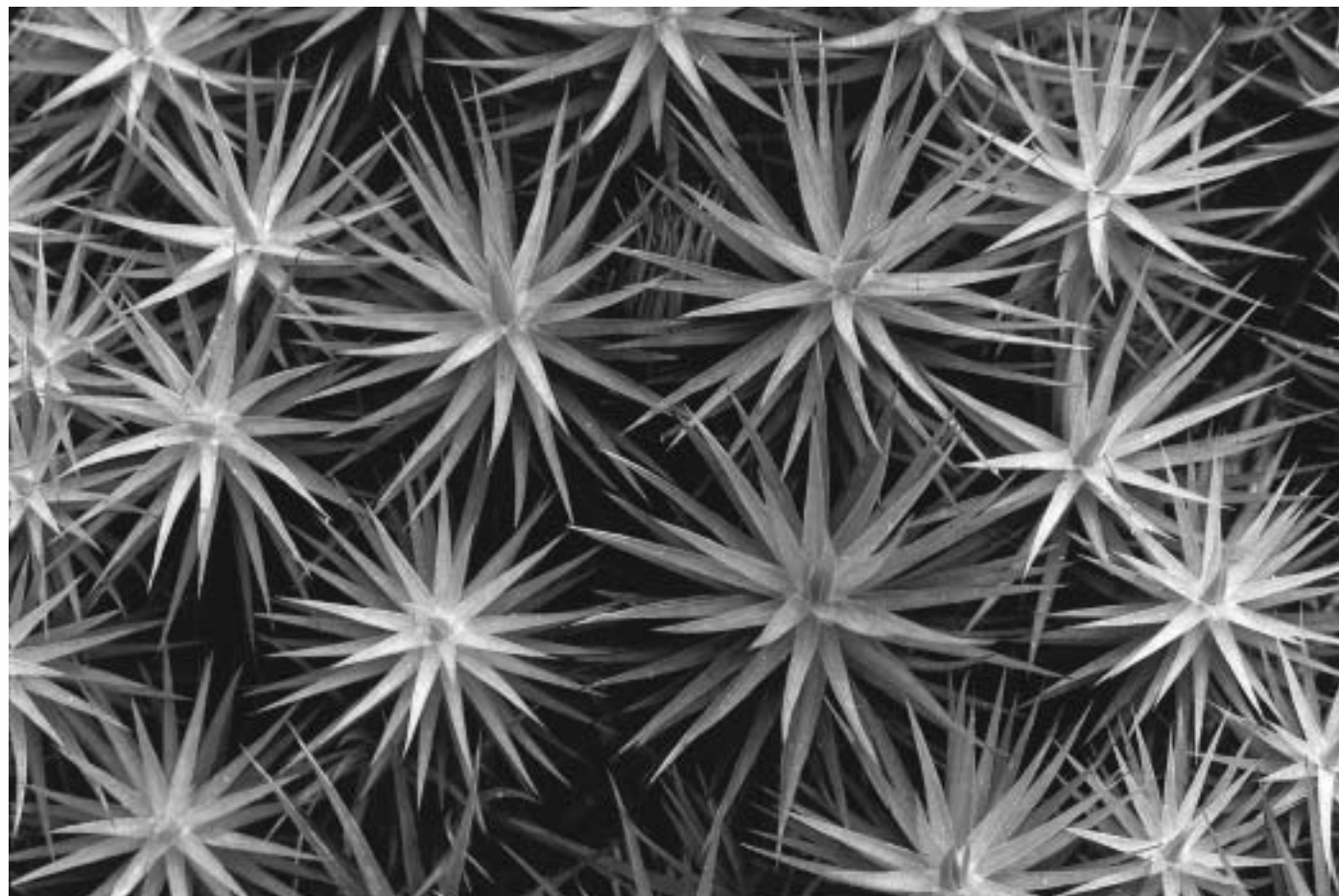




FREMONTIA

A JOURNAL OF THE CALIFORNIA NATIVE PLANT SOCIETY



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SPECIAL ISSUE: BRYOPHYTES

FREMONTIA

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California Native Plant Society

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Dedicated to the Preservation of the California Native Flora

The California Native Plant Society (CNPS) is an organization of laypersons and professionals united by an interest in the native plants of California and is open to all. Its principal aims are to preserve the native flora and add to the knowledge of members and the public at large by monitoring rare and endangered plants throughout the state; by acting to save endangered areas through publicity, persuasion, and on occasion, legal action; by providing expert testimony to government bodies; and by supporting financially and otherwise the establishment of native plant preserves. Much of this work is done by volunteers through CNPS Chapters throughout the state. The Society's educational work includes: publication of a quarterly journal, *Fremontia*, and a quarterly *Bulletin* which gives news and announcements of Society events and conservation issues. Chapters hold meetings, field trips, and plant and poster sales. Non-members are welcome to attend.

Money is provided through member dues and funds raised by chapter plant and poster sales. Additional donations, bequests, and memorial gifts from friends of the Society can assist greatly in carrying forward the work of the Society. Dues and donations are tax-deductible.

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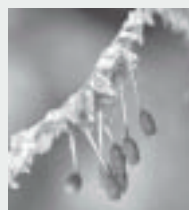
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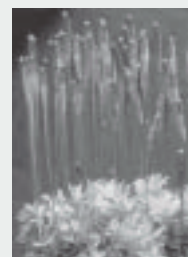


A CONVERSATION ABOUT MOSSES, LIVERWORTS, AND HORNWORTS <i>by Daniel Norris</i>	5
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Through a series of frequently asked questions, Daniel Norris, who taught bryology for years, provides an introduction to the bryophytes (mosses, liverworts, and hornworts), as well as discussing some fascinating features of these small green plants.

MOSS GEOGRAPHY AND FLORISTICS IN CALIFORNIA <i>by James R. Shevock</i>	12
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Be amazed at the great diversity of mosses in California, the habitats in which they grow, and moss geography, along with a history of moss collecting in California, as you read this article written by one of California's premier moss authorities. Then consider the fact that mosses new to California, including new species, are continually being discovered.



THE ROLE OF THE AMATEUR IN BRYOLOGY: TALES OF AN AMATEUR BRYOLOGIST <i>by Kenneth Kellman</i>	21
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Experience this journey of a commercial air conditioning mechanic with a fledgling interest in mosses, to an amateur bryologist who is authoring a "Catalog of the Mosses of Santa Cruz County"! Ken Kellman shares his joy of learning more about mosses, along with tools, resources, and encouragement for others who may wish to travel this same road.

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MOSSES IN THE DESERT? <i>by Lloyd R. Stark</i>	26
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Most of us think of mosses as being only abundant in wet habitats, festooning trees, or carpeting rocks and logs. In this article the author transforms these stereotypical images by writing of the many mosses of California deserts and where one finds them, along with many fascinating reproductive strategies employed by mosses surviving in such extreme habitats.



THE BIOLOGY OF BRYOPHYTES, WITH SPECIAL REFERENCE TO WATER <i>by Brent D. Mishler</i>	34
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Brent Mishler discusses the evolutionary history of bryophytes, and the physiological aspects of these plants that define where and how they live, with particular emphasis on mosses and water.

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THE COVER: Gametophytes (green haploid generation) of *Polytrichum commune*, haircap moss. Photograph by M. Hutten. All images in this issue by M. Hutten unless credited otherwise. See this issue in color at www.cnps.org.

GUEST EDITORIAL

I have come to increasingly appreciate the abundance of opportunity to explore and learn from the natural world. Why do I invest so much time and energy in the study of plants? The answer is quite simple: it is fascinating. I learn something new almost every day. I can't wait for my next hike where I might make an acquaintance with a new flower, and now, with each new bryophyte. Botanical exploration has been both a journey toward intellectual enrichment as well as my "mental health care package." While our lives continue to become more complex in our high-tech environment, we still have the opportunity to study nature and be amazed at the infinite ways in which it works. Several colleagues have asked me why I became interested in learning about the bryophytes. The answer is not readily pinpointed, but as the following articles attempt to convey, the bryophytes are, simply stated, a remarkable group of land plants. They are *worthy* of our attention.

