromycetes** (Reeb et al. 2004), i.e., Acarosporaceae (with a loss in the two species *Acarospora macrospora* and *Glypholecia scabra*, which have only 30–100 ascospores), *Maronea*, *Sporastatia*, *Strangospora*, and a lineage including *Thelocarpon* and *Biatoridium*.

B. Baeomycetales

The order Baeomycetales (Ostropomycetidae) (Fig. 4.5) currently includes two families, Baeomycetaceae and the monotypic Anamylopsoraaceae (Hodkinson and Lendemer 2011; Lumbsch et al. 1995). The family Baeomycetaceae comprises the three genera *Ainoa*, *Baeomyces*, and *Phyllobaeis* (Hibbett et al. 2007; Lumbsch and Huhndorf 2010) and a total of approximately 15 species with crustose to squamulose or foliose thalli, sessile to stipitate apothecia, branched paraphyses, nonamyloid asci or asci with a slightly amyloid apex, and simple to transver-

sally septate hyaline ascospores (Hibbett et al. 2007; Johnston 2001). The species grow on soils, rocks, and bryophytes in moist areas and often are primary colonizers of disturbed substrates (Johnston 2001). First placed in Lecanorales close to Cladoniaceae (Henssen and Jahns 1974; Poelt 1973), this family (including at the time the genera *Baeomyces* and *Icmadophila*) was then transferred to the predominantly nonlichenized order Helotiales (now Leotiales) based on its *Leotia*-type ascus (Chadefaud 1960, 1973; Hafellner 1988; Honegger 1983; Rambold et al. 1993; Tehler 1996).

Early molecular studies suggested that *Baeomyces* might not be related to Leotiales (Platt and Spatafora 1999; Stenroos and DePriest 1998). Later, this genus was shown to form a sister group to the Ostropales s.l., and the ordinal name Baeomycetales was then suggested for this lineage (Kauff and Lutzoni 2002). **Additional molecular data confirmed its phylogenetic placement within Ostropomycetidae** (Lumbsch et al. 2007b; Miadlikowska et al. 2006), and the order Baeomycetales was therefore formally erected for the family Baeomycetaceae (Hibbett et al. 2007).

The delimitation of Baeomycetaceae also underwent some important changes during the last two decades. Some genera previously placed in this family (e.g., *Dibaeis*, *Icmadophila*, *Siphulella*) were segregated into the new family Icmadophilaceae based on morphological evidence (Rambold et al. 1993), and subsequent molecular studies confirmed that these genera are not related to Baeomycetaceae (Platt and Spatafora 1999; Stenroos and DePriest 1998). A new genus (*Phyllobaeis*) was also described for *Baeomyces* species with squamulose primary thalli and brown apothecia (Gierl and Kalb 1993). Finally, molecular data showed that the genus *Ainoa* also belongs to Baeomycetales (Lumbsch et al. 2007b, c). This genus had previously been described to

Fig. 4.5 (continued) and Huhndorf 2010; Lumbsch et al. 2004, 2007b, 2008b; Lutzoni et al. 2004; Miadlikowska et al. 2006; Muggia et al. 2011; Reeb et al. 2004; Rivas Plata et al. 2012; Schmitt et al. 2005, 2012; Schoch et al. 2009; Wedin et al. 2009; Widhalm and Lumbsch 2011; Zhou and Wei 2007). Phylogenetic relationships among taxa (families, orders, and subclasses) were compiled using a “super tree” approach and are shown as resolved if reported with posterior probability $\geq 95\%$ or maximum likelihood bootstrap $\geq 70\%$ in multiple studies (in most cases) and are not in conflict

at the same level of support. The number of recognized families in each order is provided in parentheses after the order name. *Shaded boxes* represent subclasses and suborders. *Oblique bars* across branches indicate families with unknown placement in the Lecanoromycetidae or Ostropomycetidae. *Stars* indicate families for which no DNA sequence is currently available in GenBank. *Question mark* indicates that Dactylosporaceae may be placed outside of Lecanoromycetes (in Eurotiomycetes) (Schoch et al. 2009)

accommodate two morphologically different species of *Trapelia* that did not cluster with *Trapelia* s.s. in a molecular phylogenetic study (Lumbsch et al. 2001b).

The circumscription of the order Baeomycetales is likely to undergo more changes in the future. A morphological study of the family Anamylopsoraceae shows that this monotypic family shares several characters with Baeomycetaceae, such as the ascocarp ontogeny, stipitate ascogonia, annular exciple, and conidiophore type (Lumbsch et al. 1995). However, these two families also differ in other characters, such as the ascus type. Anamylopsoraceae had been placed tentatively in Agyriineae and Agyriales (Lumbsch et al. 1995, 2001a, respectively), but a transfer to Baeomycetales was recently suggested (Hodkinson and Lendemer 2011; Lumbsch et al. 2007b). A comprehensive phylogenetic analysis is needed to determine whether this family belongs to Baeomycetales.

