

Leaf-colonizing lichens: their diversity, ecology and future prospects

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Phyllosphere – the world on a leaf, contains an interesting symbiotic association of a photobiont and a mycobiont, called foliicolous lichens. These are widely distributed in wet or moist, highly humid or foggy tropical and subtropical forests, on leaf surfaces of plants called phorophytes and are characterized by low endemism and short life cycle, corresponding to the leaf lifespan. Species diversity of foliicolous lichens is remarkable, with a single phorophyte individual supporting 65–84, and a single leaf as many as 81 lichen species. They exhibit marked structural diversity and ecomorphological adaptations to light conditions, and are potentially sound indicators of environmental conditions. In India, so far only 116 species of these lichens have been recorded, mainly from the Andaman and Nicobar Islands, Palni and Nilgiri Hills, and the Northeast. This article highlights conspicuous lack of information on the ecology and life history of these interesting organisms.

Keywords: Biodiversity, foliicolous lichens, lichen ecology, phorophyte.

LICHENS are complex organisms involving a symbiotic relationship between a photobiont (a green alga or a cyanobacterium or both) and a mycobiont (a fungus), and have attracted considerable attention because of their perceived position on the ladder of evolution to land plants^{1,2}. The carbohydrate needs of the fungus are met by the photobiont through photosynthesis, and the fungus, in turn, helps extend the ecological and geographical range of the photobiont, besides providing protection and increasing access to nutrients and water. About 20% of all known fungi (and 40% of all known ascomycetes) are lichenized³. It is assumed that the symbiotic relationship between the photobiont and the mycobiont is obligate. However, recent studies applying phylogenetic species recognition, by analysing fungal DNA sequence data, suggest that the same fungal species can undergo its whole sexual life cycle either as a lichen or as a saprotroph, implying that lichenization may be optional, conferring the ability to use different nutritional modes⁴. It is reported that some lichen genera include species that start their life as lichen parasites, but eventually form independent lichens^{5,6}. Studies indicate that the photobiont can also occur independently of its usual mycobiont. For example, on plant surfaces in the humid tropics, the alga *Phycopeltis* (a member of the family Trentepohliaceae) commonly occurs free-living as well as incorporated within the lichen *Phyllophiale*. *Phycopeltis* appears fully capable of producing free-living progeny even while lichenized by *Phyllophiale*⁷.

There is a special group of lichens that colonize usually on live leaves: foliicolous lichens. Majority of taxa are strictly found on live leaves, while few others can grow even on plastic tape provided suitable conditions are available for their growth. Certain species are also reported to grow on barks, petioles and twigs⁸. The concept of a foliicolous taxon is consequently ecological rather than systematic⁸. These leaf-inhabiting lichens are widely distributed in wet or moist, highly humid (60 to 90%) or foggy tropical and subtropical forests throughout the world. They occur only on ephemeral substrate, i.e. surface of leaves with limited lifespan. These lichens have an accelerated life cycle and respond rapidly to changes in environmental conditions. Therefore, they have a great potential to be used as bioindicators of altitudinal zonation, microclimate and disturbance in the tropics⁹. Lücking¹⁰ has argued that these lichens can also indicate biological richness and species diversity. The species richness of foliicolous lichens in undisturbed localities was twice that of disturbed localities in the montane rainforests of Rwanda⁸. The compounds/substances present in these lichens are effective against bacterial parasites and saprophytes present in the phyllosphere¹¹, and these lichens serve as food for aphids, slugs, psosids, etc.¹². Since the foliicolous lichens can be cultured *in situ* on a transparent non-biotic surface, such as a glass slide, they afford an opportunity of learning about the mechanism of lichenization, thallus growth and reproduction through direct observation with a light microscope^{13,14}.

However, there is a pronounced lack of information on the ecology and other aspects of the life of these interesting organisms. The present article provides an overview on the distribution and diversity of foliicolous lichens, with

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emphasis on the contributing features, and on perspectives for India.

Biogeographical distribution

Lücking¹⁵ distinguished six (three tropical and three extratropical) lichenogeographical regions among the world's foliicolous lichen biota. The tropical regions are Neotropics, African Palaeotropics and Eastern Palaeotropics, and the extratropical are Valdivian region, Tethyan region, and Neozelandic–Tasmanian region. These large-scale regions share 57–77% species among them. The foliicolous lichen species are widely distributed, with 21% cosmopolitan or pantropical, 19% on at least two continents and 60% restricted to one of the three major tropical regions. Lücking¹⁵ also suggested that the three extratropical lichen biotas have resulted from partly separate evolutionary histories. In India, foliicolous lichen species are reported from Nilgiri and Palni hills¹⁶, Andaman and Nicobar Islands^{17,18}, and Northeast India¹⁹, all falling within the Eastern Palaeotropical region. The Indian and Malesian regions, within the Eastern Palaeotropical lichenogeographical region, share 84% of the species¹⁵. Of the 116 species reported from India, under 34 genera and 15 families, 72 are pantropical and only 7 species and one variety are endemic to the region, viz. *Lecidea nagalandica*, *Phyllobathelium indicum*, *Porina andamanensis*, *P. karnatakensis*, *P. multiloculata*, *P. palniensis*, *P. santessonii* and *Graphis foliicola* var. *major*²⁰. The remaining species are distributed in tropical and subtropical Asia, Africa and America.