When we consider the rate of habitat conversion caused by various land-use practices, along with the growing population that continually impacts the California landscape (e.g., urban sprawl), it is more important now than ever that we have conservation policies that provide for a network of protected areas. The protected places can (and should) run the full spectrum—from open space in urban landscapes to the most remote areas in designated national wilderness and national parks. All are important and contribute in their own way to species and habitat conservation. We are truly lucky to live in such a diverse and remarkable state, and equally fortunate to have no less than 40 percent of our state in public lands. Few states can boast of such biological diversity as found in California. However, maintaining this heritage of biodiversity requires awareness, a desire to protect it, and a framework to actually manage for it. The beginning of this process is meaningful and long-lasting change, primarily through education. *Fremontia* is one of these educational tools.

As much as we know about the California bryoflora, the process of gathering inventory is still at an early stage compared with that for vascular plants. Many regions of the state are poorly collected, and our gathering of data about rare and threatened bryophytes and their habitats is still in the preliminary stages. Nonetheless, we know that California harbors one of the most exciting and species-rich bryofloras in the entire country. We are still discovering bryophytes that are new to science—currently we have more than two dozen in the process of being described. This indeed inspires us to continue our exploration. I hope that through this bryophyte issue of *Fremontia* you may discover a sampling of what motivates bryologists like me to spend days, months, and years with these little green plants.

—Jim Shevock
Bristlecone Chapter
Member of the *Fremontia* Editorial Advisory Board

USEFUL WEBSITES AND CONTACT INFORMATION

Bryophyte websites:

See "Notes and Comments," p. 34

California Native Plant Society:

www.cnps.org, with links to conservation issues, chapters, publications, policy, etc.

To sign up for "NPCC News," e-mail news on native plant science and conservation, send a request to npcc@cnps.org.

For updates on conservation issues:

Audubon Society www.audubon.org

Center for Biological Diversity
www.sw-center.org

Natural Resources Defense Council
www.nrdc.org

Sierra Club
www.sierraclub.org

Wilderness Society
www.wilderness.org

For voting information:

League of Women Voters
www.lwv.org, includes online voter guide with state-specific nonpartisan election and candidate information.

US Senate
www.senate.gov

US House of Representatives
www.house.gov

California State Senate
www.sen.ca.gov

California State Assembly
www.assembly.ca.gov

To write letters:

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The White House
1600 Pennsylvania Ave. NW
Washington, DC 20500

Senator Barbara Boxer
or Senator Diane Feinstein
US Senate
Washington, DC 20510

Your CA Representative
US House of Representatives
Washington, DC 20515



The moss *Mnium spinulosum* with gametophyte (leafy lower portion) and sporophyte (stalks and capsules). [See moss life cycle on page 28.] Note serrated margins toward leaf apex and strong costa (leaf midrib).

A CONVERSATION ABOUT MOSSES, LIVERWORTS, AND HORNWORTS

by *Daniel Norris*

Many millennia ago, as a Michigan college freshman already ten years into bird-watching, I heard my botany professor speaking of the joys of plant collecting. Why waste time studying plants when beautiful birds beckoned? Two years later in Montana, I watched my professor's wife collecting mosses while I enjoyed the true excitement of collecting beautiful flowers. Now, after 106,000 bryophyte collections, I continue to be obsessed with the beauty of bryophytes.

Bryophyta (or *bryophytes*) is the scientific name for a group of plants including the mosses, liverworts, and hornworts. For our purpose, we can define them as green plants without flowers and fruits, and lacking a well defined system of vascular tissue for transporting plant fluids throughout the plant. They reproduce, not by seeds, but by single-celled spores. Mosses and most liverworts have clearly recognizable leaves on clearly recognizable stems but they totally lack a root system. All hornworts and some liverworts lack even a leaf-

stem differentiation but instead grow as ribbon-like *thalli* (singular, *thallus*). Bryologists typically study all groups of bryophytes despite the fact that the three groups probably evolved independently from one another. To avoid the more cumbersome term, *bryophytes*, I normally speak of mosses while meaning mosses, and liverworts and hornworts as a collective group.

Over the course of my 45 years as a bryologist, I have gradually accumulated a list of questions that I might expect from people, who

surprisingly want to continue conversing even after learning of my strange profession. For example, I am often asked, “*Will the dense mosses on my apple tree kill it?*” And I reply, “*No, your healthy apple tree will not be hurt by its moss cover.*” This is because mosses lack a root system, so they simply adhere to the bark of a tree but do not penetrate it.

Only in rare cases will bryophytes have adverse effects. In the so-called “moss forests” of montane tropical rainforests, bryophytes may become so heavy as to pull down a branch or even a tree during heavy rains. Even an apple or-

chard is sparsely covered compared with such montane tropical rainforest trees. There, the trunk, branches, and twigs may be covered to a depth of even a foot or more, and they may even have dense bryophytes on their evergreen leaves. In such conditions the *epiphyllous* (growing on leaves) bryophytes may damage coffee or cocoa by interfering with photosynthesis.

Having dispelled his worries about apple trees, my conversant may next ask about the mosses on his roof. “*Yes, they may damage roofs by interfering with drainage.*” “*How do I combat the moss cover on my roof?*” “*Move your house to a more air-pol-*

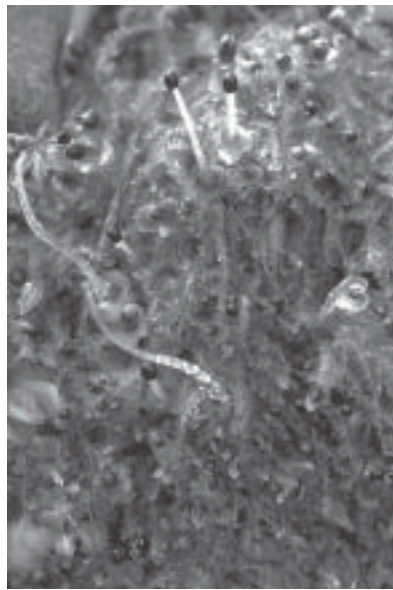
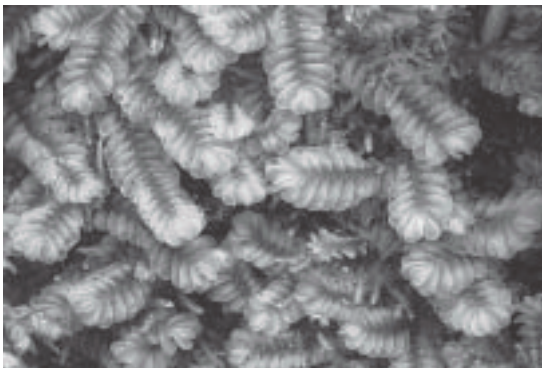
luted area.” My facetious answer elicits questions about bryophytes (and lichens) and air pollution. Without a root system, all parts of a bryophyte plant directly absorb their water from raindrops and dew-fall. Unfortunately the water that they absorb may contain dissolved substances, including harmful or potentially lethal materials from air pollution. Vascular plants are better protected from such direct air pollution damage. They take in nearly all their water via the root system, and those roots have a tissue (the endodermis) which excludes harmful materials.

“*I have heard that lichens are used in mapping air pollution.*” Historically, bryophytes and lichens have both been used for this purpose. Individual species of bryophytes and lichens differ in response to air pollution. Some can be found in highly polluted areas, and others are killed by even a small amount of air contamination. This sensitivity to pollution is often a species-specific response to levels of mineral ions such as chromium, nickel, copper, sulfur, etc. Such species-oriented studies are more advanced in lichenology, and many cities, especially in Europe, produce pollution maps based upon the presence or absence of certain lichen species.