C. Caliciales

The order Caliciales (Lecanoromycetidae) (Fig. 4.5) was **in the past recognized as a phenotypically well-delimited group that included species with mazaedium-forming ascomata and passive ascospore dispersal** (e.g., Zahlbruckner 1903–1907; see detailed review in Tibell 1984) and was erected as an order by Bessey (1907). However, this order underwent drastic changes in circumscription after a first extensive revision by Tibell (1984). Based on a careful morphological study, Tibell excluded several families and genera from Caliciales s.s. (e.g., Sphaerophoraceae and *Chaenotheca*) and restricted the order to the three families Caliciaceae, Mycolaliciaceae, and Sphinctrinaceae (Tibell 1984, 1996). More recently, a study using molecular data demonstrated that **Mycocaliciaceae and Sphinctrinaceae belong in fact to Eurotiomycetes** and that only the family Caliciaceae was strongly supported as part of the order Lecanorales (Wedin and Tibell 1997).

Subsequent studies with broader taxon samplings showed that Caliciaceae were in fact closely related to Physciaceae, in the order

Lecanorales (Wedin et al. 2000a, 2005). Both Physciaceae and Caliciaceae were later tentatively placed in Teloschistales as part of the suborder Physciineae (Miadlikowska et al. 2006). In a more recent molecular study focusing on Teloschistales s.l., Gaya et al. (2012) demonstrated phylogenetic instability for relationships among Physciineae, Teloschistineae, and Lecanorales, where the two suborders did not always form a monophyletic group. To ensure the classification was resilient to the various resolution of these three clades, Gaya et al. (2012) elevated Physciineae to the ordinal level by resurrecting the order Caliciales and restricted Teloschistales to Brigantiaeaceae, Letrouitiaceae, Megalosporaceae, and Teloschistaceae. **In this new phylogenetic context, Caliciales includes two families: Caliciaceae (with two subfamilies Calicioidea and Buellioidea) and Physciaceae.**

D. Candelariales

The order Candelariales (Candelariomycetidae?) (Fig. 4.5) **includes a single family, Candelariaceae**, and four genera: *Candelaria*, *Candelariella*, *Candelina*, and *Placomaronea* (Lumbsch and Huhndorf 2010; Miadlikowska et al. 2006; Westberg et al. 2009). It is a small group with approximately 66 lichenized species (Kirk et al. 2008) characterized by yellow to orange thalli (secondary chemistry based on pulvinic acid and derivatives), disciform apothecia, unitunicate asci (often polysporous), mostly unbranched paraphyses, and hyaline mostly simple ascospores (Hibbett et al. 2007; Westberg et al. 2007, 2009). Formerly, the family Candelariaceae had been placed in Lecanorales s.l. (Henssen and Jahns 1974; Poelt 1973). Molecular data showed that this family did not cluster within Lecanorales as currently delimited (Hofstetter et al. 2007; Miadlikowska et al. 2006; Wedin et al. 2005), and so the order Candelariales was erected for this family (Hibbett et al. 2007). Candelariales was considered to be a sister order to Acarosporales (Wedin et al. 2005) or possibly formed the second lineage to diverge within Lecanoromycetes after Acarosporales (Miadlikowska et al. 2006) or perhaps

the first diverging lineage in Lecanoromycetes (Hofstetter et al. 2007). Because of this phylogenetic uncertainty, this order was only tentatively recognized as the subclass Candelariomycetidae by Miadlikowska et al. (2006) and Hofstetter et al. (2007). A morphological and molecular revision of the family showed that the current generic delimitation does not reflect monophyletic groups, and further work will be needed to clarify the generic boundaries (Westberg et al. 2007, 2009).

E. Lecanorales

Lecanorales (Lecanoromycetidae) (Fig. 4.5) is the **largest order in Lecanoromycetes** with 19 families and approximately 250 genera (Lumbsch and Huhndorf 2010). The number of species in this order was estimated to be 5,695 (Kirk et al. 2008). It includes mostly lichenized species with varied thallus types, predominantly apothecial ascomata, usually unbranched paraphyses, mostly thick-walled unitunicate asci (often amyloid), and varied ascospores (Kirk et al. 2008). Traditionally, this apparently heterogeneous order included most lichenized apothecial ascomycetes, with the exception of those included in Ostropales (e.g., Henssen and Jahns 1974; Poelt 1973; Rambold and Triebel 1992). A new circumscription of this order based on the ascus apical structure led to the exclusion of several taxa from Lecanorales (e.g., Peltigerales and Teloschistales) (Hafellner 1988). **This circumscription was further narrowed after molecular data were used to test the relationships among the main Lecanorales taxa.** This circumscription was confirmed, and the trend continued with the advent of molecular phylogenetics, resulting in the following orders currently being recognized outside the Lecanorales: Acarosporales, Caliciales (with the Physciaceae), Candelariellales, Lecideales, Peltigerales, Pertusariales, Teloschistales, and Umbilicariales (e.g., Gaya et al. 2012; Miadlikowska and Lutzoni 2004; Miadlikowska et al. 2006; Reeb et al. 2004; Schmuell et al. 2011; Wedin et al. 2005). Among the remaining 19 families in Lecanorales are the broadly distributed and well-known

species-rich Cladoniaceae, Lecanoraceae, Parmeliaceae, and Ramalinaceae (Lumbsch and Huhndorf 2010).