A low degree of endemism to a particular region, less than 10% for any given area^{10,21,22}, seems to be a characteristic feature of foliicolous lichens. For example, Mexico harbours only 6% endemic species²³ in contrast to the vascular plant flora, where more than 50% of the species and 12% of the genera are endemic to country^{24–27}. Similarly, unlike vascular plants, few of the foliicolous lichens of New Caledonia, an island known for the remarkable uniqueness of its flora, proved to be endemic, whereas 60% were pantropical and the rest had strong affinities to continental floras. Such observations indicate a high level of long-distance dispersal, something that is rather unexpected for organisms colonizing such a specialized ecological niche.

The phorophyte

Phorophytes are plants on whose leaves these lichens establish, grow and multiply. True epiphytes are free from direct physiological relationships with their phorophytes^{28,29}, and hence phorophyte specificity in foliicolous lichens could be expected to be less marked than in parasites³⁰. Although phorophyte specificity is not pronounced in these lichens³¹, certain species may show distinct preferences. Particularly, in extratropical or semideciduous vegetation,

foliicolous lichens might be confined only to certain phorophyte species^{32,33}. The possible reasons of phorophyte preference are assignable to leaf characteristics, such as surface structure and longevity^{32,34–36}. Cuticle composition, surface and water potential, and angle of inclination are other leaf characteristics that play an important role in determining foliicolous lichen flora⁸. In India, for example, the leaves of *Mangifera* spp. are usually colonized by *Strigula smaragdula*, *S. nemathora* var. *hypothecia*, whereas those of *Pandanus* spp. by *Cryptothecia candida*, *Quercus lansaeifolia* by *Strigula maculata*, *Thea sinensis* by *Tricharia* spp. (pers. obs.). However, the above species are also found on other phorophytes. If we consider the phorophytes reported from Costa Rica and those from India (Table 1), we find that there is not a single common species of phorophyte, however, many foliicolous species are common in the two areas. However, phorophytes like *Monstera* from Costa Rica and *Rhaphidophora* sp. from India have more or less similar leaf surface texture; different species of *Piper* of both the regions act as phorophytes. The two sets of phorophyte species in Table 1 are obviously substrate equivalents as far as foliicolous lichens are concerned.

Structural diversity

There is marked diversity in the morphology of the thallus. Most frequently, the thallus structure does not resemble either that of the photobiont or the mycobiont. However, in many cases, influence of the algal or fungal component on the morphology of the lichen thallus is evident, but varies according to the lichen considered^{37,38}. In most cases, being the dominant structural component, the fungus is considered responsible for lichen thallus form. In *Phyllophiale*, the multicellular discoid thalli of the photobiont *Phycopeltis* predominate and impart a discoid shape to the young thallus, while the fungus contributes only a simple covering network and prothallus of hyphae⁷. Incorporation of additional thalli of *Phycopeltis*, and increasingly lobate growth of individual algal thalli result in larger *Phyllophiale* thalli having a lobed or discontinuous appearance. The filamentous form of the photobiont *Trentepohlia*, a close relative of *Phycopeltis*, also remains apparent in the overall form of the lichen thallus^{39–41}.

The structure of a variety of leaf-inhabiting lichens occurring in humid forests of India was examined in detail. A brief account based on this study is given in Table 2. This marked structural variability evidently reflects a rich genetic diversity, although the adaptive value of many of these inter-specific variations remains to be understood.

Physiological interactions and adaptations

Foliicolous lichens grow on upper surface of leaves (Figure 1 a–c) (supracuticular and epiphyllous species, *sensu-*

Table 1. Some selected phorophyte species in Costa Rica and India having more or less similar leaf structure

Phorophyte species in Costa Rica (Based on Lücking ³⁵)	Phorophyte species in India (Based on personal field records)
Pteridophyta (ferns)	Pteridophyta (ferns)
Athyriaceae	Nephrolepidaceae
<i>Diplazium ceratolepis</i> (H. Christ) L.D. Gómez	<i>Nephrolepis cordifolia</i> (L.) Presl.
<i>D. lindbergii</i> (Mett.) H. Christ	Thalepteridaceae
	<i>Pronephrium asperum</i> (Presl.) Halt.
Monocotyledoneae	Monocotyledoneae
Arecaceae (palms)	Arecaceae (palms)
<i>Calypptogyne condensate</i> (Bailey) Wessels Boer	<i>Carryota urens</i> L.
<i>Chamaedorea tepejilote</i> Liebm.	
<i>Cryosophila warszewiczii</i> (H. Wendl.) Burret	
<i>Geonoma cuneata</i> H. Wendl. ex Spruce	
<i>Iriarteia deltoidea</i> Ruiz & Pav.	
<i>Prestoea decurrens</i> (H. Wendl. ex Burret) H. E Moore	
<i>Welfia georgii</i> H. Wendl. ex Burret	
Araceae (Aroids)	Araceae (Aroids)
<i>Monstera tenuis</i> C. Koch	<i>Rhapidophora grandis</i> Schott. <i>R. hookeri</i> Schott
Costaceae	Costaceae
<i>Costus curvibracteatus</i> Maas	<i>Costus speciosa</i> (Koenig) Smith
<i>C. laevis</i> Ruiz & Pav.	
<i>C. malortianus</i> H. Wendl.	
Zingiberaceae	Marantaceae
<i>Ranealmia concinna</i> Standl.	<i>Phragmites capitatum</i> Willd.
	<i>P. placentarium</i> (Lam.) Mess.
Dicotyledoneae	Dicotyledoneae
Lauraceae	Lauraceae
<i>Ocotea atirrensis</i> Mez & J.D. Sm.	<i>Actinodaphne obovata</i> (Nees) Blume
	<i>Cinnamomum bejolghota</i> (Buch.-Ham.) Sweet
	<i>C. glanduliferum</i> (Wallich) Meissn in DC.
	<i>Lindera pulcherrima</i> sub. sp. <i>pulcherrima</i> (Nees)
	Hook. f.
	<i>L. assamica</i> (Meisner) Kunz.
	<i>L. neesiana</i> (Wallich ex Nees) Kunz.
Piperaceae	Piperaceae
<i>Piper glabrescens</i> (Miq.) C.DC. in DC.	<i>Piper</i> spp.