Compared with lichenological studies, bryologists mapping air pollution are less concerned with species distribution around pollution sources. Instead they focus on mineral analyses of bryophytes in various air pollution regimes. Because mosses absorb all the minerals contained in incoming water, scientists in Europe have been hanging cloth-enclosed bags of mosses from freeway overpasses. Harvest of these bags at specific intervals is followed by mineral analyses. Interestingly, these studies show recent improvement in air quality in most cities in northern Europe.

“*Can I clean the mosses from my roof after they are killed by the drought*

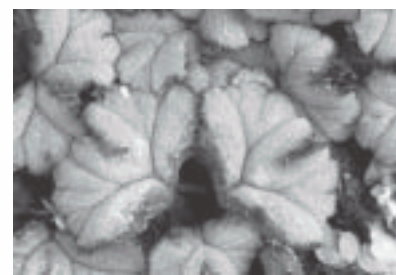
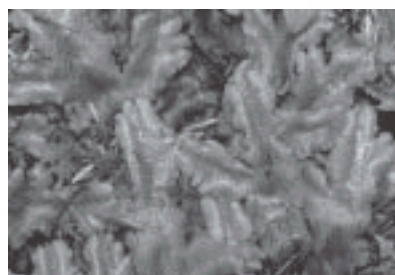
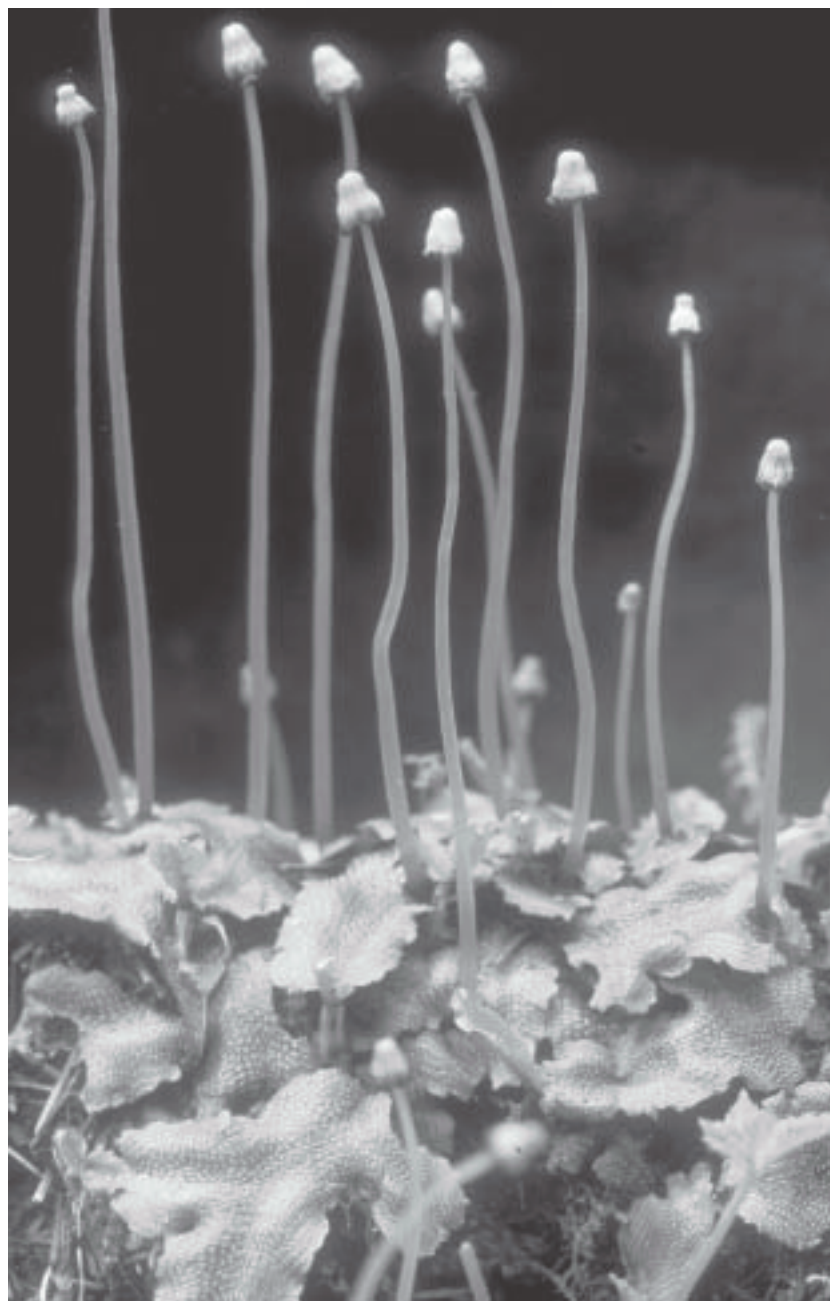
Clockwise from top: *Lophocolea cuspidata*. Most leafy liverworts have lobed or divided leaves, whereas mosses never do. • *Jungermannia* sp., a leafy liverwort, with capsules. Capsules in the leafy liverworts are relatively fragile and short-lived, and are normally dark and spherical. • The leafy liverwort *Gyrothyra* sp. Leafy liverworts appear to have leaves in two ranks, and unlike mosses, the leaves never have a costa.



of summer?" Most mosses are not killed by drying. Without a root system, mosses must survive drying rather than merely resisting it. Flowering plants may use the rain-water of last month and even last year by continuously tapping the underground soil reservoir penetrated by their roots. Bryophytes, on the other hand, can only use the water of yesterday and today. Flowering plants resist the loss of water by covering leaves and stems with a waxy covering, the cuticle. While bryophytes may have a thin cuticle, it does not protect them from drying. In fact, protection from drying would run counter to their need for being able to absorb surface water. Because bryophytes must have plant parts capable of rapid water absorption, those same plant parts lose water with equal rapidity.

Species of bryophytes differ in rapidity of water loss and water uptake, and these differences bear close relationship to the substrate on which they grow. Some bryophytes get virtually all of their water from precipitation (rain, dew, and mist). This is termed an *ecthydryc* strategy, and the extreme of such a strategy is shown by bryophytes growing on the extreme branchlets of trees. In contrast, bryophytes of wet soil or logs exhibit a more *endhydryc* strategy in that they typically take their water from the substrate surface and conduct that water throughout the plant in such capillary spaces as those formed by the wick of filamentous hairlike processes (rhizoids) on the stem surfaces. These two strategies are merely polar distinctions; in-between the extremes are innumerable variations of water uptake depending on the substratum.

Easterners have often asked me, "Why, in California, are there so many epiphytic mosses (growing on the trunks of trees)?" These epiphytic mosses are, of course, ecthydryc, and such mosses are completely hydrated by only a few millimeters of rain or even by water-droplet-laden fog



Conocephalum conicum (top) with sporophytes. • The thallus of *Conocephalum conicum* (bottom left) is several cell layers thick, with air chambers and air pores, as indicated by the compartmentalization apparent in this image. • *Ricciocarpus natans* (bottom right), a thallose liverwort. The photosynthetic tissue of thallose liverworts is thickened, whereas leafy liverwort leaves are usually one cell thick.



Mature hornwort, *Anthoceros* sp. (top). In this genus the spores are black, as indicated by the dark tips of the sporophytes. • *Anthoceros* sp. (bottom), displaying both developing columnar sporophytes and gametophytes. The gametophytes of hornworts can be distinguished from those of thallose liverworts by their blue-green, greasy appearance.

banks. Most of the eastern United States contains fewer epiphytic mosses despite generally higher total rainfall. We are contrasting here the areas of summer maximum rainfall (eastern United States) with ar-

eas of winter maximum rainfall (the Mediterranean climate regions of the west). In the East, the great thunderstorms of summer are followed by a hot drying period which soon leaves the mosses no better off than before the rain. Winters in California have frequent periods of small and sustained drizzle or mist, and during those winters, the heavy mass of epiphytic bryophytes shows most of its growth.