Parmeliaceae is the largest family within Lecanorales, with approximately 2,500 species and 88 genera (Kirk et al. 2008). Earlier, many groups within Parmeliaceae had been tentatively segregated from this family based on morphological, anatomical, and chemical characters (e.g., Alectoriaceae, Anziaceae, Hypogymniaceae, and Usneaceae). But most of these segregate families were not confirmed by molecular phylogenies (e.g., Arup et al. 2007; Mattsson and Wedin 1999; Wedin et al. 1999), and a wider circumscription of Parmeliaceae is currently accepted (Eriksson 2006; Kirk et al. 2008; Lumbsch and Huhndorf 2010). This family comprises a large variety of growth forms (e.g., parmelioid, usneoid, or cetrarioid species), which do not define large monophyletic groups within Parmeliaceae but nevertheless were found to be useful in characterizing and identifying smaller clades within the family (Crespo et al. 2007).

The generic concept is a strongly debated area in lichen research (e.g., Elix 1993; Hale 1984a; Nimis 1998). In Parmeliaceae, large genera (e.g., *Parmelia* s.l.) have been split into multiple smaller genera (e.g., Culberson and Culberson 1981; Elix and Hale 1987; Elix et al. 1986; Hale 1974, 1984b). Molecular phylogenetic studies have shown that many of these newly segregated genera are not monophyletic (e.g., Blanco et al. 2004, 2005; Crespo et al. 2010; Nelsen et al. 2011), and the taxonomic importance of some characters traditionally used to classify parmelioid lichens (e.g., chemistry of the cortex, presence or absence of pores and pseudocyphellae) may have been overestimated (Blanco et al. 2006).

Similar problems were found in other families of Lecanorales (e.g., Lecanoraceae, Ramalinaceae). In the predominantly crustose groups of Lecanorales, which were mainly classified based on ascus characters (Hafellner 1984), molecular phylogenetic studies reported that many of these crustose groups (e.g., Bacidaceae, Lecanoraceae, Micareaaceae) were not monophyletic and that the evolution of the ascus was more complex than had been anticipated and of limited value for classification at this taxonomic level (Andersen and Ekman 2004; Ekman 2001; Ekman and Wedin 2000;

Ekman et al. 2008). Because of a similar composite thallus, Cladoniaceae was placed together with Stereocaulaceae and two other families within the suborder Cladoniineae (Lecanorales s.l.) (Poelt 1973). Molecular phylogenies showed that, although the composite growth form evolved several times in Lecanoromycetes (Stenroos and DePriest 1998), Cladoniaceae and Stereocaulaceae do form a sister group to which the suborder Cladoniineae is now restricted (Miadlikowska et al. 2006; Myllys et al. 2005; Wedin et al. 2000b).

F. Lecideales

Lecideales (Lecanoromycetidae) (Fig. 4.5) is an order recently resurrected for a single family, Lecideaceae, now restricted to the genus *Lecidea* s.s. (sensu Hertel) and some species of *Porpidia* (Schmull et al. 2011). In Zahlbruckner's classification system (1903–1907), **Lecideaceae was a large artificial family within the order Lecanorales that included a heterogeneous assemblage of crustose taxa with lecideine or biatorine apothecia** (e.g., *Bacidia*, *Catillaria*, *Toninia*), among which *Lecidea* was one of the largest lichen genera. The delimitation of this poorly studied family was questioned in later taxonomic works and classification systems (Henssen and Jahns 1974; Hertel and Rambold 1985; Poelt 1973; Santesson 1952; Timdal 1987). In his classification of Lecanorales, Hafellner (1984) was the first to attempt to recircumscribe the two families Lecideaceae and Lecanoraceae. Based on ascus characters, he segregated several new families from the Lecideaceae, among which was Porpidiaceae. His system was broadly accepted (e.g., Eriksson and Hawksworth 1993; Hafellner 1994; Rambold and Triebel 1992), although also sometimes criticized (e.g., Timdal 1992).