Serusiaux⁸) with the exception of the hypophyllous *Strigula janeirensis*, which is found on the lower surface of leaves (Figure 1 d). These leaf colonizers apparently do not show any damage or negative effect on their phorophyte¹¹, although some species that grow between the cuticle and epidermis, may utilize nutrients from their host leaf⁴². Such subcuticular thalii (Figure 1 d, e) also are expected to receive moisture from the host leaves during periods of drought, and therefore, can also occur on phorophytes in drier climates. The cover of lichens on leaves may be substantial, and in several cases, particularly in the understory, all leaves may support copious growth of foliicolous lichens (Figure 2). For example, a mean cover of 40% on leaves of *Wilkiea macrophylla* (with as much as 100% cover on individual leaves) was recorded in a subtropical rainforest in Australia⁴³. Such a situation is common also for Indian plants (Figure 1 a). In many cases, the whole

leaf of the phorophyte is covered by these epiphylls, but such luxuriant colonization is often encountered on older leaves. Such a dense cover of foliicolous lichens may significantly shade and reduce the photosynthetic output of the phorophyte leaf⁴⁴⁻⁴⁶, especially where the incident radiation is low⁴⁷. In careful experiments conducted by Anthony *et al.*⁴², absorptance spectra of foliicolous lichens were similar to those of their host leaves, and the photosynthetically usable light reaching the underlying photosynthetic layer of leaves was reduced by about 50%. However, concentration of chlorophyll in tissues under lichens was increased by 10–20% and photosynthesis-saturation irradiance was reduced, as an acclimatory response to shading. Further, greater allocation of photosynthate to the lower side of the phorophyte leaf could maximize the use of diffuse light. Monte Carlo estimates of total daily carbon gain based on assimilation-irradiance curves showed

Table 2. Structural diversity of foliicolous lichens occurring in India (Pinokiyo, unpublished)

Growth form	Most of the foliicolous species are of crustose form (crust like) except for some species of <i>Cococarpia</i> and <i>Leptogium</i> , which are foliose.
Thallus	Thallus may be smooth (<i>Porina</i> spp., most of <i>Strigula</i> spp., <i>Tapellaria nana</i> , etc.) or verucose (<i>Sporopodium antonianum</i> , <i>Mazosia melanophthalma</i> , <i>Strigula multipunctata</i> , <i>Tricharia santessonii</i> , etc.) or provided with trichomes or hairs (<i>Tricharia</i> spp.), corticated (<i>Asterothyrium</i> spp., <i>Aulaxina</i> spp., <i>Bullatina</i> spp., <i>Phyllobathelium indicum</i> , etc.) or ecorticated in most of the other species. Anatomy of thallus consists of fungal hyphae (mycobiont) and algal cells (photobiont). Photobiont cells may be rectangular, rounded or irregular (<i>Phycopeltis</i> , <i>Trentepohlia</i> or <i>Trebouxia</i> , etc.) and arranged in the form of plates (<i>Mazosia rotula</i> and in some <i>Porina</i> spp.) or irregularly dispersed (<i>Calopadia</i> spp., <i>Sporopodium</i> spp., <i>Bacidia</i> spp.). Thickness of the thallus ranges from 10 to 300 µm.
Vegetative propagules	These are represented by conidia (ovoid to bacillar or filiform, occasionally branched) which are produced in conidiomata (<i>Mazosia</i> spp., <i>Strigula</i> spp., <i>Echinoplaca</i> spp., <i>Sporopodium</i> spp., <i>Calopadia</i> , etc.), thallus outgrowths like isidia (small cylindrical to globular, corticated structures e.g. isidia of <i>Cococarpia</i> spp.) and soredia (tiny, non corticated, flour-like thallus granules, e.g. soredia of <i>Fellhanera bouteillei</i>). Conidiomata may be hair or whip-like (hyphophores, e.g. hyphophores of most <i>Echinoplaca</i> spp.), ear-shaped (Campylidia – a characteristic feature of family Ectolechiaceae) and globose or flask-shaped (Pycnidia – found in <i>Mazosia</i> spp., <i>Strigula</i> spp., etc.).
Fruiting body (ascomata)	These may be Perithecia (pyriform as in <i>Strigula</i> spp., <i>Porina</i> spp., <i>Phyllobathelium</i> spp., <i>Phylloblastia</i> spp. etc.) or Apothecia (disc shaped as in <i>Bacidia</i> spp., <i>Bapulmuia</i> spp., <i>Calopadia</i> spp., <i>Fellhanera</i> spp., <i>Tapellaria</i> spp., etc.) either ascolocular or ascohymental, found within stromata or single.
Perithecial walls	The walls may be differentiated into an outer wall (involucrellum) and an inner wall (excipulum) as in many species of <i>Porina</i> , <i>Strigula</i> , <i>Aspidothelium fugiens</i> , etc. or both walls may be fused (<i>Phylloblastia dolichospora</i>).
Excipulum	It may be paraplectenchymatous (cells with elongated lumens) as in <i>Byssolecania</i> spp., <i>Gyalectidium</i> spp., <i>Echinoplaca</i> spp.; prosoplectenchymatous (cells with angular lumens) as in <i>Bacidia</i> spp., <i>Calopadia</i> spp., or in the form of loosely intricate hyphae – a characteristic feature of the genus <i>Byssoloma</i> . Hymenium, the fertile part of fruiting body, is protected by excipulum.
Hymenium	It mainly consists of an epithecium (thin layer on the apices of paraphyses), paraphyses (sterile fungal filaments) and asci (sac-like cells in which ascospores are produced). Paraphyses may be simple (<i>Byssolecania</i> spp., <i>Strigula</i> spp., <i>Porina</i> spp.) or branched (<i>Echinoplaca</i> spp., <i>Mazosia</i> spp., <i>Tapellaria</i> spp.).
Asci	These are of various shapes and may be clavate (<i>Mazosia</i> spp., <i>Calopadia</i> spp.), globose (<i>Arthonia</i> spp.), obclavate (<i>Porina</i> spp.), cylindrical (<i>Strigula</i> spp.), oblong to sac-like (<i>Tricharia</i> spp.). They may be one-spored (<i>Tapellaria nana</i> , <i>Gyalectidium</i> spp.) to eight-spored (<i>Mazosia</i> spp., <i>Porina</i> spp., <i>Bacidia</i> spp.).
Ascospores	These are mostly colourless, but light brownish in the mature spores of <i>Arthonia</i> spp. and of various shapes such as fusiform (<i>Mazosia</i> spp., <i>Porina</i> spp.), acicular-subulate (<i>Bacidina mastothallina</i> , <i>Bapulmuia palmularis</i>), oblong (<i>Tricharia</i> spp., <i>Tapellaria molleri</i> , <i>Calopadia</i> spp.), simple (<i>Lecidea nagalandica</i>), transversely septate (<i>Bacidia</i> spp., <i>Coenogonium</i> spp., <i>Fellhanera</i> spp., <i>Byssolecania</i> spp., <i>Strigula</i> spp., <i>Porina</i> spp.), muriform (many-celled) as in <i>Gyalectidium</i> spp., <i>Echinoplaca epiphylla</i> , <i>Tapellaria molleri</i> , <i>T. nana</i> , <i>Phyllobathelium</i> spp., <i>Sporopodium</i> spp. etc., submuriform (transversely septate cells with single vertical septa (<i>Calopadia nymanii</i> , <i>Loflammia intermedia</i> , etc.)).