In vascular plant ecology, we speak of *hydryc*, *mesic*, and *xeric* plants and plant communities. Such terms do not work for bryophytes. It is better to speak of habitats on the basis of 1) frequency of hydration/dehydration, 2) duration of hydration, 3) duration of dehydration, and 4) intensity of dehydration. The eastern United States has occasional short periods of bryophyte hydration after the rainstorms of the summer, but these are quickly followed by long periods of dehydration because of the temperature of those summer months. Winters in most of the East are characterized by frozen conditions without the possibility of fluid water necessary for growth. In contrast, winters outside the high mountains of California allow for the continuous hydration of the bryophytes, due to the frequent mists and drizzles and low evaporation of the cool winter months.

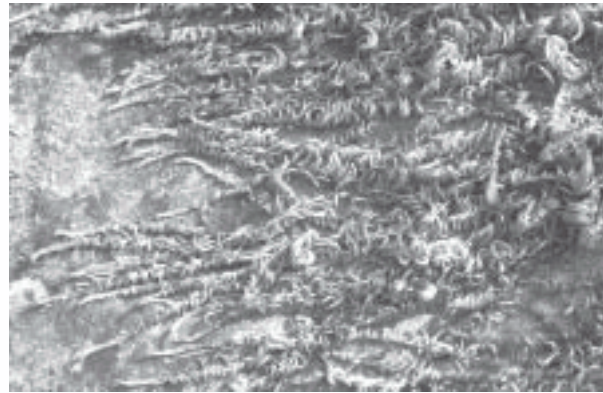
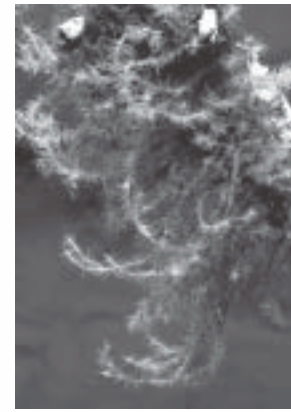
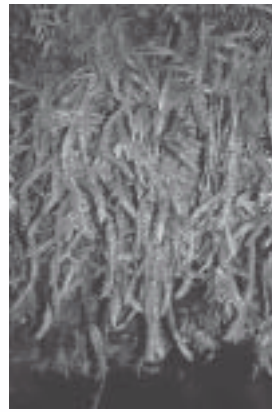
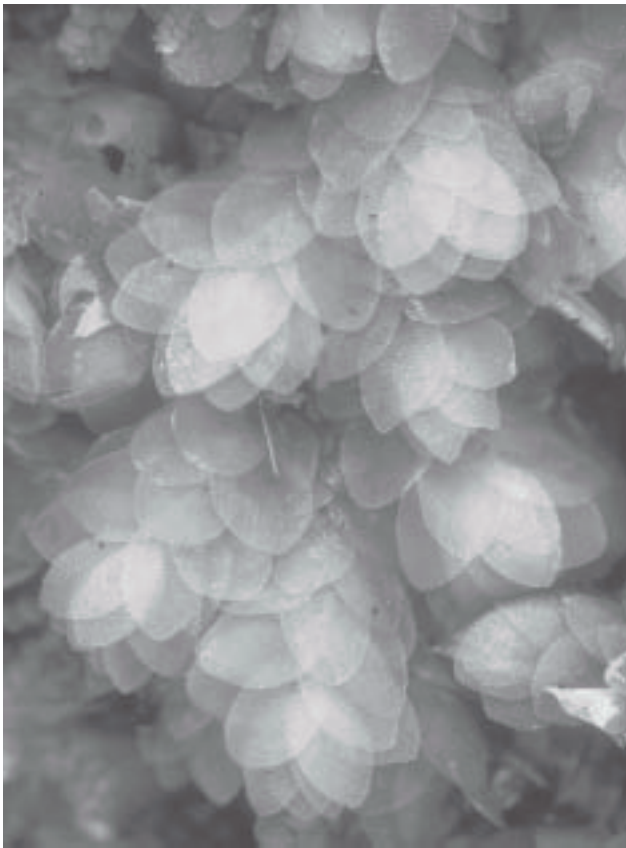
"Why do mosses grow on the north side of trees?" This is not necessarily true! Mosses on the north side of trees do not receive direct sunlight with its heating and associated drying effects. They may therefore remain hydrated and photosynthetically active for a longer period of time. Many trees have abundant bryophytes, not only on their northern base but also on all the rest of the trunk, limbs and even twigs. The total mass of bryophytes on a tree will be reflective of the duration of effective photosynthesis as opposed to the duration of drought-induced dormancy. In more open

forests, the south side of a tree may even be limited by temperature effects. Bryophytes are largely cold-weather plants with little or no photosynthetic effectiveness above about 80°F.

"Why did the moss on the rock in my front yard die when I sprayed it with water last summer?" Mosses can be exposed even to the temperatures of a Death Valley summer if they are dry and dormant. When wet and warm, mosses will usually use more food than they manufacture, resulting in starvation.

"I was skiing the other day and noticed some thawing patches of snow. Mosses and liverworts were protruding from that snow and apparently growing. How can that be?" Most flowering plants cannot realize a net gain from photosynthesis at temperatures much lower than 50°F. It is true that some flowering plants can grow through snow, but that growth involves the use of food manufactured and stored the previous year. In contrast, bryophytes can often realize a net gain of photosynthesis at temperatures very near freezing.

"Why are you crawling on the cold winter ground?" My usual answer, "I am testing the soil," is the answer of a coward fearful of the recruiters for the local mental institution. I am not really crazy. Many mosses and liverworts appear in late fall and early winter, and they dry to invisibility in the summer. Such bryophytes often grow and complete the lifecycle from spore to spore in a period of 6–10 weeks. They begin growth with the first moistening of the soil surface in the autumn, and they must end growth when the grasses begin to shade them in the spring. California is a place of great diversity of these ephemerals because many of its regions have winters with unfrozen soil surface left unshaded by vascular plants for several months at a time. Northward, there is reduced duration of such unshaded



Variation in moss gametophytes (clockwise from top left): *Hookeria lucens*, recognized by its transparent overlapping leaves. In California, this moss is the species most likely to be mistaken for a leafy liverwort. • *Buckiella undulata*, a large pleurocarpous moss in California primarily found in the redwood forest zone. Photograph by J. Shevock. • *Orthotrichum papillosum* (with a few sporophytes). *Orthotrichum* is one of the larger moss genera in the state. • *Homalothecium* sp. This large pleurocarpous moss forms mats on rocks and tree trunks.

and moist soil surfaces and with that reduction we see reduced diversity of ephemeral bryophytes.

"I was in the redwood forests of northwestern California. The broad-leaved trees were drenched with mosses but the conifers were almost bare. Why?" Conifers and angiospermous trees differ in many respects in the habitats provided for bryophytes. Conifer bark is typically more acid than angiosperm bark; it is usually somewhat harder; and it continues to be shaded during the high bryophyte growth times of winter.