Molecular phylogenetic studies confirmed the heterogeneity of early circumscriptions of Lecideaceae and Lecanoraceae (Andersen and Ekman 2004, 2005; Buschbom and Mueller 2004; Ekman 2001; Ekman et al. 2008; Schmull et al. 2011). For example, the genus *Bacidia*, included in Lecideaceae in early classifications

(Henssen and Jahns 1974; Poelt 1973; Zahlbruckner 1903–1907), was shown to belong to Ramalinaceae, a family classified within Lecanorales (Ekman 2001). Molecular phylogenies also shed a light on Hafellner's classification system (1984). Characters of the ascus tip used by this author to redelimitate genera and families within Lecanorales do not seem to characterize monophyletic entities in Lecideaceae and related taxa (e.g., Porpidiaceae) (Buschbom and Mueller 2004). Some taxa previously attributed to Lecideaceae were shown to belong to different lineages within Lecanoromycetes, and genera within this family were shown to be poorly delimited (Schmull et al. 2011). **The phylogenetic positions of most members of Lecideaceae are still unknown or unsettled** (Miadlikowska et al. 2006; Schmull et al. 2011). However, they were found to form five distinct groups within Lecanoromycetidae, one of which included only saxicolous species belonging to the genera *Lecidea* and *Porpidia*, including the type species *Lecidea fuscoatra*, which led to the resurrection of the order Lecideales s.s. (Schmull et al. 2011). Additional molecular data are greatly needed to further investigate this species-rich and broadly defined lichen group.

G. Ostropales

Ostropales (Ostropomycetidae) (Fig. 4.5) is a **large order of mostly crustose lichenized and nonlichenized species, with high species diversity in the tropics**. It includes approximately 2,750 species (Kirk et al. 2008) currently classified in ten families: Coenogoniaceae, Graphidaceae (including Gomphillaceae and Thelotremaaceae), Gyalectaceae, Myeloconidaceae, Odontotremataceae, Phaneromycetaceae, Phlyctidaceae, Porinaceae, Sagirolechiaceae, and Stictidaceae (Baloch et al. 2010; Lumbsch and Huhndorf 2010; Rivas Plata et al. 2012). This order is characterized by ascomata ranging from perithecial to apothecial, with unbranched or anastomosate paraphyses, unitunicate non-amyloid asci, and morphologically variable ascospores (Kirk et al. 2008; Lücking et al. 2004; Lumbsch et al. 2007b).

The circumscription of the order Ostropales has undergone many changes in the past. It was originally described to accommodate the nonlichenized family Ostropaceae (Nannfeldt 1932), now known as Stictidaceae. Gilenstam (1969) was the first to include lichenized taxa within Ostropales. He recognized the close relationship between the lichenized genus *Conotrema* and the nonlichenized genus *Stictis* and attributed *Conotrema* to Ostropales. He also suggested that the lichenized genera *Diploschistes*, *Graphis*, and *Thelotrema* should be transferred to Ostropales because of their close relationship with *Conotrema* (Gilenstam 1969). Henssen and Jahns (1974) considered these genera and further lichenized groups (then included in Asterothyriaceae, Graphidaceae, and Thelotremataceae) as part of Ostropales. Subsequently, in a morphological revision of Ostropalean fungi, Sherwood (1977a, b) restricted Ostropales to *Odontotrema*, *Ramonia*, most current genera of Stictidaceae, and other genera now excluded from Lecanoromycetes. In this classification, many lichenized taxa (e.g., Graphidaceae and Thelotremataceae) were excluded from Ostropales based on differences in ascospore type (Sherwood 1977a, b).

Early molecular phylogenetic studies confirmed the close relationship between *Stictis* and *Conotrema*, and between Stictidaceae and both Graphidaceae and Thelotremataceae (Winka et al. 1998). The two families Coenogoniaceae and Gyalectaceae (Gyalectales) were then shown to be related to Graphidaceae and Thelotremataceae based on molecular data, and a broad delimitation was adopted for Ostropales (Kauff and Lutzoni 2002): Ostropales s.l. with Coenogoniaceae, Graphidaceae [including Thelotremataceae, as shown by Mangold et al. (2008)], Gyalectaceae, Stictidaceae, and Trapeziaceae. Other families were subsequently attributed to Ostropales s.l. based on additional molecular data: Asterothyriaceae and Gomphillaceae (Lücking et al. 2004), Phlyctidaceae and Solorinellaceae (Miadlikowska et al. 2006), the reinstated family Sagirolechiaceae (Baloch et al. 2010), and, more surprisingly, Porinaceae, a family of lichenized perithecioid ascomycetes (Grube et al. 2004). Trapeziaceae (as Agyria-

ceae) is now excluded from Ostropales s.l. (Grube et al. 2004; Miadlikowska et al. 2006). Although still recently largely debated (Grube et al. 2004; Lücking et al. 2004; Lumbsch et al. 2004; Miadlikowska et al. 2006), the broader delimitation of Ostropales (but without Trapeziaceae) has been accepted in current classification systems (Hibbett et al. 2007; Lumbsch and Huhndorf 2010).