that leaf areas covered by lichens compensated fully for shading by lichens⁴². Evidently, because of such acclimatory responses, phorophytes have not developed defence mechanisms against lichen colonization, except that the presence of hair and glands on the leaf surface discourages lichen colonization.

For their food and nutrient requirements, foliicolous lichens usually do not depend on phorophytes, as shown experimentally by Sipman⁴⁸, who reported successful growth of foliicolous lichens on plastic tape. Sanders¹³, and Sanders and Lücking¹⁴ have shown that the crustose foliicolous lichens from the humid tropics can be grown on artificial

transparent substrates. Therefore, it is likely that they may derive majority of their nutrients from the atmosphere and atmospheric depositions (but see Anthony *et al.*⁴²). Passive leaching of substances from leaf may provide some nutrients to these epiphylls⁴⁹.

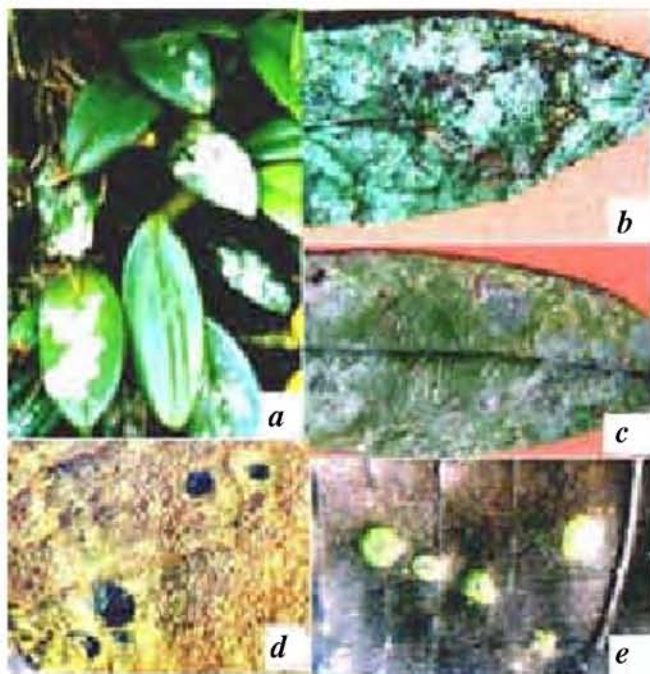


Figure 1. *a*, Whitish thalli of *Fellhanera bouteillei* (Desm.) Vřzda covering almost the entire upper surface of some leaves of *Dendrobium chrysanthum* Lindl. in a subtropical humid forest of Meghalaya. Copious growth of thallus is due to formation, dispersal and germination of soredia near the parent thalli. *b*, Whitish thalli of *Echinoplaca pellicula* (Müll. Arg.) R. Sant. covering the upper surface of the leaf of *Glomerata sumuntia* G. Don in a subtropical humid forest of Sikkim Himalaya. *c*, Whitish thalli with black apothecia of *Byssoloma subdiscordans* (Nyl.) P. James covering the upper surface of *Symplocos glomerata* Keng. ex Clarke in a subtropical humid forest of Sikkim Himalaya. *d*, Subcuticular thalli and black perithecia of *Strigula janeirensis* (Müll. Arg.) Lücking on lower surface of leaf in tropical forests in Arunachal Pradesh. *e*, Subcuticular green thalli of *Strigula smaragdula* Fr. (having wide ecological amplitude), on upper surface of leaf of *Mangifera indica* L. in a tropical dry forest of Sikkim Himalaya.