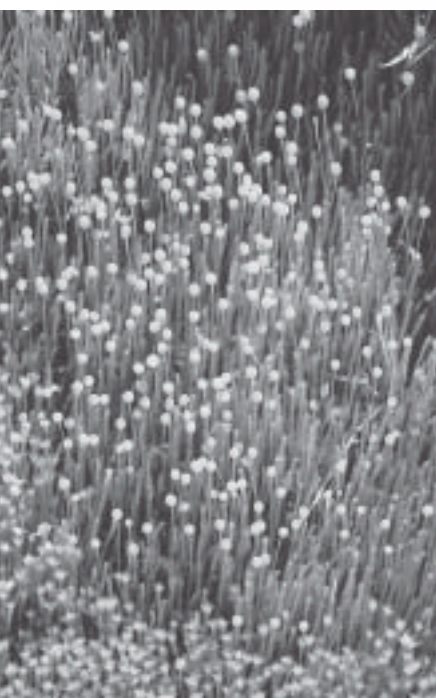
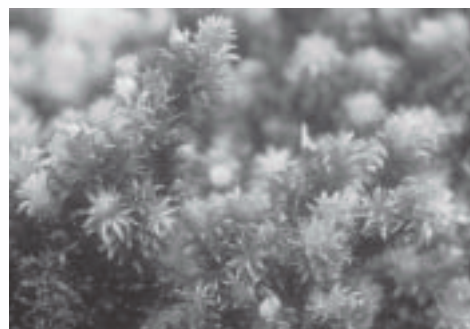
Perhaps more important is the greater amount of water and mineral nutrients provided to the epiphytes on broad-leaved trees. Conifer-branching architecture can be looked upon as an adaptation to the breakage effects of snow load due to leaf retention during the winter.

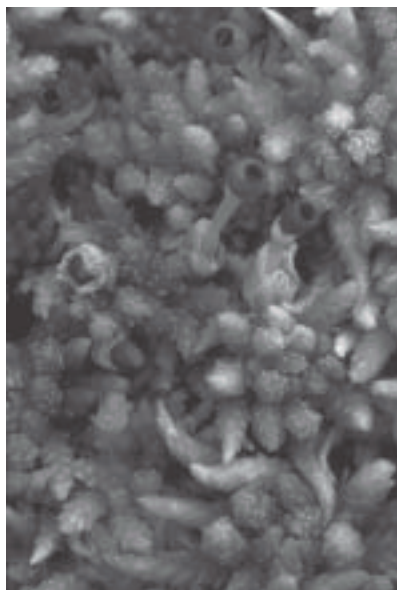
Conifers typically have the branches angled down from the point of insertion on the trunk. Such a pattern allows the snow to slide off the branch tips. Without leaves during the winter, most of our broad-leaved trees can have branches upwardly directed from their insertion on the trunk. Such upwardly-directed branches allow water with contained mineral nutrients to drain down to the trunk and from there to the soil at the tree base. The bryophyte growing on a broad-leaved tree thus gets more water and mineral nutrients than the one on a conifer. Because it gets more water, it grows more, and can therefore intercept even more water and minerals.

"Why are you so opposed to people earning their living by stripping mosses from trunks of trees and selling them for floral designs?" Mosses intercept

the water and minerals that flow down the trunks of trees. They only slowly meter out that material to the soil where it may be taken up again by the roots of the trees. The loss of the moss mat from the trunks of broad-leaved trees means that the mineral nutrients enter the soil too rapidly, and will therefore be lost into the water table and thence into the streams. Stripping mosses from tree trunks seriously depletes the fertility of the forest soil.

"If all that is true, why isn't the soil of the coniferous forest rapidly depleted of its mineral nutrients?" Conifers use and lose mineral nutrients at a much reduced rate compared to broad-leaved trees. The low mineral content of water leached from the canopy of a conifer is spread around the forest floor from the descending branch tips of





Variation in moss sporophytes: Opposite page, clockwise from top left: *Buxbaumia viridis*. Species in this genus are called “bug on a stick”! *Buxbaumia* is unique in that you only see the plant when sporophytes are present because the gametophytes are so inconspicuous. • *Trachybryum megaptitum*. This moss and other pleurocarpous mosses have capsules attached on lateral stems, as opposed to acrocarpous mosses, with capsules attached at the tips of the stems. • *Scouleria aquatica*. At maturity, the capsules of this moss turn chestnut brown, and are shaped like an inner-tube. It is found seasonally submerged in rivers and fast flowing streams; when dessicated, the plants turn jet black. • *Polytrichum juniperinum*, called the haircap moss for the netted coverings (calyptra) over the capsules. • *Philonotis fontana* is named the green apple moss, for its spherical capsules. Primarily found in springs and seeps. Photograph by J. Shevock. • *Neckera douglasii*. In California, this epiphyte is found in the coastal rainforest. Note the pendulous sporophytes and ring of appendages (peristome teeth) at the mouth of the capsules. This page, left to right: *Sphagnum* sp. Members of this family (Sphagnaceae) are unique among mosses: sporophytes lack peristome teeth and the leaves contain water-holding cells and lack chlorophyll. • *Heterocladium macounii*. Note the peristome teeth.

that conifer. The high mineral content of water leached from the canopy of a broad-leaved tree is instead held in the moss mat on the tree trunk. In California those nutrients are leached out of that moss mat, especially once the rains resume in the late fall and winter. It might also be noted here that late fall and winter, the time of maximum leaching, coincides with the maximum growth of tree roots. This results in more rapid uptake both through the root hairs and by the fungi that cloak the roots (mycorrhizae).

One of the most frequent comments that I receive on a day of heavy rain is, “A nice day for mosses isn’t it?” My usual reply of “Maybe not!” is motivated by studies I conducted in an area of temperate rainforests in coastal northern Cali-

fornia. I found maximum epiphytic bryophyte growth on years when there was little rainfall in the normally wet months of October through January. Minimum epiphytic bryophyte growth occurred in times of extremely high late fall and early winter precipitation. This counter-intuitive observation seems to be related to excessive leaching of the epiphytic moss mat with the consequence of reduced mineral nutrients for growth.

“How can I grow bryophytes in my yard?” Japanese gardeners are famous for their moss gardens, but such gardens are so labor intensive as to be daunting to a westerner [see Book Reviews, page 41]. More appropriate is the growing of mosses on trees or rocks in your yard. Especially with trees, it is often possible to take a large clump of moss

