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family, though they could still show a lot of diversity between genera.

Genus

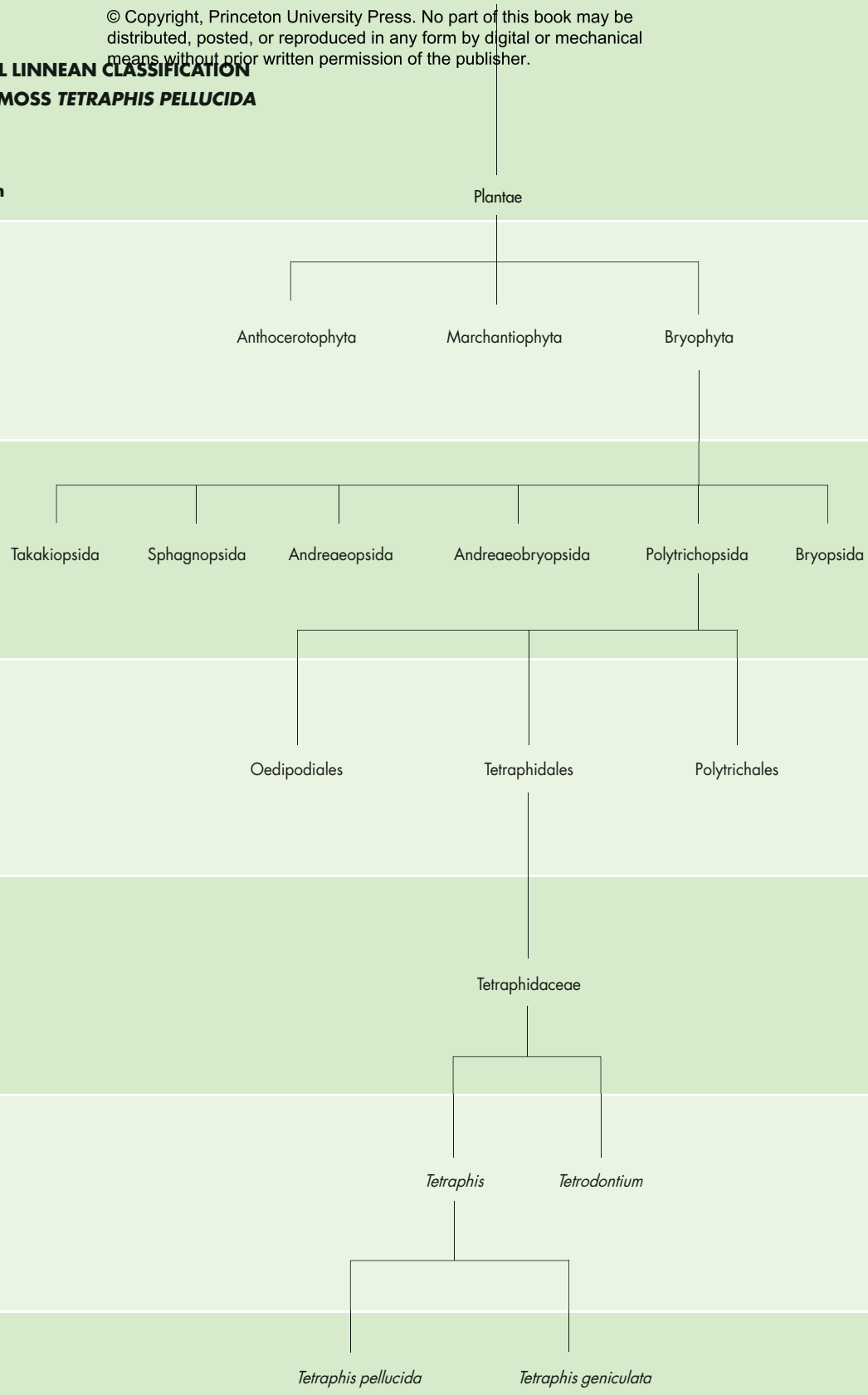
Generally speaking, bryophytes should be identifiable to genus level with a few morphological characters. Genera should also reflect a grouping with a shared ancestry, and this has led to something of a shake-up in larger genera that have been found to be derived from more than one ancestral group.

Species

At the most basic level, a species represents the groupings a person would recognize when separating out different types of plants based on their shared characters. It is an extremely important level of classification, as it is a concept most people have some familiarity with and is used extensively in conservation metrics and targets.

BELOW | *Tetraphis pellucida* is a common moss of temperate northern hemisphere.

THE FULL LINNEAN CLASSIFICATION OF THE MOSS *TETRAPHIS PELLUCIDA*



SELECTED GENERA

At the time of writing, the diversity of bryophytes is classified into 73 orders, 1,344 genera, and over 15,000 species. The classification used here is based on the latest research from the international community of bryologists and represents a phenomenal amount of research culminating over many decades.

Every order of bryophytes across the hornworts, liverworts, and mosses is represented in this section by at least one genus and the more diverse orders by two or three genera. An exception is made for the Hypnales, where six genus profiles have been included since this order of mosses has the most genera of any bryophyte order.

For those orders that include only one genus, the decision was easy! Where genera had to be selected from a range of potential candidates, the following criteria were considered. Some genera are so charismatic that they simply had to be included. For example, *Schistostega*—a moss that glows in the dark, no less—was essential to feature in the Dicranales along with other examples of this order. An attempt was made to include the most species-diverse and globally widespread genera—such as *Bazzania*, *Herbertus*, and *Plagiochila*—within the liverwort order of the Lepidoziales. Particularly striking and beautiful genera were included to illustrate the orders where possible—such as *Dawsonia*, the world's tallest moss. The 100 genera chosen here aim to illustrate the rich structural and evolutionary diversity of bryophytes from around the world.

Notes on the profiles

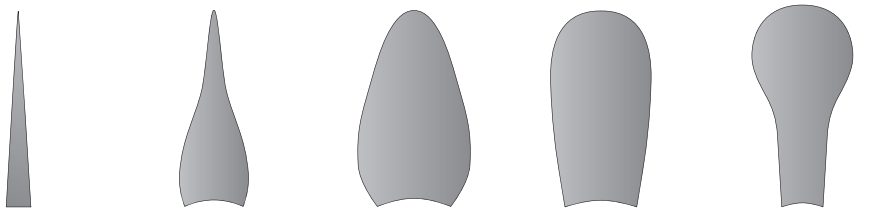
Each genus profile includes an information panel highlighting key features as well as a small distribution map.

The estimated number of species described for each genus is based on a wonderful online resource provided by the Missouri Botanical Garden based on their immense nomenclatural database Tropicos. It is worth noting, of course, that the number of species names accepted across the scientific literature may not tally with the actual number of "real" species. These figures are constantly changing as new findings are published.

BELOW LEFT | The liverwort *Bazzania trilobata* has a dichotomously branched or Y-shaped leaf pattern.