The phylogenetic placement of Ostropales within Lecanoromycetes has also long been unclear due to an unstable backbone of the Lecanoromycetes phylogeny (Lumbsch et al. 2007b). Ostropales has been found to be sister to all other Lecanoromycetes (Grube et al. 2004; Lücking et al. 2004; Lumbsch et al. 2004), sister to Trapeliales and Hymeneliaceae (Kauff and Lutzoni 2002; Miadlikowska and Lutzoni 2004) or to a lineage including Trapeliales and Baeomycetales (Miadlikowska et al. 2006), sister to Fuscideaceae, a family incertae sedis in Lecanoromycetes (Reeb et al. 2004), and sister to a lineage including *Anzina* and *Arthroraphis* (Wedin et al. 2005), although none of these relationships were strongly supported. Schmitt et al. (2005) reported the Thelenellaceae as sister to the Ostropales s.l. with a high posterior probability, supporting the resolution shown in Fig. 4.5. Nevertheless, more loci and broader taxon samplings are needed to establish the sister taxa of Ostropales with high phylogenetic confidence (Lumbsch et al. 2007b).

H. Peltigerales

Peltigerales (Lecanoromycetidae) (Fig. 4.5) is an order of mainly foliose species, with rounded apothecia, unbranched paraphyses, bitunicate asci with fissitunicate dehiscence, and multiseptate ascospores (Honegger 1978; Kirk et al. 2008). They have a worldwide distribution and colonize diverse substrates, mostly in humid habitats. **Most species in this order are associated with cyanobacteria, either as primary or secondary photobionts.** All Lecanoromycetes with cyanobacteria as their primary photobiont belong to this order [with the only exception being Arctomiaceae, which are classified in Ostropomycetidae (Lumbsch

et al. 2005)]. When cyanobacteria occur only as secondary photobionts, the primary photobionts are then green algae from the genera *Coccomyxa*, *Dictyochloropsis*, or *Myrmecia* (Tschermak-Woess 1988a), and the cyanobacterial secondary photobionts are restricted to gall-like structures called cephalodia. Peltigeralean species associated only with a green alga are rare. The most recent common ancestor of Peltigerales was inferred to be associated with a cyanobacterium as its primary photobiont, which means that the **green algal photobionts were most likely acquired secondarily in this order** (Miadlikowska and Lutzoni 2004). Moreover, the anatomically nonlayered gelatinous thalli mostly found in some genera of Collematineae (e.g., *Collema* and *Leptogium*) seem to have evolved from more complex and anatomically layered thalli (Wedin et al. 2009). The phylogenetic relationships, an overview of phenotypic characters, and the major types of ascus structures within Peltigerales are reported in Spribille and Muggia (2013).

Peltigerales currently includes two suborders, Collematineae and Peltigerineae (Miadlikowska and Lutzoni 2004), and ten families (Spribille and Muggia 2013). Collematineae includes four families: Coccocarpiaceae, Collemataceae, Pannariaceae, and Placynthiaceae. Peltigerineae includes six families: Koerberiaceae, Lobariaceae, Massalongiaceae, Nephromataceae, Peltigeraceae, and Vahliellaceae (Miadlikowska and Lutzoni 2004; Muggia et al. 2011; Spribille and Muggia 2013; Wedin et al. 2007, 2011). Previously, peltigeralean lichens had been recognized at either the ordinal level (Peltigerales) (Hafellner 1988; Kirk et al. 2001) or the subordinal level within the order Lecanorales (Peltigerinae) (Eriksson et al. 2003; Henssen and Jahns 1974; Poelt 1973; Rambold and Triebel 1992; Tehler 1996). Despite this ranking inconsistency, all large-scale molecular phylogenetic studies confirmed the placement of this lineage within Lecanoromycetes (e.g., Kauff and Lutzoni 2002; Lutzoni et al. 2001, 2004; Miadlikowska et al. 2006; Wedin and Wiklund 2004). The current recognition of this clade at the ordinal level and the establishment of the **two suborders Peltigerineae and Collematineae** were proposed by Miadlikowska

and Lutzoni (2004) and are now largely adopted (Hibbett et al. 2007; Lumbsch and Huhndorf 2007b, 2010).