Figure 2. Rich foliicolous lichen growth (several species) on understorey shrub *Symplocos* spp. in a subtropical humid forest of Sikkim.

These epiphylls exhibit various ecomorphological adaptations to light conditions. Whitish thalli, together with dark ascomata (Figure 1 *c*) are considered adaptations to exposed situations⁵⁰. Features such as reduced, whitish thallus with encrustation of crystals or formation of cortex, dark pigments of exciple and margin of apothecia or perithecia are ecomorphological adaptations towards reduced light condition, high irradiation in light gap or canopy species, protection of reproductive tissue from too much UV radiation respectively⁵¹. Spectral properties of lichens generally correspond to the colour and morphology of the thallus, which in turn are correlated with habitat preference⁴². For example, Anthony *et al.*⁴² found that about 70% of the light was transmitted through *Arthonia trilocularis*, which had a thin thallus and weak reflectance. Also, reflectance of the dark-pigmented lichens was significantly reduced and reflectance of lichens from the gap was often more than twice that of lichens from the understorey, suggesting a protective mechanism against high irradiance. Examples of Indian species possessing such adaptations are: reduced thallus of *Porina* species in reduced light condition; whitish, compact fungal covering of the thallus in species of *Asterothyrium*, *Aulaxina*, *Bullatina*, *Phyllobathelium*, etc. and dark exciple and margin of apothecia in *Tapellaria* spp. in exposed situations.

These leaf inhabiting lichens also compete with other epiphylls, like bryophytes present in the phyllosphere. Bryophytes are usually competitive and overgrow young lichen thalli, but some lichen species are known to prevent and even overgrow and kill small bryophytes¹². N₂ fixing cyanobacteria, which often grow between bryophytes and lichen thalli, may contribute substantially to the nitrogen economy of the phorophyte. However, such studies are yet to be carried out on the phorophyll–lichen system.

Reproduction, dispersal and colonization

These lichens have a relatively short life cycle of 1–3 years corresponding to the longevity of their phorophyte leaves^{55,52}. Therefore, they exhibit a short life cycle, rapid reproduction and reduced thallus size^{53–55}. They appear to complete their life cycle strictly on living leaves. Except for the subcuticular species of *Strigula*, thalli of foliicolous lichens are easily removed from dried leaves of phorophytes, e.g. herbarium specimens. Thallus becomes fertile within a few months⁵⁰. Reproduction is successfully carried out through asexually or sexually produced diaspores. As already mentioned, asexual diaspores include conidia, isidia and soredia, while sexual diaspores are represented by ascospores. The sexual mode of reproduction is predominant. The ascospores from different species vary in shape and size (Figure 3). Availability of wind current seems to be important for growth and successful establishment of diaspores of foliicolous lichens^{55,56}, as well as for the development of fruiting bodies, as most of the species fertile

in such conditions, are often found in sterile conditions in dry areas, where there is lack of wind current. High humidity (66 to 99%) and smooth surfaces of leaves of phorophytes promote successful establishment of reproductive devices with adherent cells⁵⁷. The ecological significance of types of ascospores is difficult to assess, however, ascospore size is possibly related to dispersal and germination⁵¹. Large ascospores may be dispersed by invertebrates^{58,59}. Dispersal of diaspores from the conidiomata (hyphophore and campylidium) is probably by animals or water, either running down the leaf or via a 'splash cup' mechanism⁶⁰⁻⁶⁴. This mechanism is suitable for dispersal over short distances^{65,66}. We suggest that large numbers of light, sexually produced ascospores are lifted by air currents which carry them to long distances; these gradually settle down indiscriminately on various habitats, but germinate preferably on leaves where the environment does not violate any of their tolerance axes. Thus, the appropriate phorophyte leaves and climatic conditions, including particularly, the humidity regime, act as an environmental filter. Subsequently, the growing fungus prothallus (hyphal network) traps an appropriate photobiont, and a lichen thallus begins to develop. This way, perhaps, the extraordinary wide dispersal of many species resulting into limited endemism, is accomplished. A general lack of specificity for phorophyte and photobiont species facilitates this process. For example, members of the family Chlorococcaceae were found

to be lichenized in as many as 124 fungi, those of Trentepohliaceae in 109 species and Scytonemataceae in three species⁶⁷. The asexually produced isidia and soredia, which already contain both the photo- as well as the mycobiont components, largely facilitate short-distance dispersal, i.e. within a forest type or a phorophyte. The isidia and soredia are generally heavier and can be transported to small distances such that after germination the growing thallus may coalesce with the parent thallus and help enlarge it⁶⁸.

Biodiversity and niche differentiation

The legendary high species richness of the tropical rainforest⁶⁹ is also reflected in the diversity of foliicolous lichens. One hectare of the tropical rainforest may harbour as many as 280 species of these lichens, one phorophyte species may support 130 species and one individual of a phorophyte species may account for 65-84 foliicolous lichen species^{10,35}. This means that a single individual, on average, may support more than one-third of the foliicolous lichen species potentially growing on the phorophyte species³⁵.