BELOW RIGHT | The moss *Ptilium crista-castrensis* has pinnate or feather-like branching.

COMMON MOSS LEAF SHAPES



Linear—long and narrow with pointed tip

Lanceolate—wider at the base and tapering to a point

Ovate—egg-shaped with a pointed tip

Lingulate—tongue-shaped with parallel sides

Spathulate—wider above the middle than below

The maps serve to include the global range of the plants and are based on the available scientific literature. One of the challenges here is that a genus may be described in print as occurring across Africa, Southeast Asia, and Australia, but when it comes to imprinting this description on a map, some important details are missing! While every effort was made to ensure accuracy at this scale, the maps represent the level of information available at the time of writing.

TAXONOMIC TERMINOLOGY

All natural-history enthusiasts employ a certain amount of jargon for their areas of special interest and bryologists are no different! Taxonomic jargon is kept to a minimum in this book but some scientific terms are necessary. Some of the terms that occur repeatedly through these pages are explained in more detail below.

Leaf shape

There are a number of commonly used terms to describe the shape of bryophyte leaves, and the most frequently used of these are illustrated above.

Branching patterns

Bryophytes can show a variety of branching patterns (see opposite), which are informative taxonomic characters.

Sexual condition

Whether plants produce male or female sexual organs—or both—is an important taxonomic characteristic. If the male and female sex organs are produced on different plants, they are called dioicous; if they are produced on the same plant, they are called monoicous. Monoicous plants can further be divided into those that produce the sex organs on different branches (autoicous) and those that produce the sex organs together in the same cluster (synoicous).

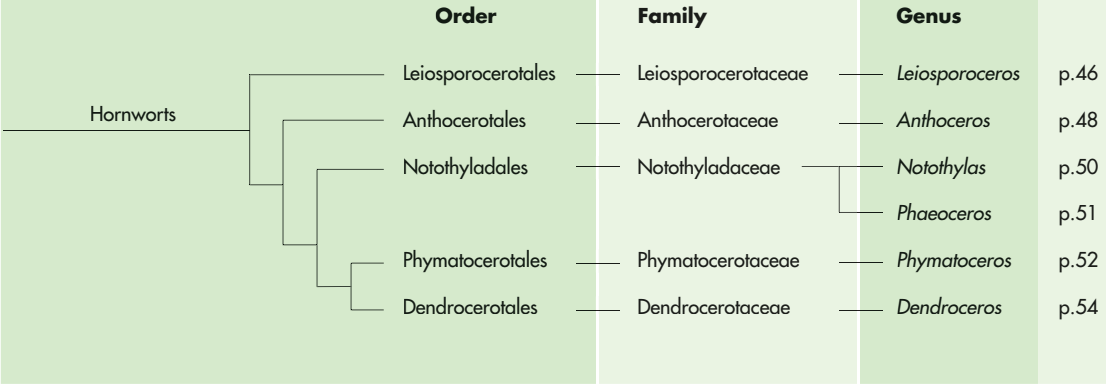
Bryophytes that grow on other plants

Many species of bryophytes grow directly on other plants, and these are called epiphytes. They are using the trees and shrubs simply as a convenient structure to perch themselves on. Those species that grow specifically on leaves are called epiphyllous.

Parasitic and symbiotic relationships

Many liverworts have symbiotic associations with fungi, which means both partners gain something from the relationship. Only the liverwort *Aneura mirabilis* is known to have a parasitic relationship, in this case with a fungus, from where it sources its carbon.

PHYLOGENETIC TREE OF HORNWORT ORDERS AND FEATURED GENERA



OPPOSITE | The hornwort *Phaeoceros laevis*, showing female plants with horn-like sporophytes and male plants with yellow antheridia.

ANTHOCEROTOPHYTA: THE HORNWORTS

The hornworts have a number of unique aspects to their biology. Most have a symbiotic association with cyanobacteria; their large solitary chloroplasts have similarities to those of the algae, and the narrow, elongate "horns" of the spore-producing structures are immediately recognizable. In fact, they are so distinct from any other land plant lineage and yet so sparse in distinct taxa compared to other groups that some scientists suggest they may have been more diverse in the past.

Hornworts are the least taxonomically diverse of the three bryophyte groups, with an estimated 200 to 250 species classified within 5 orders and 14 genera. The first two decades of the twenty-first century have been an exciting time for hornwort research, with major new insights into their structures, evolutionary relationships, and classification.

The Leiosporocerotales are considered particularly distinct and a sister group to all other hornworts. The characters used to define the different orders of hornworts mainly rely on a combination of DNA sequence data to reveal past evolutionary relationships and on microscopic anatomical features such as details of the spores and features of the chloroplasts.

LEIOSPOROCEROS

The species *Leiosporoceros dussii* is considered so unique among hornworts that it warrants its own order and is considered a sister group to all other hornworts because it is both morphologically and genetically distinct.

The plants form elongate rosettes and the projecting cells on the surface give the plant a velvety feel. Most striking are the long blue lines drawn

BELOW | A spectacular colony of *Leiosporoceros* showing the elongated branches of the thallus and abundant sporophytes.

DISTRIBUTION
Mexico, Central America (Costa Rica, Panama), northern Andes, Lesser Antilles

ETYMOLOGY
Greek *leios* = "smooth" + *kéras* = "horn," referring to the smooth unornamented spores

NUMBER OF SPECIES
1 accepted species

APPEARANCE
Robust, fleshy thallus forming rosette, branches ¾ in (2 cm) in diameter. Cells 1–2 chloroplasts, no pyrenoid. Mature sporophytes 1½ in (4 cm) long. Pseudoelaters long, thick-walled. Antheridia up to 70 per chamber. Cyanobacterial *Nostoc* colonies visible as blue strands

HABITAT
On rocks or sandy soils, usually near water bodies

ABOVE | The distinctive spores of *Leiosporoceros* are slightly elongated and have a single linear scar.

BELOW | Perhaps the most striking feature of *Leiosporoceros* are the blue strands of the cyanobacteria colonies.

along the thallus. These are *Nostoc* colonies oriented longitudinally inside the thallus in mucilage-filled canals. This linear arrangement of the colonies running parallel to the main axis of the thallus is not only unique among the hornworts but is unknown in any other land plant. These colonies initiate when *Nostoc* enters the thallus and establishes behind the cell at the growing tip of the thallus. As the thallus then elongates, so does the *Nostoc* colony within an advancing canal of mucilage.

Leiosporoceros also has distinctive spores that are nearly smooth, transparent, and slightly elongated. When spores are being formed they are initially attached to each other in groups of four. When these are formed in a tetrahedral arrangement they leave a trilete (Y-shaped) scar on each spore from where they were initially joined with three other spores. If they originated in a tetragonal formation then each of the four initial spores would have been in contact with only two of their neighbors, and the resulting scar is called monolete (linear-shaped). Most hornworts have spores with a trilete mark except for *Leiosporoceros*, which have the monolete mark, demonstrating a clear divergence in early development processes.