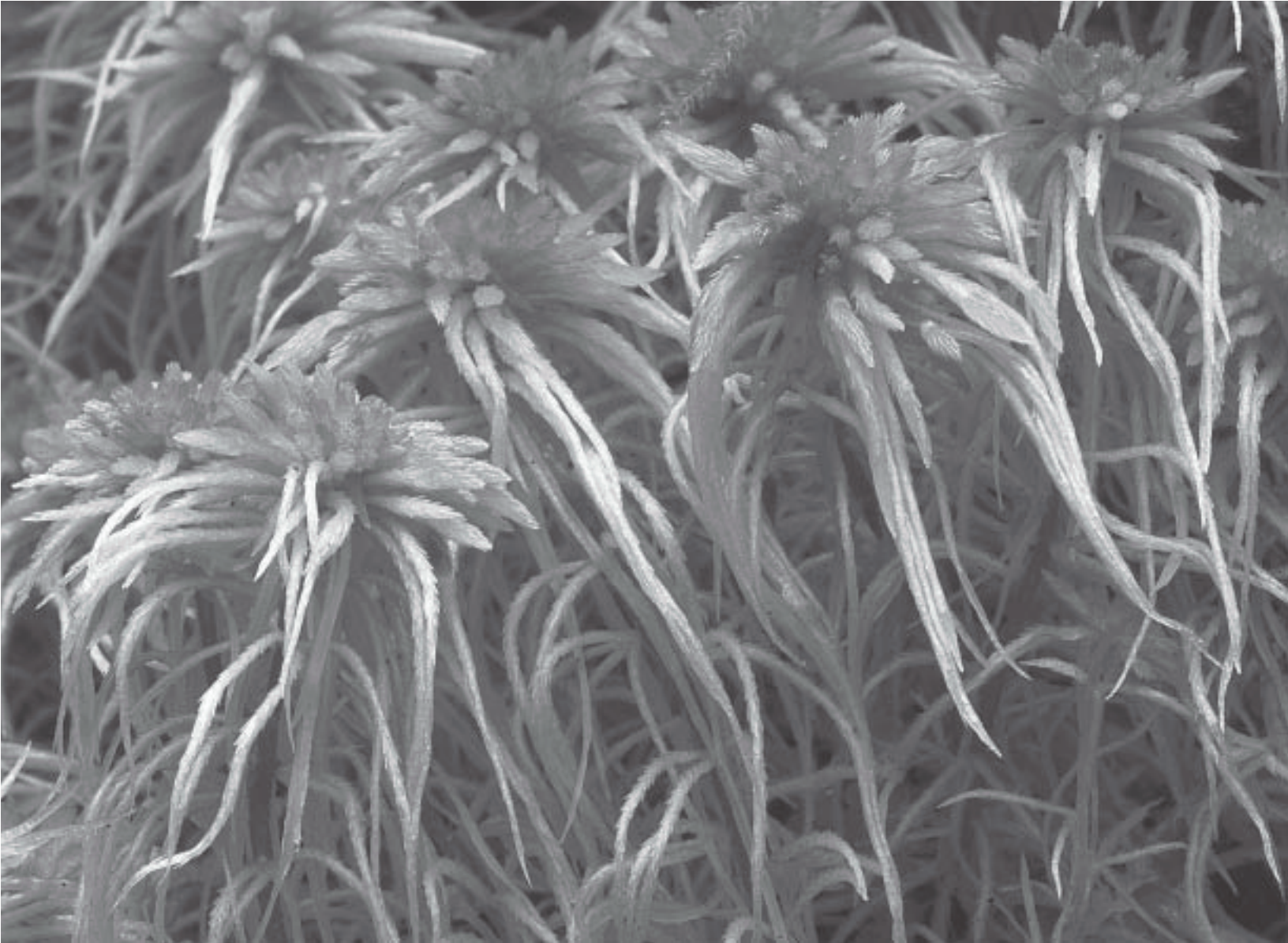
from a tree and to tie it on to the tree with fish line. It is important that one take a fairly large patch because mosses operate on what I call a “Catch-22.” They can survive if there are enough of them to intercept and hold sufficient water during a dry time. In nature, one wonders how they get from being small and easily dried to becoming large and less easily dried.

Another approach to planting bryophytes, and one that works especially well on rocks, is the use of plant fragments. Any living cell of almost any bryophyte has the potential to grow into a mature plant. A bryophyte can grow from fragments processed in a blender and sprayed onto a suitable surface. Buttermilk is often included in the blender brew to provide a suitably acid glue for these fragments.

“Can I simply take the spores from a moss capsule and tap them out onto a suitable surface?” Probably not. Most bryophytes reproduce primarily from plant fragments—whether from the dirty toenails of squirrels or the dried materials adhering to a duck’s legs. Sporic reproduction seems to primarily be an adaptation to very occasional long-distance dispersal, something that is probably not very common. Experimental work in The Netherlands has shown that most bryophyte spores died when exposed on the wings of airlines for even a single transatlantic flight.

As you might now more fully appreciate, bryophytes are a fascinating group fully justifying my life-long obsession. There is enough yet to be learned about these plants to justify an obsession of a similar length, or a passion equaling mine, for a few tens of thousands of appropriately curious amateur or professional bryologists.

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Sphagnum girgensohnii. Most people have heard of peat moss, which is the common name for members of the genus *Sphagnum*. Although peat moss covers large expanses of the northern hemisphere, and is ecologically one of the most important groups of mosses in the world, it is relatively uncommon and relictual in California.

MOSS GEOGRAPHY AND FLORISTICS IN CALIFORNIA

by James R. Shevock

Mosses are the largest of the three lineages of bryophytes. With nearly 1,200 species of mosses recorded for North America, California has nearly half of them. So what accounts for this great diversity of mosses within the state? California is well known throughout the world for its vascular flora, a flora influenced and evolved in relation to a

Mediterranean climate. Only five regions in the world have such a climatic pattern of cool wet winters followed by long hot and dry summers. The Mediterranean climate is the defining factor in explaining the species rich moss flora in California as well.

Then why do plant enthusiasts and professional botanists generally know so little about the mosses?

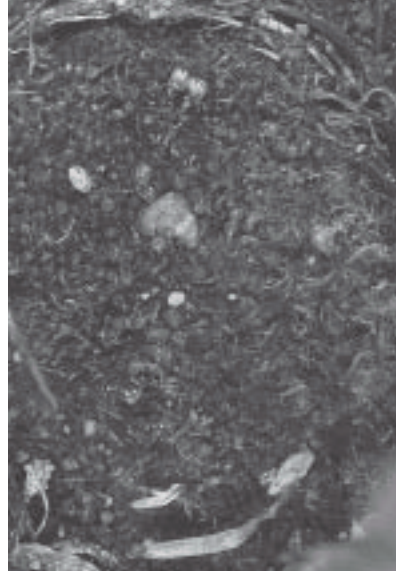
The best answer seems to be that mosses are just the wrong size and have little or no recognized economic value when compared to the flowering plants. Our smallest moss in California is probably *Ephemerum serratum* that forms a green filamentous growth on soil after the winter rains. The capsules of *Ephemerum* are around 0.25 millimeter in diameter. The other size extreme

is found in the genus *Fontinalis*, the water mosses, with plants up to one meter in length.

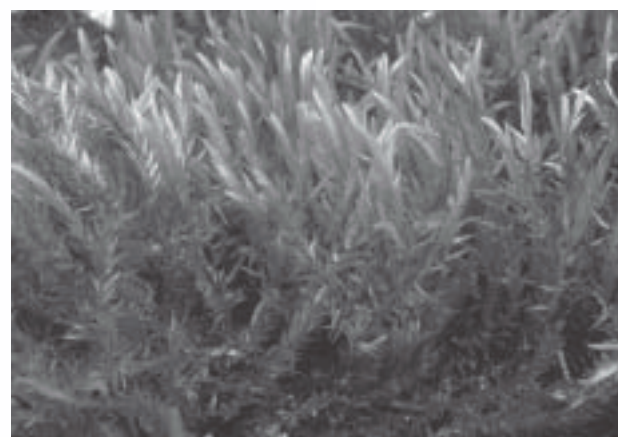
Mosses are perceived to be hard to identify, have no showy features like flowers, and are just overlooked by many of us. But upon closer observation of our environment, mosses are actually all around us if we take a moment and focus our attention at a different scale. Viewed through a hand lens or microscope, mosses are simply stunning [For an introductory article to this group, see *Fremontia* 26(2): 3–8, 1998, summarized on page 39 of this issue]. Mosses are no more difficult to learn and identify than vascular plants once some basic new terminology and microscope techniques are learned.

The major difference between mosses and vascular plants is that identifying most mosses to the species level generally will require greater magnification than can be obtained with a hand lens alone. Another reason why the mosses appear to be overlooked seems to be that botanists have placed an inordinate amount of value on being *vascular* at the expense of the rest of the plant kingdom. The result of this is that all of the plants and plant-like organisms without vascular tissue are often simply lumped in botany textbooks as non-vascular plants, or *cryptogams*.

We now recognize and acknowledge that mosses actually play a key role in ecosystem function, especially how they regulate the release of water and assist in protecting soil from erosion. Mosses can also tell us much about climate change. This is why the California Native Plant Society (CNPS) and botanists affiliated with land management agencies are looking at the mosses in a new conservation light. To learn more about mosses from a non-technical approach, I highly recommend the recently published book *Gathering Moss, a Natural and Cultural History of the Mosses* by Robin Kimmerer. [See review on page 41.]



Ephemenum serratum (above left) is perhaps the smallest moss in the state of California, with capsules smaller than a pinhead, and is seen only during the winter months in western North America. It is found on soil. Photograph by J. Game. • *Fontinalis gigantea* (above right), commonly called the water moss. Plants are generally found submerged in streams and rivers, and can reach one meter in length.