The number of families within Peltigerales changed greatly over time [see details in Miadlikowska and Lutzoni (2004)]. The two families Lobariaceae and Peltigeraceae have always been included in Peltigerales (Hafellner 1988; Poelt 1973), but Coccocarpiaceae, Collemataceae, and Pannariaceae have sometimes been excluded and transferred to the Lecanorales s.l. or classified as incertae sedis within Lecanorales s.l. (Eriksson et al. 2003; Hafellner 1988; Henssen and Jahns 1974; Kirk et al. 2001; Poelt 1973). Moreover, Nephromataceae and Solorinaceae were recognized as separate families from Peltigeraceae by certain authors (Hafellner 1988; Poelt 1973). Molecular phylogenetic studies have confirmed the placement of Coccocarpiaceae, Collemataceae, Pannariaceae, and Placynthiaceae within the Collematineae, and Lobariaceae, Nephromataceae, and Peltigeraceae within the Peltigerineae (Miadlikowska and Lutzoni 2004; Miadlikowska et al. 2006; Wedin and Wiklund 2004; Wedin et al. 2009). The families Massalongiaceae, Vahliellaceae, and Koerberiaceae were more recently described and attributed to Peltigerineae (Spribille and Muggia 2013; Wedin et al. 2007, 2011).

I. Pertusariales

The order Pertusariales (Ostropomycetidae) (Fig. 4.5) mostly comprises crustose species with disciform to poriform apothecia, thick-walled asci, branched paraphysoids, and generally large ascospores (Lumbsch et al. 1994; Schmitt et al. 2006). They have a worldwide distribution and colonize a broad range of habitats and substrates. Earlier, these species were classified in the suborder Pertusarineae within the order Lecanorales s.l. (Henssen and Jahns 1974; Poelt 1973) and later as the order Pertusariales (Hawksworth and Eriksson 1986). Molecular phylogenies revealed that Pertusariales belongs to Ostropomycetidae (Lutzoni et al. 2004; Miadlikowska et al. 2006; Reeb et al. 2004), and this order was accepted in all recent classifications of Ascomycota (Hibbett et al. 2007; Lumbsch and Huhndorf 2010).

A recent molecular study showed that the type species of *Agyrium* did not cluster with other Agyriaceae but nested within Pertusariales (Schmitt et al. 2010). As a result, these authors reduced the order Pertusariales to synonymy with Agyriales based on the priority

principle. The name Agyriales would then be used for a group including a large majority of species traditionally classified in Pertusariales and only a few mostly nonlichenized and poorly known species of *Agyrium*. Hodkinson and Lendemer (2011) proposed that **the name Pertusariales should be retained over Agyriales** because the principle of priority is not mandatory for taxa above the family rank, and because the name Agyriales was most recently misapplied to a monophyletic group, including the family Trapeliaceae, now recognized as Trapeliales.

Pertusariales currently includes seven families: Agyriaceae (currently only represented by its generic type *Agyrium rufum*), Coccotremataceae, Icmadophilaceae, Megasporaceae, Miltideaceae, Ochrolechiaceae, and Pertusariaceae (Hodkinson and Lendemer 2011; Lumbsch and Huhndorf 2010; Schmitt et al. 2010; Widhelm and Lumbsch 2011), but its circumscription has been problematic. Only species from the families Coccotremataceae, Pertusariaceae, and Ochrolechiaceae had traditionally been included in Pertusariaceae/Pertusariales (Eriksson and Hawksworth 1986; Henssen 1976; Henssen and Jahns 1974; Poelt 1973). Species from the Coccotremataceae family were segregated from Pertusariaceae based on differences in ascomata structure and ontogeny (David and Hawksworth 1991; Henssen 1976). Because species of Coccotremataceae also differ from those of Pertusariaceae in other aspects (e.g., the ascus structure, the presence of cephalodia), members of Coccotremataceae had previously been excluded from Pertusariales (Lumbsch et al. 1994), but molecular phylogenetic analyses confirmed their placement within this order (Lumbsch et al. 2002). The segregation of *Ochrolechia* from Pertusariaceae was first suggested by Harris (1990). Schmitt et al. (2006) then formally described and redelimited this family to also include the genus *Varicellaria*. Icmadophilaceae had earlier been classified within Baeomycetaceae (Henssen and Jahns 1974; Poelt 1973), but molecular phylogenies supported the placement of this family within Pertusariales (Miadlikowska et al. 2006; Reeb et al. 2004). The family Megasporaceae was erected for *Megaspora verrucosa*, a species previously classified as part of the genus *Aspicilia* (Clauzade and Roux 1984) and placed in Pertusariales (Lumbsch et al. 1994). This species was later shown based on molecular data to be sister to *Aspicilia* and part of Pertusariales (Schmitt et al. 2006). The genera *Aspicilia* and *Lobothallia* were therefore transferred to Megasporaceae, and Aspiciliaceae ined. was regarded as a synonym of this family (Lumbsch and Huhndorf 2010; Schmitt et al. 2006).