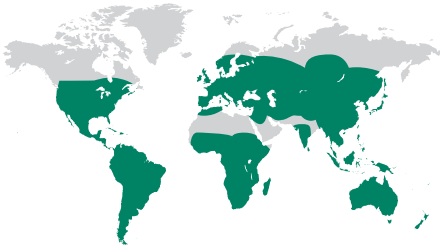
ANTHOCEROS

The Anthocerotales includes just the two genera: the widespread *Anthoceros* and the tropical *Folioceros*. *Anthoceros* was the first hornwort genus ever to have been described and features in Linnaeus's landmark publication *Species Plantarum* in 1753. It is also the most species-rich hornwort genus, with over 60 species recognized.

Although some well-known species of *Anthoceros* can be distinguished by features seen with a hand lens, some species of *Anthoceros* from tropical regions can only be identified by examining minute characteristics of the dark-brown spores. Other features needed to identify this order include the details of the male reproductive structures, where there are numerous antheridia in each chamber, contrasting with most other hornwort orders that only have one or two antheridia in each chamber.

Anthoceros agrestis is increasingly being used as the model system for the study of hornwort biology, plant and cyanobacteria interactions, biochemistry, and detailed genomic information. It is a plant that copes very well as a laboratory rat due to its small size and easy propagation. Its genome has been sequenced and is providing insights into the innovations for early land plant evolution. There is also future potential to explore genetic engineering by transferring useful hornwort traits into crop plants to increase yields, such as efficient mechanisms for photosynthesis using pyrenoids or the symbiosis with cyanobacteria. These detailed studies into the mechanics of hornwort biology have the potential to dramatically impact various fields and support food security in the face of increasing pressures on agriculture.

LEFT | Colonies of the cyanobacterium *Nostoc* are visible as dark spots on the surface of the hornwort thallus.



DISTRIBUTION
Globally widespread, temperate, tropical

ETYMOLOGY
Greek *ánthos* = "flower" + *kéras* = "horn," referring to the horn-shaped sporophytes

NUMBER OF SPECIES
67 accepted species

APPEARANCE
Dark-green rosettes, frilly margins, no midrib. Sporophytes 3/8–2 in (1–5 cm) tall. Dark-brown spores, trilete mark, bumps on surface. Cells 1–4 chloroplasts with/without pyrenoid. Antheridia 4–45 per chamber. Thallus with mucilage-containing cavities. *Nostoc* scattered across thallus surface visible as black dots

HABITAT
Pioneer of open environments on disturbed ground such as arable fields, banks, and path sides

LEFT | *Anthoceros punctatus* is a widespread species that typically forms small rosettes with frilly margins.

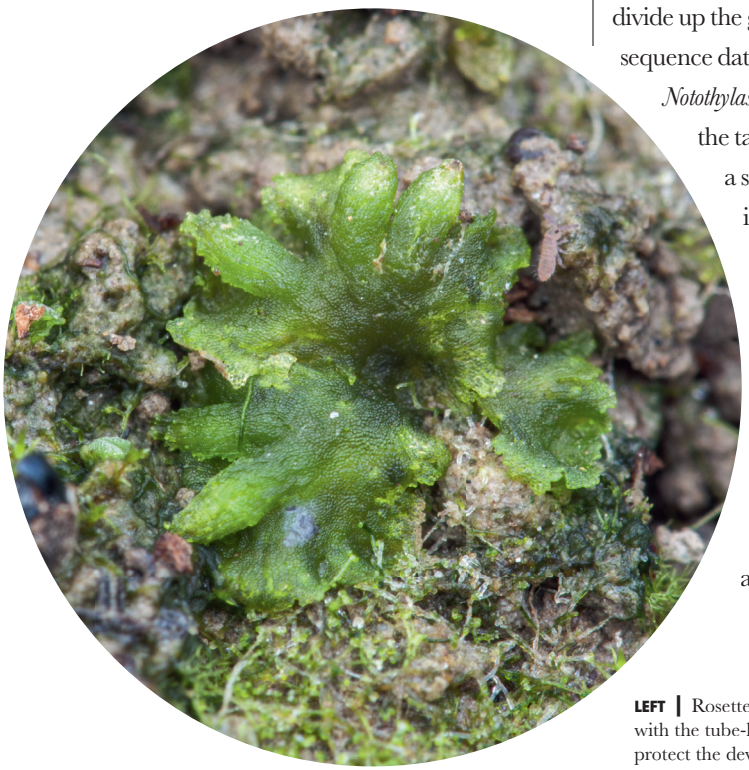
BELOW | *Anthoceros fusiformis* can be distinguished by the upright flaps of thallus tissue, as can be seen in the lower part of this image.

NOTOTHYLAS

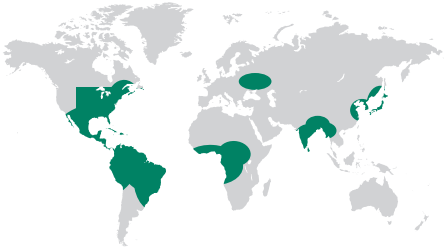
Notothyladales is an order particularly notable for the heterogeneity of its four genera. Within the order, *Notothylas* is distinguished by a number of features, but most apparent is the length of the sporophytes, which are the shortest of all the hornworts.

The remaining features are very variable even within the genus. A particularly unusual variation is the spore color, which is usually consistent within hornwort genera but here can vary from yellow to dark brown or black. In an attempt to bring some order to this rather chaotic grouping, taxonomists have previously proposed various subsections to divide up the genus, though analysis of DNA sequence data does not support these divisions. *Notothylas* is defined as monophyletic, meaning the taxonomic grouping includes a single common ancestor plus all of its descendants, albeit one with a wide range of defining characteristics.

Despite its lack of conformity, *Notothylas* is an easy genus to recognize due to its short, stumpy sporophyte "horns" lying almost flat on the thallus surface. It is widely distributed in tropical to temperate regions, with its highest diversity across the Indian subcontinent.



LEFT | Rosettes of *Notothylas orbicularis* with the tube-like involucres that protect the developing sporophyte laying flat against the thallus.



DISTRIBUTION
A pantropical and northern-temperate genus

ETYMOLOGY
Greek *nôto* = "dorsal" + *thylakos* = "pouch," referring to position of sporophyte on dorsal surface of thallus and protective structures enclosing the developing sporophyte

NUMBER OF SPECIES
26 accepted species

APPEARANCE
Small rosettes 3/16–1 1/4 in (0.5–3 cm) in diameter. Cells contain 1–3 chloroplasts. Sporophytes enclosed within the involucre. Spores with trilete (Y-shaped) mark, pseudoelaters without spiral band. Antheridia 2–6 per chamber. Globose *Nostoc* colonies across thallus, visible as black dots

HABITAT
Disturbed soil in open habitats

PHAEOCEROS

Demonstrating just how variable the Notothyladales really are, the genus *Phaeoceros* looks strikingly different from *Notothylas*. These larger plants are ¾–1¼ in (2–3 cm) in diameter and can be rather robust and fleshy. The sporophytes grow long and upright, sometimes reaching heights of 3½ in (9 cm), though they are usually more modest.