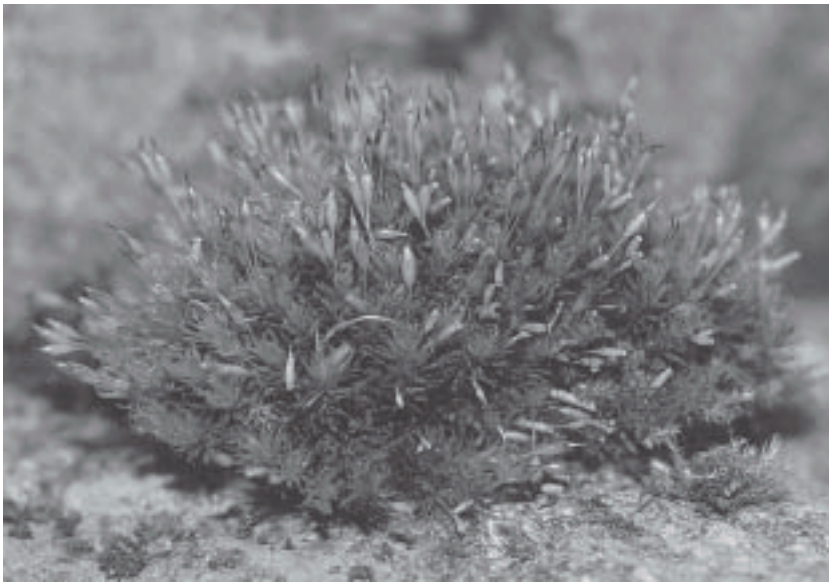
Mosses can grow on surfaces that are generally not available to vascular plants. Mosses are also extremely important as pioneering species as they can cover bare exposed soil caused by fire, landslides, or other perturbations. Even in urban centers, mosses can grow on the sides of buildings, on concrete retaining walls, and even asphalt walkways!

Mosses use a different strategy to regulate water loss than do vascular plants. Since they lack roots, they are not restricted to growing on soil. Many mosses are quite

content to grow on rock surfaces, such as members of the genus *Grimmia* with over 30 of the 75 species world-wide residing in California. *Grimmia* species can be found in every county of the state. Other mosses prefer tree bark, and as a general rule, favor hardwood trees over conifers. Bark characteristics like chemical composition, texture, and water-holding capacity are important in moss colonization of this particular habitat. Mosses occurring as epiphytes on tree bark and branches do not adversely affect the trees. In fact, mosses have

Dendroalsia abietana (when dry, below left), a species endemic to western North America, is a large moss, and especially common in the foothill woodland. When dry, the stems curl, similar to a fern frond or the head of a violin. • *Dendroalsia abietana* (when moist, below right) with capsules arising from the underside of the branches. Photographs by J. Shevock.





Ptychomitrium gardneri, an acrocarpous moss, found on rock. This is one of the few mosses with several sporophytes arising from a single sexual bud (perichaetium). Photograph by J. Shevock.

exploited just about every ecosystem in California from sea level to the summit of Mt. Whitney, from areas receiving barely an inch of water a year in parts of Death Valley to the temperate rain forests dominated by coast redwoods.

Of course the lack of both identification field guides or an illustrated moss flora for California has not made it easy for plant conservationists, enthusiasts, or professional botanists to learn about the mosses. However, plans are underway to provide such publications for our state. Currently one has to use a variety of regional moss floras in the United States to aid in moss identifications. Lawton (1971) and Flowers (1973) are the two most important moss floras available for California botanists. Dan Norris and this author have a catalogue of California mosses and a key to species ready for publication in *Madroño* that is due to be published in early 2004.

HISTORY OF MOSS COLLECTING IN CALIFORNIA

Many of the great botanical explorers of the 1800s in California were also involved in the collection

of mosses. The botanists Bolander, Brewer, Bigelow, and Coville have all contributed to this effort. In fact, Bolander was the principal collector of mosses during the 1860s, and many mosses new to science were subsequently named for him to commemorate his efforts. In the 1900s, other botanists collected mosses in California, too. Leo Koch and Fay MacFadden were the two prominent bryologists who added many moss collections to herbaria in the 1950s. MacFadden was on staff at Fullerton College, while Koch taught at Bakersfield College, Tulane University, and then at Illinois. In 1950 Koch published his list of California mosses in *Leaflets of Western Botany*, just after completing his PhD on the distribution of California mosses while at the University of Michigan.

Other nationally known bryologists during this era came out of Stanford. William Campbell Steere spent much of his professional career at the New York Botanical Garden, and Wilfred Schofield trained many bryologists while teaching at the University of British Columbia, Vancouver. Wilf's *Introduction to Bryology* textbook has recently been reprinted in a paperback edition (available at www.blackburnpress.com) and will be of

considerable interest to those wanting to learn more about this fascinating group of plants. In addition, another great book to begin a study of bryophytes is *Structural Diversity of Bryophytes* by the late Howard Crum. It can be ordered from the herbarium at the University of Michigan, Ann Arbor.

During the past 30 years or so the indefatigable bryophyte collector Dan Norris has nearly doubled the number of mosses recorded from the state since Koch's list. Dan's collections, numbering over 106,000, come from all corners of the globe and are permanently housed at the University of California, Berkeley. Probably many CNPS readers are not aware that prominent botanists such as Alice Eastwood, John Thomas Howell, Willis Linn Jepson, Philip Munz,

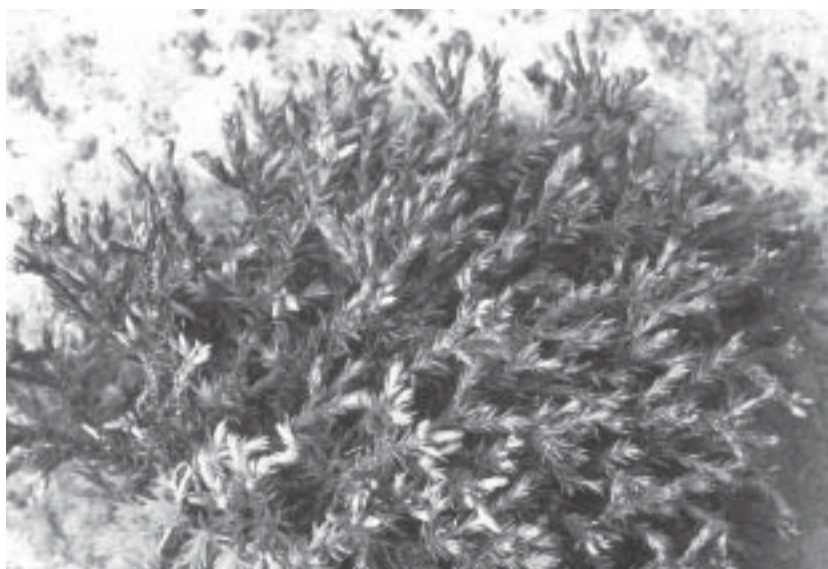
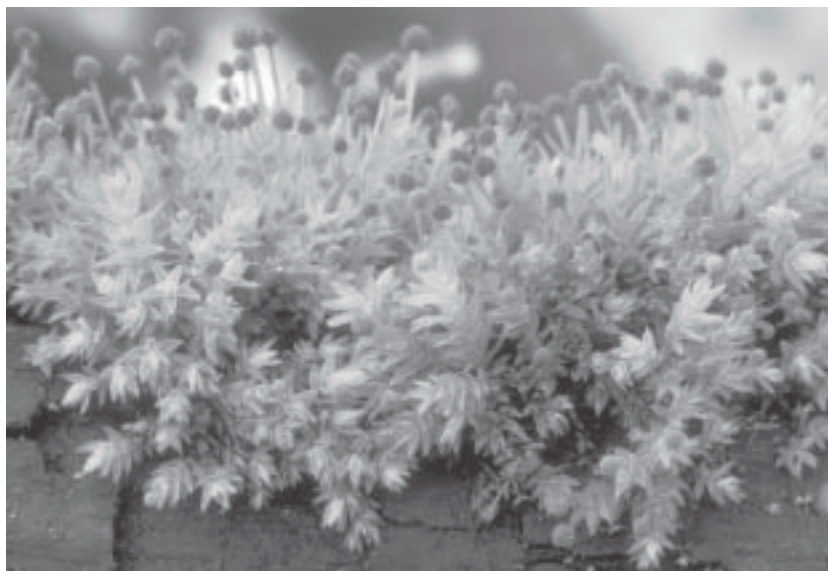
Meesia triquetra (below top), a relatively rare moss in California, found in Sierran fens. Photograph by J. Shevock. • Close-up of *Meesia triquetra* (below bottom), showing the three-ranked leaves, as the specific epithet implies. Photograph by J. Game.