J. Rhizocarpales

The order Rhizocarpales (Lecanoromycetidae?) (Fig. 4.5) **includes two families, Rhizocarpaceae and part of the Catillariaceae** (the genus *Sporastatia*), and approximately 489 species (Kirk et al. 2008). They are characterized by crustose areolate thalli, immersed to sessile apothecia, branched and often anastomosed paraphyses, asci with an amyloid apex, and simple to muriform ascospores (Hafellner 1984). The sister relationship between *Sporastatia* (Catillariaceae) and *Rhizocarpon* (Rhizocarpaceae) was first demonstrated in the study by Reeb et al. (2004). Further studies confirmed this result (Buschbom and Mueller 2004; Lutzoni et al. 2004), and the order Rhizocarpales was proposed by Miadlikowska et al. (2006) to accommodate selected taxa from these two families (many members were never subjected to phylogenetic studies). The phylogenetic position of Rhizocarpales as the first split within Lecanoromycetes has rarely been supported. If confirmed, this order should be considered as a member of Lecanoromycetidae.

K. Sarrameanales

The order Sarrameanales (Ostropomycetidae) (Fig. 4.5) includes a single family, Sarrameanaaceae, and the two genera *Loxospora* and *Sarrameana*. It is a small family of approximately ten species occurring mostly in cool temperate regions of both Northern and Southern Hemispheres (Kantvilas 2004). They are crustose species with dark lecideine to lecanorine apothecia, simple to sparingly branched paraphyses, asci with an amyloid domelike tholus lacking an ocular chamber, and simple to transversally septate hyaline ascospores. The genus *Loxospora* was segregated from Haematommataceae and placed in Loxosporaceae (Staiger and Kalb 1995), which was later synonymized with Sarrameanaaceae (Kantvilas 2004). **Because of a unique combination of morphological characters, the systematic position of the**

genus *Sarrameana* has always been problematic, possibly as related to Fuscideaceae (Eriksson and Hawksworth 1986), Haematommataceae (Hafellner 1984; Vězda and Kantvilas 1988), Lecideaceae (Vězda and James 1973), and Ophioparmaceae (Kantvilas and Vězda 1996). Recent molecular phylogenetic analyses that included several species of *Loxospora* showed that Sarrameanaceae is not related to any of these families (Lumbsch et al. 2007a, b, 2008b). In several studies, the genus *Loxospora* forms the earliest diverging lineage within the subclass Ostropomycetidae (Lumbsch et al. 2007b; Miadlikowska et al. 2006; Schoch et al. 2009). As a result, Hodkinson and Lendemer (2011) erected the new order Sarrameanales for Sarrameanaceae.

L. Teloschistales

Teloschistales (Lecanoromycetidae) (Fig. 4.5), as recently recircumscribed by Gaya et al. (2012), comprises four families classified in the two suborders Teloschistineae (Megalosporaceae and Teloschistaceae) and Letrouitiineae (Brigantiaeaceae and Letrouitiaceae). It includes mostly lichenized species with crustose to foliose or fruticose thalli with a yellow to orange color (anthraquinone pigments), apothecial ascomata, unbranched paraphyses, unitunicate asci with an apical thickening, and mostly hyaline polarilocular ascospores (Kärnefelt 1989; Kirk et al. 2008). They are found worldwide and often favor nutrient-rich substrates.

First recognized as a suborder within Lecanorales s.l. (Teloschistineae; Henssen and Jahns 1974) or placed within the suborder Buelliineae (Poelt 1973), the families Letrouitiaceae, Teloschistaceae, and, tentatively, Fuscideaceae were grouped by Eriksson and Hawksworth (1986) in the order Teloschistales, which they formally described. With the advent of molecular phylogenetics, several taxa were added to Teloschistales, namely, Megalosporaceae (Helms et al. 2003; Lutzoni et al. 2004) and both Caliciaceae and Physciaceae (Miadlikowska et al. 2006), which were shown to form a monophyletic group (Helms et al. 2003; Wedin et al. 2000a). As a result, two suborders

were recognized within Teloschistales (Miadlikowska et al. 2006): Physciineae (Physciaceae, including Caliciaceae) and Teloschistineae (Letrouitiaceae, Megalosporaceae, and Teloschistaceae). However, the relationship between Physciineae and Teloschistineae never obtained strong support (Miadlikowska et al. 2006).

In a more recent molecular study, Gaya et al. (2012) detected two competing hypotheses for the relationships among the three clades Lecanorales, Physciineae, and Teloschistineae: either Lecanorales is sister to a lineage including Physciineae and Teloschistineae, or Physciineae is sister to a lineage including Lecanorales and Teloschistineae. To avoid this phylogenetic uncertainty contributing to taxonomic instability, Gaya et al. (2012) proposed **to restrict the name Teloschistales to the Teloschistiineae and resurrect the order Caciiales for the Physciineae**. This study also showed that Brigantiaeaceae, a family classified as incertae sedis in Lecanoromycetidae (Lumbsch and Huhndorf 2010) or as part of Lecanorales (Kirk et al. 2008), belongs to Teloschistales and is sister to Letrouitiaceae (Gaya et al. 2012).