Despite being classified in a different order, *Phaeoceros* can look very similar to *Anthoceros* in the Anthocerotales and the two genera can be easily confused when they grow together in similar habitats. *Phaeoceros* can be distinguished in the field by its yellow spores in contrast to the blackish spores of *Anthoceros*. On a more microscopic level *Phaeoceros* lacks the numerous large mucilage-containing cavities characteristic of *Anthoceros*.

Phaeoceros has a worldwide distribution, with highest species diversity in the tropics, where examining details of the spores may be needed to identify species.

ABOVE | *Phaeoceros minutus* on bare soil of the Western Cape, South Africa.

DISTRIBUTION
Worldwide

ETYMOLOGY
Greek *phaeo* = "dark colored" + *kéras* = "horn," although genus described with yellow spores

NUMBER OF SPECIES
35 accepted species

APPEARANCE
Dark green with thallus forming rosettes ¾–1¼ in (2–3 cm) diameter. Cells contain 1–2 chloroplasts. Sporophytes 1–4 up to 3½ in (9 cm) tall. Spores with spinose to bumpy ornamentation. Antheridia 2–4 per chamber

HABITAT
On soil in open environments

PHYMATOCEROS

BELOW | *Phymatoceros bulbiculosus*, showing the upright green sporophytes emerging from the tube-like involucres.

OPPOSITE | This *Phymatoceros phymatodes* colony is growing surrounded by the liverwort *Solenostoma rubrum* on soil in British Columbia, Canada

Phymatoceros was only established in 2005 when subtle yet significant differences in a species previously described as *Anthoceros bulbiculosus* were considered to be sufficiently different from all other hornwort genera to justify creating a new genus. Since then, two additional species have been assigned to this genus, with one species, *Phymatoceros binsarensis*, described in 2023 based on plants discovered in India, extending the distribution of this genus from the Americas, Europe, and Africa eastward into Asia. Further analysis of hornwort classification has found this small genus to be so different from other hornworts that it is placed in its own order, the Phymatocerotales. Two of these species had previously been placed in *Phaeoceros*.

Rather than forming the typical rosette of most hornworts, *Phymatoceros* grows in a more linear fashion, with a narrow parallel-sided branching thallus. Another striking feature is the prolific long, stalked tubers in the upper region of the thallus. There are one to two chloroplasts per cell, but in contrast to most other

DISTRIBUTION
Widespread in Mediterranean Europe and Africa, India, and North and South America

ETYMOLOGY
Greek *phȳma* = "tumor" or "growth" + *kéras* = "horn," in reference to the prolific number of tubers produced

NUMBER OF SPECIES
3 accepted species

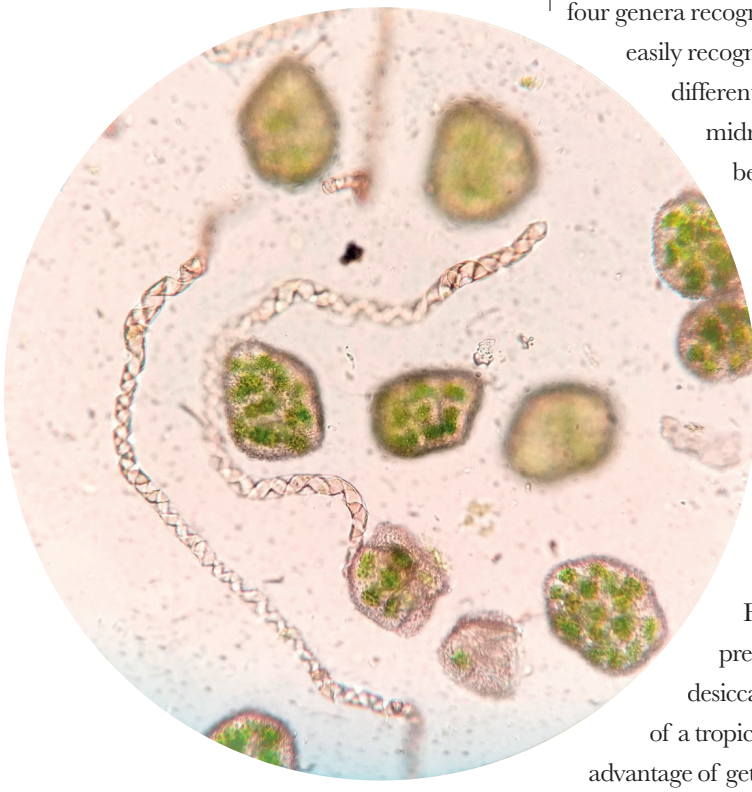
APPEARANCE
Narrow linear thalli up to 9/16 in (14 mm) long. Cells 1–2 chloroplasts with or without a pyrenoid, depending on species. Spores brown-black, bumps/dimples distinguish species. Pseudoelaters short, thin-walled. Antheridia 1 or 2–5 per chamber. Globose *Nostoc* communities on thallus

HABITAT
A colonizer of bare soil in open environments

hornworts, not all species in *Phymatoceros* possess a pyrenoid. These species are dioicous, meaning that male and female reproductive organs are produced on separate plants. The female plants are slightly smaller than the males and produce a short robust sporophyte. Although united by their molecular data and some morphological similarities, the three species placed in this order are morphologically quite divergent from each other, and summarizing diagnostic features for the genus is challenging.

DENDROCEROS

BELOW | Under the microscope these green *Dendroceros* spores can be seen to be multicellular, intermixed with the long, spiraled pseudoelaters.



The Dendrocerotales differ from the other hornwort orders in their choice of habitat as they have specialized to grow on living plants as epiphytes rather than as colonizers of bare soil. They may even grow on the surface of leaves in areas with high humidity. The Dendrocerotales are predominately tropical, and *Dendroceros* is one of four genera recognized in the order. *Dendroceros* is easily recognized by the crisped thallus that is differentiated into a central thickened midrib and lateral wings that may be perforated with holes.