About 716 species of foliicolous lichens have been reported so far from the world⁷⁰. These are unevenly distributed and show interesting patterns. Species richness of these epiphylls does not seem to depend on the size of the country, since Costa Rica covers less than 1% the size of Brazil and 2.5% the size of Mexico, and yet has 20-30% more species²³. On a broader scale, there is a diversity gradient from the equator towards tropical areas north and south^{15,21,23,71}, with species richness declining as one moves away from the equator. This broad-scale pattern is similar to that of higher plants^{69,72} and reflects the impact of climatic factors. Similarly, the number of species declines with increase in altitude⁹. The altitude range 700-900 m harbours maximum foliicolous lichen diversity in humid forests of the Indian mainland compared to altitudes below and above this range. A comparison of lowland and montane rainforest sites in Mexico, Guatemala, Costa Rica and Ecuador showed that on average lowland (150-650 m) sites had twice as many species as montane (≥ 700 m) sites²³. Further, species richness is maximum in wet tropical forest with no or short dry period within the annual cycle; it decreases towards dry evergreen and is reduced to only a few species in dry deciduous forest⁹. This is in conformity with the rainfall regime and leaf lifespan of the phorophytes.

On a narrower scale, altitude affects foliicolous species composition more strongly than geographical distance. For example, among the neotropical sites, differentiation in species composition between lowland and montane locations, within the same region, was more pronounced (37-25% dissimilarity) than that between adjacent regions (only 4-1% dissimilarity among lowland sites and 17-13% dissimilarity among montane sites)²³. It is not surprising because environmental conditions and species composition

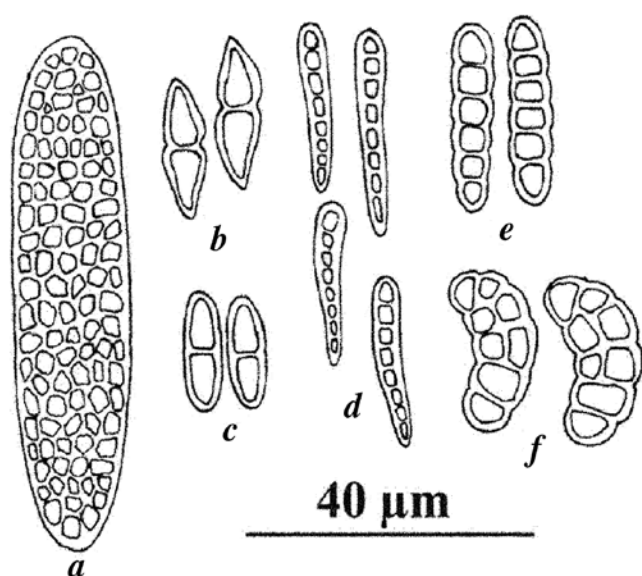


Figure 3. Some selected ascospores of foliicolous lichens having various shapes and sizes. *a*, Muriform and oblong ascospore of *Tapellaria epiphylla* (Müll. Arg.) R. Sant. *b*, Transversely 1-septate, fusiform ascospores of *Strigula melanobapha* (Krempelh.) R. Sant. *c*, transversely 1-septate and bacillar ascospores of *Strigula maculata* (Cooke & Masee) R. Sant. *d*, submuriform and subulate ascospores of *Tricharia santessonii* D.L. Hawks. *e*, Transversely seven-septate and acicular ascospores of *Bacidina mastothallina* (Müll. Arg.) Zahlbr. *f*, Transversely five-septate and oblong ascospores of *Tapellaria nigrata* (Müll. Arg.) R. Sant.

of vegetation change more rapidly along elevational gradients than along spatial gradients.

At a still narrower scale, i.e. at microhabitat level, species assemblies tend to be more strongly differentiated. For example, studies on lowland forests indicated three well-defined species associations corresponding to the three major microhabitats^{51,73,74}: (i) shady understory association, composed of members of families Arthoniaceae, Opegraphaceae, Strigulaceae, Trichotheliaceae and Pilocarpaceae, with green alga *Phycopeltis* (Trentepohliaceae) as the predominant photobiont; (ii) natural light gap association, dominated by the families Strigulaceae, Gomphillaceae and Ectolechiaceae, with *Trebouxia* (Chlorococcaceae) as the common photobiont, and (iii) canopy association, mainly characterized by families Asterothyriaceae and Gomphillaceae and Ectolechiaceae; the photobiont is mostly *Trebouxia* (Chlorococcaceae). This differentiation is mostly due to the differences in light regimes of the microhabitats and is related to the ecomorphological characteristics of the lichen thalli. For example, in the exposed canopy association, the thalli are often dispersed into small, inflated patches encrusted with crystals and provided with a cortex, whereas in the shady understory communities, the thalli are usually thin and reduced, with a smooth surface or provided with small, hydrophobic verrucae^{51,73}. Such compositional differentiation can indicate the ecological conditions of a site; the occurrence of a particular guild of foliicolous lichens or even a dominant taxon of a guild can provide information on the successional status of the forest (primary vs. secondary) or the degree of anthropogenic disturbance which resulted in canopy opening. Interestingly, this information can be garnered even from herbarium specimens, suggesting the prevalent ecological conditions described above during the time period of specimen collection.

At the scale of phorophyte, apparently, due to a relative lack of phorophyte preference, host diversity does not seem to influence species richness of foliicolous lichens. Irrespective of the phorophyte species, spatially adjacent individuals are more similar in their foliicolous lichen flora than distant individuals belonging to the same species³⁵. This could result from a dispersal limitation, but requires further in-depth study, particularly on phorophyte–microclimate complex. Thus, the foliicolous on different phorophyte species may be more similar to each other than to those on different individuals of the same species. As a result, a few phorophyte species may account for most of the foliicolous lichen diversity on a site. Presence of a large number of leaves, both old and young, on a phorophyte, each a discrete, potential microsite for colonization, and, together, representing a large gradient in light and other microclimatic conditions, can permit almost unlimited diversity of the epiphylls. However, why only some phorophyte species and not others, show such an extremely high foliicolous lichen species richness, remains to be understood.