M. Trapeliales

Trapeliales (Ostropomycetidae) (Fig. 4.5) currently includes a single family, Trapeliaceae (Hodkinson and Lendemer 2011). This family had been described for the four genera *Orceolina*, *Placopsis*, *Trapelia*, and *Trapeliopsis* (Hertel 1970). Originally, Trapeliaceae was placed in the Agyriineae, a suborder of Lecanorales with a similar ascus structure (Hafellner 1994). In a comprehensive morphological revision of Agyriineae, the placement of this suborder within Lecanorales was questioned (Lumbsch 1997). Early molecular studies showed that Agyriineae were indeed not related to Lecanorales, and Agyriales was resurrected for this group (Lumbsch et al. 2001a). More recent molecular studies showed that the type species of *Agyrium* (*A. rufum*) belongs to Pertusariales (Lumbsch et al. 2007c; Schmitt et al. 2010). **Because no ordinal name was then available for the lineage including all genera of**

Trapeliaceae and other genera previously placed in Agryriaceae, Hodkinson and Lendemer (2011) proposed to erect the new order Trapeliales for them. Previous molecular data had confirmed the placement within Trapeliaceae of the four genera originally included in this family (Lumbsch et al. 2007b, c; Miadlikowska et al. 2006; Poulsen et al. 2001; Schmitt et al. 2003).

In addition, the genera *Aspiciliopsis*, *Placynthiella*, *Ptychographa*, *Rimularia*, and *Xylographa* had also been shown to belong to this family based on molecular data (Lumbsch et al. 2001b; Schmitt et al. 2003). The genera *Amylora*, *Coppinsia*, *Lignoscripta*, and *Sarea* have also been suggested as belonging to Trapeliaceae (Hodkinson and Lendemer 2011), but their phylogenetic placements still need confirmation from molecular phylogenetic studies.

N. Umbilicariales

The order Umbilicariales (Lecanoromycetes incertae sedis) (Fig. 4.5) is an order of approximately 191 species classified in four families: Elixiaaceae, Fuscideaceae, Ophioparmaceae [including Rhizoplacopsidaceae, as it is now considered a synonym of Ophioparmaceae (Lumbsch and Huhndorf 2010)], and Umbilicariaceae (Kirk et al. 2008). The delimitation of the order Umbilicariales has changed greatly over the last decade. Diverse lichen families have recently been shown to belong to this order: Elixiaaceae (Lumbsch et al. 2007a), Ophioparmaceae and Fuscideaceae (Bylin et al. 2007; Miadlikowska et al. 2006), Rhizoplacopsidaceae (Zhou and Wei 2006), and Ropalosporaceae, although without support for this last family (Bylin et al. 2007). Umbilicariales was formally described in two different publications during the same year (Hibbett et al. 2007; Zhou and Wei 2007), but the authorship was attributed to the earliest one (Zhou and Wei 2007).

Umbilicariaceae, the largest family within this order, includes lichenized foliose umbilicate species, with disciform apothecia, mostly

unbranched paraphyses, unitunicate asci with a small amyloid cap, and simple to muriform ascospores (Hibbett et al. 2007; Louwhoff 2009). They mostly grow on rocks at high altitudes or high latitudes (Davydov 2007). They were traditionally placed in Lecanorales s.l. (Henssen and Jahns 1974), sometimes in a separate suborder, Umbilicariineae (Poelt 1973). Early molecular studies showed that Umbilicariaceae was not related to Lecanorales (Kauff and Lutzoni 2002; Lutzoni et al. 2001; Stenroos and DePriest 1998). **They form a well-supported monophyletic group, and although their placement within Lecanoromycetes is not resolved, they do not seem to belong to any of the three currently recognized Lecanoromycetes subclasses Acarosporomycetidae, Lecanoromycetidae, and Ostropomycetidae** (Hofstetter et al. 2007; Lumbsch et al. 2004; Miadlikowska et al. 2006; Reeb et al. 2004; Wedin et al. 2005). Miadlikowska et al. (2006) suggested that this group might be recognized as a separate subclass in the future.

VIII. Conclusion

Morphological, anatomical, and chemical characters have traditionally been used to classify orders, families, and genera within Lecanoromycetes, the class of Ascomycota with the largest number of lichen-forming fungi. In the last two decades, molecular phylogenies showed that traditional classification systems were not always consistent with the evolutionary history of this fungal class, resulting in changes in the delimitation of orders and families. For example, many families were segregated from the large and heterogenous order Lecanorales and raised to the ordinal level. As a result, the classification system of the Lecanoromycetes is now more on par with the overall supraordinal classification of the Fungi (Hibbett et al. 2007) and comprises 14 orders and 3 subclasses. Additional changes are expected in the future when better taxon and gene sampling will be available to resolve phylogenetic relationships within Lecanoromycetes.

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