The spores, which are so heavily relied upon in hornwort taxonomy, are particularly interesting in *Dendroceros* since they exhibit endosporic germination, which means the spore cell starts dividing within the cell wall before a protonemal filament emerges, resulting in multicellular spores. For a plant that grows in rather precarious habitats prone to desiccation, such as on the surface of a tropical tree leaf, it is easy to see the advantage of getting an early start and reaching

DISTRIBUTION
Widespread across tropical and extending into subtemperate regions

ETYMOLOGY
Latin *dendro* = "trees" + *kéras* = "horn," referring to the epiphytic habit of these plants

NUMBER OF SPECIES
Around 39 accepted species

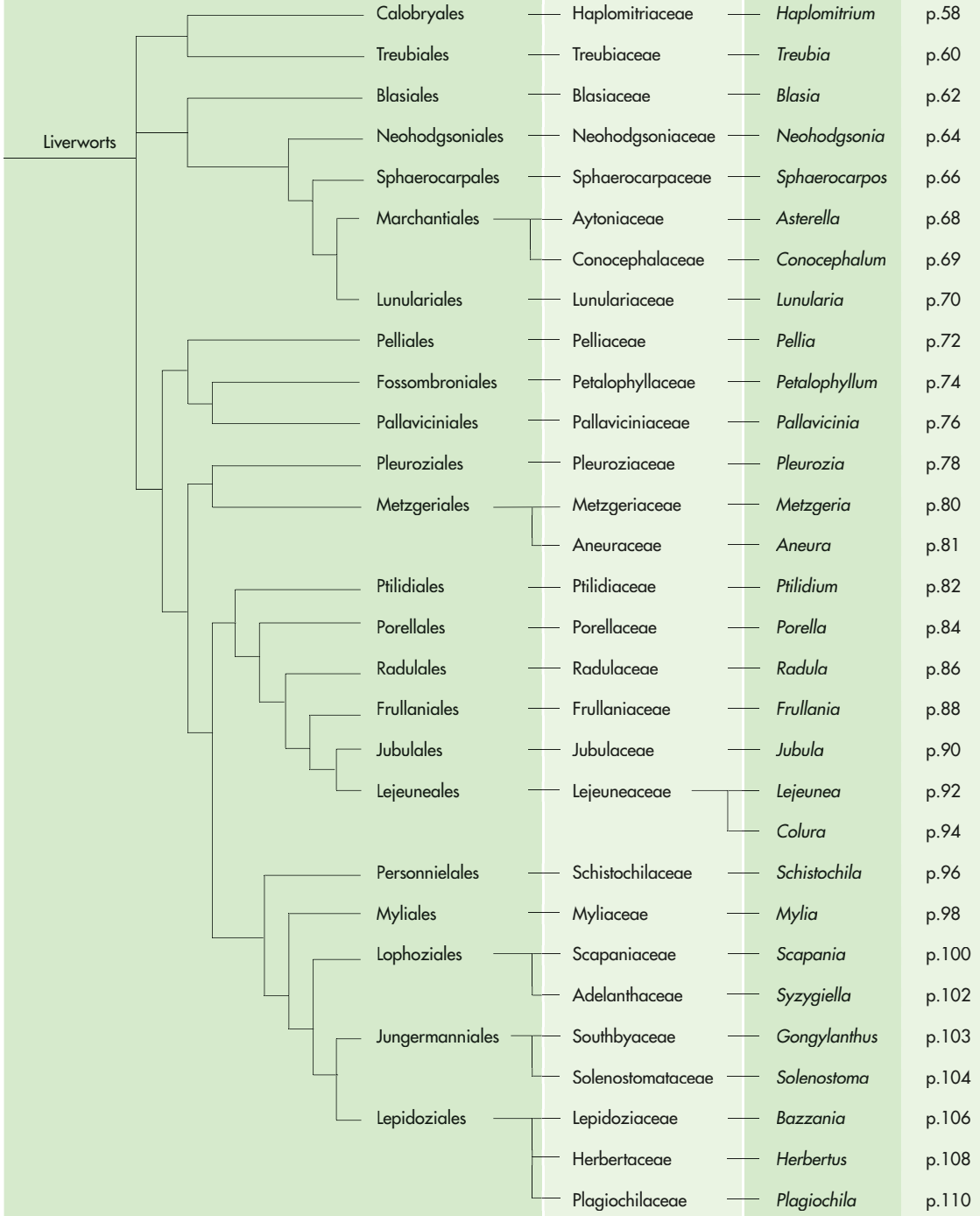
APPEARANCE
Yellow-green. Solid thallus 1/16–3/16 in (2–5 mm) wide, midrib, lateral wings. Cells 1 large chloroplast. Mature sporophytes 3/8–2 in (1–5 cm) tall. Pseudoelaters narrow, spiraled. Spores colorless, yellow, pale green. Antheridia 1–2 per chamber. *Nostoc* on thallus appear as black dots

HABITAT
Twigs, branches, living leaves in humid temperate/tropical forests

maturity to reproduce as soon as possible. The spores of the Dendrocerotales are colorless or yellow-green, which is typical of the tropical species associated with this order, where the spores are short lived. Darker spores typical of other hornwort orders have thicker walls and are filled with lipids, which means they are more desiccation tolerant and longer lived.

BELOW | *Dendroceros borbonicus* growing as an epiphyte on a tree in the tropical forest of Réunion Island.

PHYLOGENETIC TREE OF LIVERWORT ORDERS AND FEATURED GENERA



MARCHANTIOPHYTA: THE LIVERWORTS

The liverworts are morphologically an extremely diverse group, with a vegetative body plan varying from green thalloid plates to leafy shoots and a variety of complex leaf structures. The shared ancestry of the Marchantiophyta only really becomes apparent when the plants produce sporophytes and the uniform features of the setae and capsules become apparent.

There are around 7,000 known species of liverworts, which are recognized in 23 orders and 363 genera. The evolutionary relationships within the liverworts have been a puzzle to decipher. Some lineages have lost features and have become more structurally simple than their ancestors, and leaf-like structures have actually evolved more than once within the liverwort dynasty. But DNA sequencing has helped reach a more stable classification reflective of the relationships and origins of these plants.

Although the liverworts have ancient origins, some of the most species-diverse orders—such as the Lejeuneales and Lepidoziales—evolved more recently in parallel with the rise of the angiosperms and the tropical forests. These groups were able to diversify rapidly into these new habitats and are a significant part of forest epiphyte communities to this day.

HAPLOMITRIUM

Calobryales is a very ancient order that diverged early in the evolutionary history of the liverworts. *Haplomitrium* is the only living representative of this order, giving it a special significance in the study of early land plants.

The green leaves are positioned in three rows up the stems, giving a spiraled appearance. These small leafy shoots look very simple, but that overlooks some rather advanced adaptations at a cellular level. Some species have a central strand in the stem made up of long narrow cells that act as an internal water-conducting system. The lower part of the plant consists of a unique thick colorless rhizome, the branches of which bury themselves in the substrate. Symbiotic associations with fungi are common across the liverworts,

BELOW | A single plant of *Haplomitrium hookeri*, showing the pale rhizome from which the leafy shoots arise.

OPPOSITE | Typically found on damp ground, such as lake margins, these tiny green plants require careful searching on hands and knees to find.