At the small scale, i.e. at the level of a leaf, the niche differentiation almost completely disappears and a large number of foliicolous lichen species occupy the same niche. Lücking and Matzer⁷⁵ examined two individual dicotyledonous leaves (125 and 98 cm² in size) and one composed palm leaf (c. 6800 cm² in size) from Costa Rica and Amazonian Ecuador, and found 49 lichens on the dicotyledonous leaf from Costa Rica and 46 lichens on that from Ecuador. The palm leaf yielded 81 lichens. The earlier highest species count (45 spp.) was recorded for the leaves of a palm in New Guinea⁷⁶. In India, maximum number of species (20–30) is estimated to occur on the leaves of *Rhapidophora grandis*, *Phrynium* spp. (pers. obs.). Current ecological theories, unless unreasonably stretched, cannot explain the co-occurrence of such a large number of species on a uniform habitat, viz. a single leaf. Facilitative interaction among co-inhabiting lichens cannot be ruled out.

Perspectives for India

Region-wise distribution of all species reported from India is given in Table 3. Not surprisingly, the number of species confined to the Northeast and the Andaman and Nicobar Islands is the largest, and only 16 species occur in all the three regions (i.e. Northeast, Andaman and Nicobar Islands and Palni and Nilgiri hills).

The available information on foliicolous lichens from India, as presented here, is far from complete, because of lack of explorations and laboratory investigations. The richest sites of their distribution in India, viz. NE India, the Western Ghats and Andaman and Nicobar Islands, have yet to be explored fully. Quantitative data on diversity parameters, such as species richness of a leaf, a phorophyte individual, a phorophyte species, or of an unit area, are completely lacking. Similarly, their physiological, biochemical and molecular characteristics, as well as life history, including preferences for photobiont species, need to be investigated thoroughly. The Convention on Biological Diversity clearly indicates that diversity of all groups of organisms needs to be identified for its conservation and sustainable use. Follicolous lichens are not an exception to this. Some of the interesting areas for investigation include their biotic interactions within the phyllosphere, phorophyte preference in respect of economically important phorophytes, such as mango, tea, etc. their role as a protectant of phorophylls from bacteria and other minute leaf tissue feeding organisms, their physiological relation with their substrate, etc. Significantly, foliicolous lichens are sensitive to changes in environmental conditions; they develop well-defined ecomorphological adaptations and occupy a distinct ecological niche. Therefore, they (even through herbarium specimens) may prove to be the best indicators of environmental conditions, including global change, and therefore, have the potential of being used in

Table 3. Region-wise distribution of foliicolous lichen species reported from India (based on Pinokiyo and Singh²⁰)