DISTRIBUTION
North and South America, Europe, Asia, Africa, Australia, Pacific Islands

ETYMOLOGY
Greek *haplóos* = "simple" + *mitrium* = "little cap," referring to the calyptra that functions as a protective sleeve for the sporophyte

NUMBER OF SPECIES
7 accepted species

APPEARANCE
Up to ¾ in (2 cm) tall, 2⅜ in (6 cm) for some species. Leafy shoots, rounded leaves, pale root-like rhizome. Capsules cylindrical. Antheridia at shoot tips, ball-like, often orange, in leafy splash cups

HABITAT
Mostly soil or gravel in humid habitats but also wood or rocks

and these underground branches are colonized by fungi. These are being studied to provide insights into how the earliest land plants may have adapted to terrestrial habitats with the help of fungal partners.

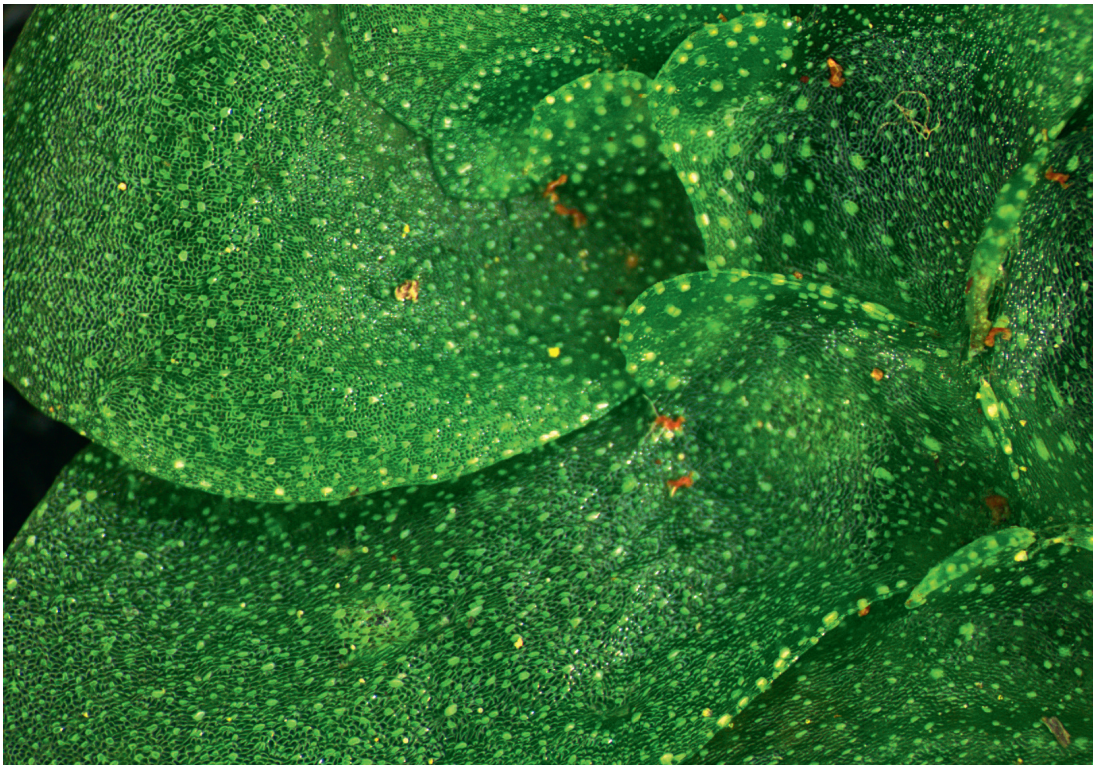
The sporophyte is also unique and surrounded by a fleshy calyptra while developing. The capsules are cylindrical, which is also striking as almost all other liverwort capsules are round. The setae are unusually thick and can extend up to 1 ¼ in (3 cm).

The greatest species diversity for the genus is in the southern hemisphere. Although only seven species are accepted, these show high levels of genetic diversity, and it is likely more species will be recognized with future study.

TREUBIA

The Treubiales represent an ancient group that, along with the Calobryales, diverged very early on in the evolution of the liverworts. The liverworts broadly fit into two structural groups: the thalloid liverworts, which form flat green mats without stems or leaves, and the leafy liverworts,

BELOW | A close-up view of the lobule of a *Treubia lacunosa* plant; the yellow dots are the large oil bodies.



DISTRIBUTION
Only found in the southern hemisphere—Chile, Southeast Asia, Australasia, and South Pacific islands

ETYMOLOGY
After Melchior Treub (1851–1910), a Dutch botanist

NUMBER OF SPECIES
7 accepted species

APPEARANCE
Thallus fleshy, brittle, bright green with yellow dots of oil body cells on the surface, branches up to 4 in (10 cm) long and ⅝ in (1.5 cm) wide with 2 rows of leafy lobes along the axis. Leaf cells dimorphic. Dioicous. Sporophytes arising from shoot tips. Asexual reproduction by gemmae

which have stems and leaf-like structures. The Treubiales is a particularly fascinating order from an evolutionary perspective because the structural complexity of these plants appears intermediate between these leafy and thallose forms. The result is a thalloid plant's innovation for a version of leaves!

Treubia has a unique leafy growth form for what is essentially a thalloid body plan. The thallus has a thick central axis with two rows of leaf-like lobes and smaller dorsal lobes along the upper surface. The leaves have two kinds of cells, some containing a large oil body scattered among other cells containing chloroplasts. The upper surface of the thallus is covered in a layer of mucilage produced from specialist mucilage-secreting cells. Sporophytes are positioned at the end of the thallus branches and have an unusually large seta.

There are two extant genera within the Treubiales: *Treubia* and *Apotreubia*. *Treubia* is a remarkable genus in terms of its unique morphology and evolutionary significance. It is distributed across the southern hemisphere, reflecting a time when the southern continents were united in the ancient supercontinent of Gondwana.

ABOVE | The structure of *Treubia tasmanica* illustrates how these plants are intermediate between leafy and thalloid liverwort forms.

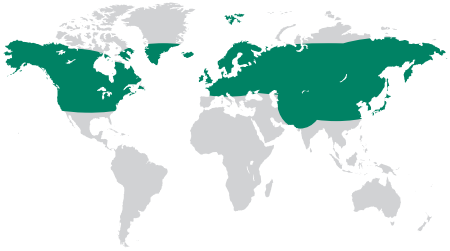
HABITAT
Growing over soil or rotting logs in humid sites, tropical forests

BLASIA

The Blasiales have a series of features that make them unique among the liverworts. Symbiotic relationships with cyanobacteria are common among the hornworts but in liverworts are restricted to the Blasiales, where the scattered dark spots of *Nostoc* colonies can be seen on the surface following a single line on each side of the thallus.

Blasia produces two distinct kinds of gemmae that play different roles in its vegetative reproduction. The green spiky gemmae balls produced on the upper thallus surface are short lived and develop in the summer months when they disperse and grow into new plants. These gemmae plan ahead and carry within them a tiny piece of the *Nostoc* symbiont to pastures new. The smooth, pale-yellow gemmae are produced in long, narrow, flask-shaped receptacles and contain nutrient reserves allowing them to overwinter in a dormant state and then start to grow in the spring. These are initially lacking a *Nostoc* symbiont, which needs to be acquired later. Sometimes both types of gemmae are produced on the same plant. All the sporophyte-bearing gametophyte thalli die off in the fall and the green sporophyte stays protected among the dead thallus throughout the winter, maturing and producing its spores in the following spring.

Blasia shares some features with the more complex thalloid liverworts. Its short, linear branches with lobed and ruffled margins have two rows of scales on the underside and are similar to those in Marchantiales. However, the thallus of *Blasia* is not internally differentiated with air chambers and pores.



DISTRIBUTION
Circumpolar boreo-temperate—Europe, Russia, Himalaya, China, Japan, North America

ETYMOLOGY
After Blasius Biagi (c.1670–1735), a Benedictine monk and botanist

NUMBER OF SPECIES
Only 1 species

APPEARANCE
Thallus branches to 1 in (2.5 cm) long with midrib and lobed margins. Dioicous. Antheridia arranged in two rows embedded in thallus surface. Sporophytes at tips of thallus lobes, large seta, capsule with elaters. Two kinds of gemmae produced. *Nostoc* colonies visible as dark spots on surface

HABITAT
Areas of disturbed soil such as roadside banks, on moist gravel or sand

OPPOSITE | The *Nostoc* colonies on this *Blasia* are visible as dark-green dots on the thallus surface.

RIGHT | One of *Blasia*'s smooth gemmae balls produced at the end of a long receptacle.

BELOW | *Blasia pusilla* showing both the spiky green gemmae on the thallus surface and also two rows of rounded bumps housing the male antheridia.

NEOHODGSONIA

The Neohodgsoniales is one of several orders of complex thalloid liverworts that are broadly defined as having a differentiated thallus with an upper layer with pores and air chambers and a lower layer of solid tissue. Rhizoids are abundant on the underside of the thallus and may occur in two forms: those that attach the plant to its growing surface and those that can form a capillary conducting system for water retention. The underside of the thallus may have rows of flap-like scales that also have a role in water conduction. Many of these complex thalloid liverworts produce unique, elaborate structures to house the sex organs, which resemble small umbrellas and are formed from the vegetative thallus.

The Neohodgsoniales contains just one species, *Neohodgsonia mirabilis*. It differs wildly from any other thalloid liverworts in having a uniquely branched carpocephalum—the umbrella-like structure that bears the female sex organs. It is also unusual in possessing gemmae cups on its surface, a feature found in a few other liverworts such as the common *Marchantia*. Genetic sequence data has confirmed the uniqueness of this species and its status as the sole representative of this order.

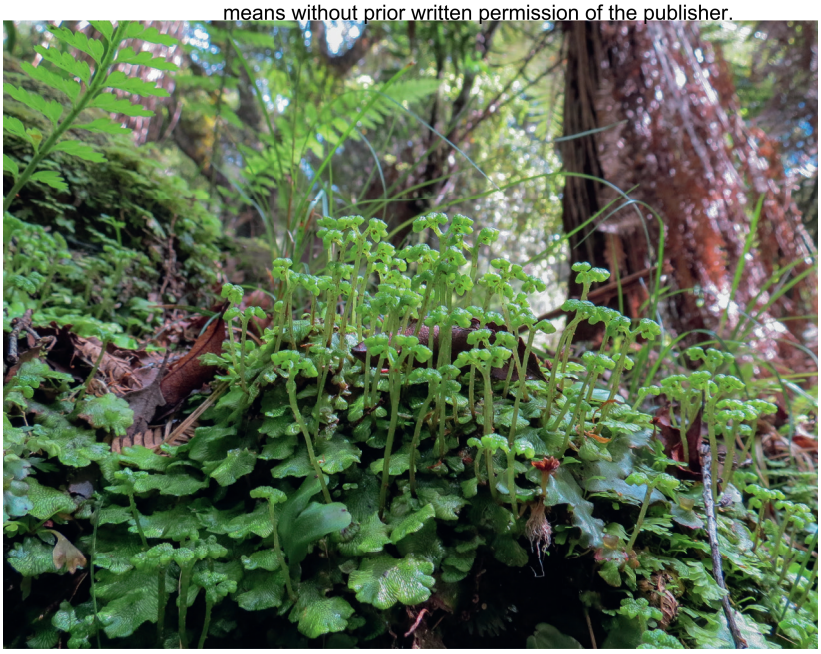
Neohodgsonia lacks the detailed distribution data needed to accurately assess its conservation status,

DISTRIBUTION
New Zealand, Tristan da Cunha, Gough Island

ETYMOLOGY
Originally described as *Hodgsonia* after Eliza Amy Hodgson (1888–1983), New Zealand bryologist

NUMBER OF SPECIES
1 known species

APPEARANCE
Thallus dark green with lighter green specks, branches ⅓–⅜ in (8–10 mm) wide, underside with 2 rows of scales. Cells with single large oil bodies. Monoicous. Antheridia and archegonia in separate stalked structures with disc-shaped lobed receptacles. Gemmae cups with frilly margins on thallus surface with discoid gemmae



LEFT | The rare *Neohodgsonia mirabilis* photographed in woodland in New Zealand.

but it is certainly a rare species known to occur only in New Zealand and the remote Tristan da Cunha islands. Its disjunct distribution is intriguing. In New Zealand it is known to require moist conditions of montane forests since it is not drought tolerant.

OPPOSITE | The round gemmae cups on the thallus surface, similar to those found in *Marchantia*, are visible in this photo.

RIGHT | The unique branching of the carpocephalum can be seen here.

HABITAT
Usually growing over forest soil in areas of high rainfall

SPHAEROCARPOS

BELOW | *Sphaerocarpos europaeus* belongs to a very distinctive group of thalloid liverworts found on disturbed bare soils.

The Sphaerocarpales are sometimes referred to as the "bottle" liverworts in reference to the inflated bottle-shaped protective structures—involucres—that surround the sex organs. They form a very distinctive group of complex thalloid liverworts and are adapted to living in disturbed temporary habitats where they are short lived, completing their life cycle within a year.

Sphaerocarpos has a worldwide distribution, though its range is not continuous and it is usually quite rare.