Species reported only from Northeast India	
<i>Asterothyrium pittieri</i> Müll. Arg	<i>Lecidea nagalandica</i> Sinha & K. Singh
<i>Asterothyrium rotuliforme</i> (Müll. Arg.) Sérus.	<i>Loflammia intermedia</i> (R. Sant.) Vřda
<i>Aulaxina uniseptata</i> R. Sant.	<i>Mazosia rotula</i> (Mont.) Massal.
<i>Bacidina mastothallina</i> (Vainio) Vřda	<i>Mazosia tumidula</i> (Stirton) Müll. Arg.
<i>Bapalmuia palmularis</i> (Müll. Arg.) Sérus.	<i>Phyllobathelium indicum</i> Sinha & K. Singh
<i>Byssolecania deplanata</i> (Müll. Arg.) R. Sant.	<i>Strigula concreta</i> (Fée) R. Sant.
<i>Byssoloma tricholomum</i> (Mont.) Zahlbr.	<i>Strigula maculata</i> (Cooke & Masee) R. Sant.
<i>Calenia conspersa</i> (Stirton) R. Sant.	<i>Strigula melanobapha</i> (Krempelh.) R. Sant.
<i>Calopadia nymanii</i> (R. Sant.) Vřda	<i>Strigula phyllogena</i> (Müll. Arg.) R. C. Harris
<i>Calopadia perpallida</i> (Nyl.) Vřda	<i>Tapellaria epiphylla</i> (Müll. Arg.) R. Sant.
<i>Coenogonium luteum</i> (Dicks.) Kalb & Lücking	<i>Tapellaria molleri</i> (Henriques) R. Sant.
<i>Cryptothecia candida</i> (Krempelh.) R. Sant.	<i>Tapellaria nigrata</i> (Müll. Arg.) R. Sant.
<i>Echinoplaca epiphylla</i> Fée	<i>Tricharia santessonii</i> D. L. Hawks.
<i>Echinaplaca pellicula</i> (Müll. Arg.) R. Sant.	<i>Tricharia triseptata</i> R. Sant.
	<i>Tricharia vainioi</i> R. Sant.
Species reported only from Andaman and Nicobar Islands	
<i>Arthonia trilocularis</i> Müll. Arg.	<i>Lasioloma arachnoideum</i> (Krempelh.) R. Sant.
<i>Aspidothelium fugiens</i> (Müll. Arg.) R. Sant.	<i>Lofflammia gabrielis</i> (Müll. Arg.) Vřda
<i>Aulaxina epiphylla</i> (Zahlbr.) R. Sant.	<i>Loflammia epiphylla</i> (Fée) Lücking & Vřda
<i>Bacidia micrommata</i> (Krempelh.) R. Sant.	<i>Opegrapha puiggari</i> Müll. Arg.
<i>Bacidina pallidocarnea</i> (Müll. Arg.) Vřda	<i>Porina albicera</i> (Krempelh.) Van Overeem-de Haas
<i>Badimia polillensis</i> (Vainio) Vřda	<i>Porina andamenensis</i> Upreti & Singh
<i>Calenia thelotremella</i> Vainio	<i>Porina atrocoerulea</i> Müll. Arg.
<i>Calopadia phyllogena</i> (Müll. Arg.) Vřda	<i>Porina papillifera</i> (Stirt.) F. Schilling
<i>Chroodiscus coccineus</i> (Leighton) Müll. Arg.	<i>Porina thaxteri</i> R. Sant.
<i>Coccocarpia aeruginosa</i> Müll. Arg.	<i>Strigula obducta</i> (Müll. Arg.) R. C. Harris
<i>Coenogonium dilucidum</i> (Krempelh.) Kalb & Lücking	<i>Trichothelium annulatum</i> (Karst.) R. Sant.
<i>Lasioloma trichophorum</i> (Vainio) R. Sant.	
Species reported only from Palni and Nigiri hills and surrounding regions	
<i>Badimia pallidula</i> (Krempelh.) Vřda	<i>Porina palniensis</i> Awasthi & K. Singh
<i>Graphis foliicola</i> var. <i>major</i> Awasthi & K. Singh	<i>Porina santessonii</i> Makh., Adaw. & Patw.
<i>Porina multiloculata</i> Makh., Adaw. & Patw.	<i>Tapellaria phyllophila</i> (Stirton) R. Sant. & Thorold
<i>Porina nilgiriensis</i> D. Awasthi & K. Singh	<i>Trichothelium alboatrum</i> Vainio
<i>Porina octomera</i> (Müll. Arg.) F. Schilling	
Species common between Andaman and Nicobar Islands and Northeast India	
<i>Aulaxina quadrangula</i> (Stirton) R. Sant.	<i>Porina lucida</i> R. Sant.
<i>Bacidia olivaceorufa</i> Vainio	<i>Porina nitidula</i> Müll. Arg.
<i>Badimia galbinea</i> (Krempelh.) Vřda	<i>Porina trichothelioides</i> R. Sant
<i>Byssoloma chlorinum</i> (Vainio) Zahlbr.	<i>Porina virescens</i> (Krempelh.) Müll. Arg.
<i>Chroodiscus mirificus</i> (Krempelh.) R. Sant.	<i>Sporopodium argillaceum</i> Zahlbr.
<i>Mazosia bambusae</i> (Vainio) R. Sant.	<i>Sporopodium phyllocharis</i> (Mont.) Massal.
<i>Mazosia paupercula</i> (Müll. Arg.) R. Sant.	<i>Strigula janeirensis</i> (Müll. Arg.) Lücking
<i>Phylloblastia dolichospora</i> Vainio	<i>Strigula orbicularis</i> Fr.
<i>Porina conica</i> R. Sant.	<i>Trichothelium epiphyllum</i> Müll. Arg.
<i>Porina imitatrix</i> Müll. Arg.	
Species common between Northeast India and Palni and Nilgiri hills and surrounding regions	
<i>Bacidina apiahica</i> (Müll. Arg.) Vřda	<i>Fellhanera semecarpi</i> (Vainio) Vřda
<i>Byssolecania fumosonigrans</i> (Müll. Arg.) R. Sant.	<i>Gyalectidium filicinum</i> Müll. Arg.
<i>Byssoloma leucoblepharum</i> (Nyl.) Vainio	<i>Porina chrysophora</i> (Stirton) R. Sant.
<i>Byssoloma subdiscordans</i> (Nyl.) P. James	<i>Porina cupreola</i> (Müll. Arg.) Schilling
<i>Bullatina aspidota</i> (Vainio) Vřda and Poelt	<i>Porina fulvella</i> Müll. Arg.
<i>Calopadia puiggarii</i> (Müll. Arg.) Vřda	<i>Porina karnatakensis</i> Makh.
<i>Fellhanera bouteillei</i> (Desm.) Vřda	<i>Porina monocarpa</i> (Krempelh.) Schilling
<i>Fellhanera fuscata</i> (Müll. Arg.) Vřda	<i>Opegrapha filicina</i> Mont.
<i>Fellhanera rhapidophylli</i> (Rehm.) Vřda	<i>Tricharia albostrigosa</i> R. Sant.
Species common between Andaman and Nicobar Islands and Palni and Nilgiri hills	
<i>Porina semecarpi</i> Vainio	<i>Strigula antillarum</i> Fr.
Species common to all the three regions (Andaman and Nicobar Islands, Northeast India and Palni and Nilgiri hills)	
<i>Calopadia fusca</i> (Müll. Arg.) Vřda	<i>Porina rufula</i> (Krempelh.) Vainio

(Contd...)

Table 3. (Contd...)

<i>Calopadia subcoerulescens</i> (Zahlbr.) Vřda	<i>Strigula nemathora</i> Mont.
<i>Mazosia melanophthalma</i> (Müll. Arg.) R. Sant.	<i>Strigula nitidula</i> Mont.
<i>Mazosia phyllosema</i> (Nyl.) Zahlbr.	<i>Strigula smaragdula</i> Fr.
<i>Porina atriceps</i> (Vainio) Vainio	<i>Strigula subelegans</i> Vainio
<i>Porina epiphylla</i> (Fée) Fée	<i>Strigula subtilissima</i> (Fée) Müll. Arg.
<i>Porina limbulata</i> (Krempelh.) Vainio	<i>Sporopodium xantholeucum</i> (Müll. Arg.) Zahlbr.
<i>Porina pallescens</i> R. Sant.	<i>Tapellaria bilimbioides</i> R. Sant.

ecosystem management. However, this potential can be tapped only after generating information through integrated field and experimental studies.

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