Sphaerocarpos forms tiny pale-green rosettes with lobed thalli. The dense cluster of balloon-like involucres are extremely distinctive once you get close enough to see them. *Sphaerocarpos* plants are sexually dimorphic, with female plants much larger than the males, sometimes even growing over the male plants. The male antheridia are in the flask-shaped "bottles" on the upper surface of the thallus while the female archegonia are in rounded to cylindrical structures. These plants do not raise their capsules

DISTRIBUTION
Pacific North America, South America, Europe, South Africa, southeastern Australia

ETYMOLOGY
Greek *sphaîra* = "sphere" + *karpos* = "fruit," referring to the involucres enclosing the capsules

NUMBER OF SPECIES
10 accepted species

APPEARANCE
Tiny pale-green rosettes with foliose lobes. Dioicous. Male plants only around 3/16 in (5 mm) in diameter, antheridia in perigonial involucres on thallus surface. Female plants much larger around ¾ in (2 cm) in diameter, sporophyte enclosed in flask-shaped structure

up on setae like most other liverworts but instead the sporophyte is hidden, completely enclosed within the leafy "bottle" produced from the gametophyte thallus. The capsules do not have lids that open to release the spores; instead, the spores are released when the capsule wall disintegrates. Another anatomical feature of the sporophyte that sets this order apart from other liverworts is the absence of elaters in the capsule, which when present would help to disperse the spore mass. Dispersing spores over long distances is clearly not a priority for *Sphaerocarpos*, and this life strategy may be reflected in the ephemeral habitats that it occupies.

ABOVE RIGHT | A close-up view of *Sphaerocarpos texanus* showing the balloon-like structures that contain the reproductive organs.

RIGHT | *Sphaerocarpos stipitatus*, pictured here in the West Coast National Park, Western Cape, is known only from South Africa and Chile.

HABITAT
On damp soil of disturbed and temporary habitats such as agricultural fields or gardens

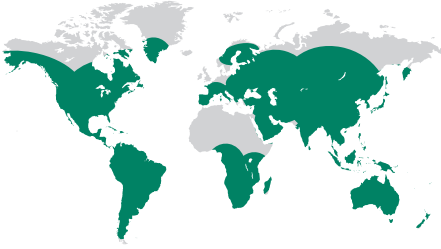
ASTERELLA

Marchantiales is a large order containing over 25 genera of complex thalloid liverworts. They have pores on the thallus surface that are surrounded by differentiated cells and an internal thallus structure with air chambers, photosynthesizing cells, and storage tissue. They also have archegoniophores that are tall stalks with a disc-shaped receptacle at the top housing the reduced sporophytes.

Asterella forms dense mats or scattered branches, bright green above and dark wine red to black underneath. Many species of liverworts are highly aromatic, and *Asterella* species can have a characteristic smell of rotten fish.

The archegoniophores in *Asterella* are unique among the complex thalloids. The receptacles are rounded with four or more lobes and each lobe houses a single reduced sporophyte surrounded by a protective sheath or involucre. When the spores are mature this sheath splits into ribbons allowing the spores to disperse. The tattered ribbons are usually conspicuous white or lilac and are a characteristic sight identifying the genus before getting close enough to test for a fishy whiff.

LEFT | The white sheaths surrounding the sporophytes can be seen in this specimen of *Asterella saccata* hanging down below the green receptacles.



DISTRIBUTION
Worldwide extending from the Arctic, temperate to tropical regions; the Americas, Europe, Africa, Asia, Australasia, and Oceania

ETYMOLOGY
Greek *astḗr* = "star," referring to the star-like appearance of the female receptacle

NUMBER OF SPECIES
53 accepted species

APPEARANCE
Thallus green to purple, branches up to ⅜ in (9 mm) wide, underside of thallus with large, often purple scales in 2 rows. Monoicous or dioicous. Antheridia on thallus. Archegoniophores with a conspicuous fringe surrounding each reduced sporophyte

HABITAT
Usually growing on soil, sometimes rock

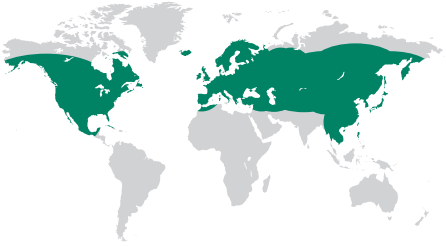
CONOCEPHALUM

Conocephalum is another example of the complex thalloid liverworts in the Marchantiales with air chambers within the thallus. Looking at the surface of the plants, the borders between the air chambers are clearly outlined with a roughly hexagonal line, giving most species a snakeskin pattern. The openings to the air chambers are via pores that are raised up from the surface like mini volcanoes.

The archegoniophores elongate very rapidly and the stalks holding up the female receptacle can sometimes reach up to 2¾ in (7 cm) high, which is huge for a bryophyte! The female receptacles are conical and a distinctive feature of the genus. Like many of the Marchantiales genera, *Conocephalum* produces aromatic compounds and some species have a strong smell of turpentine when crushed.

These liverworts can form large mats and are commonly encountered in the right kind of damp habitat across the northern hemisphere. Common names are not often applied to bryophytes, yet *Conocephalum* is such a large and easily recognized plant that in English-speaking regions it has acquired two aliases: Great Scented Liverwort and Snakeskin Liverwort.

ABOVE | The clear outline of the air chambers with their central pore gives a distinctive pattern to the surface of this *Conocephalum salebrosum*.



DISTRIBUTION
Predominantly in temperate to boreal regions of the northern hemisphere, spanning North America, Europe, and eastern Asia

ETYMOLOGY
Greek *konos* = "cone" + *kephalos* = "head," alluding to the conical-shaped receptacles

NUMBER OF SPECIES
5 accepted species

APPEARANCE
Large, branched thallus up to 8 in (20 cm) long, surface with raised pores with conspicuous border to air chambers. Dioicous. Archegoniophores produced at ends of thallus branches with long stalks and conical receptacles

HABITAT
Damp areas in woodland, such as near water courses, growing over soil or rocks

LUNULARIA

OPPOSITE | *Lunularia* with its characteristic crescent-shaped gemmae cups housing the tiny green propagules.

BELOW | *Lunularia* is a rather weedy species commonly found around gardens and nurseries where its delightful gemmae cups are always worth a closer look.

The single species representing the Lunulariales, *Lunularia cruciata*, was formerly placed in Marchantiales. However, research into its evolutionary history based largely on DNA sequencing has shown that *Lunularia* is the only living representative of a lineage of plants that diverged from the rest of the complex thalloids early on in their history.

DISTRIBUTION
Worldwide

ETYMOLOGY
Latin *lunula* = "little moon," referring to the crescent-shaped gemma cups

NUMBER OF SPECIES
Only 1 species

APPEARANCE
Thallus bright green, branches up to 2 in (5 cm) long, upper surface with pores, borders to air chambers faintly seen on surface forming reticulate pattern, underside of thallus with 2 rows of scales. Dioicous. Usually sterile. Asexual reproduction by discoid gemmae in lunate gemmae cups on thallus surface

HABITAT
Commonly found in human-made habitats such as gardens or in damp areas near water

(continued...)

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