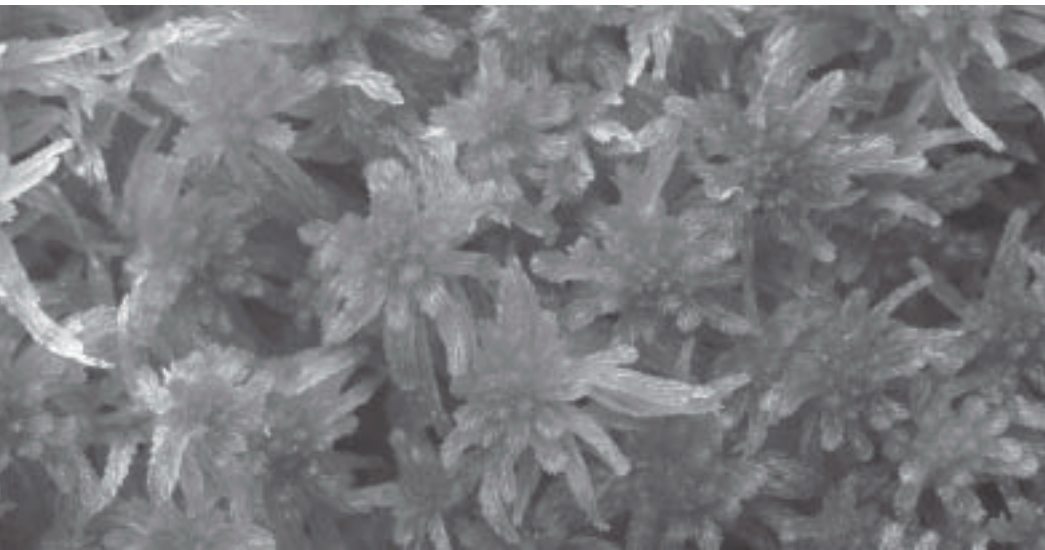
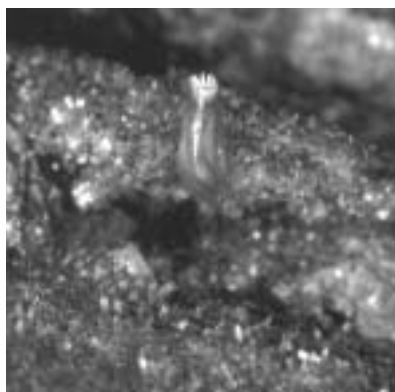


Peter Raven, Ledyard Stebbins, and Louis C. Wheeler collected mosses among their flowering plant work. However, their moss collections were generally few in number. Besides these prominent botanists, several moss floras at either county level or other administrative units were developed as part of master's theses at the state universities at Humboldt, Pomona, and San Francisco during the 1970s and early 1980s.

Amateurs and botanists working within the land management agencies are primarily responsible for the current interest in the study of California bryophytes. Rarity and conservation of bryophytes are now being included as components of large landscape management strategies to provide for biodiversity at various scales in both the Pacific Northwest and in the Sierra Nevada. The Northwest Forest Plan, a major Environmental Impact Statement planning document established in the 1990s within the species range of the northern spotted owl, specifically requires surveys for cryptogams thought to be rare and restricted to old growth forests. These survey requirements facilitated a need for botanists to expand their scope of knowledge to include the identification of and survey protocols for bryophytes as well as other cryptogams.

Top to bottom: *Andreaea rupestris*. Members of this genus are commonly called the granite mosses, and are restricted to acidic rock types. The capsules on *Andreaea* are unique: note the four splits on the burgundy-colored capsule. In the field, the whole plants are usually about the size of a human thumbnail. • *Aulacomium androgynum* is a common species on logs and rotting wood. Note the spherical gemmae which are asexual reproductive structures, that are, simply speaking, a whorl of modified moss leaves. • *Schistidium rivulare* always occurs on rock, usually on seasonally wet areas such as boulders along a stream, or rocks of intermittent streamlets. The peristome teeth of the capsules are bright red to orange.





Clockwise from top left: *Hylocomium splendens*, called the stair-step moss. Although abundant as a forest floor covering in North America, it is rare in California, restricted to the California-Oregon border. Photograph by J. Shevock. • *Buxbaumia piperi*, a species seen only when sporophytes are present. *Buxbaumia* is generally found on logs, and occurs in the northwest corner of California. Note the extension of the peristome teeth. Photograph by J. Game. • *Racomitrium varium*, commonly found on coastal rocks. The whitish tips (hyaline awns) of the leaves give this moss a frosted appearance when dry. Photograph by J. Game. • *Sphagnum capillifolium*. This *Sphagnum* species, although rare in California, is very distinctive due its reddish-tinged hue.

MOSS FLORISTICS

While California lacks an illustrated moss flora, moss floras and checklists have been produced for the state going back to the 1860s. Leo Lesquereux presented the first paper on California mosses to the American Philosophical Society in 1863, and in 1868 the California Academy of Sciences published his *Mosses From the Pacific Coast of North America*. Mosses documented from California were prominently referenced in that work. Again, it was the moss specimens acquired by Bolander that contributed most to this undertaking.

In 1880, the second volume of the *Botany of California* edited by Sereno Watson was published, and it now included the mosses. This was the first flora to address all of the mosses recorded or presumed to occur in California at that time. This moss flora documented 181 mosses for California. By the time of Koch (1950) the number of mosses documented for California had nearly doubled to 317. A new catalogue of California mosses referenced earlier by Dan Norris and this author will nearly double the number of mosses documented for California since the Koch publication.

While mosses have been recorded for each of the 58 counties in California, some portions of the state have been more systematically sampled. In part, this reflects the location of educational institutions where bryology was taught in the past. The coast redwood forest region and adjacent coastal environments from Santa Cruz County north through Del Norte County have been fairly well sampled when compared to other regions of the state. Moss catalogues, checklists, or floras have either been developed or are in preparation for Del Norte, Lake, Marin, San Francisco, and Santa Cruz counties. The master theses produced at Cal Poly Pomona in the 1970s focused on

other types of landscape units such as mountain ranges or wilderness areas within southern California.

But with the demise of many field-oriented university biology programs in the 1990s, all of the campuses that once taught bryology in California have ceased to offer such training and education. It is through the efforts of Dan Norris as well as the Jepson Workshop Series [see page 40] that current taxonomic training in bryology is being provided, much of this training directed to expanding the skills of amateur and professional botanists, especially those employed with land management institutions.

MOSS GEOGRAPHY

Much has been written about the "California Floristic Province," an area not confined to the state boundary but excluding the Great Basin and Desert regions. The California Floristic Province extends northward into Southern Oregon near the Medford and Grants Pass region, and southward to the northern portion of Baja California Norte, Mexico. As already noted, winter precipitation is a key feature of a Mediterranean climate, and the rainfall increases northward and westward across the California Floristic Province.

Beyond the California Floristic Province, the eastern portion of California is influenced by the Great Basin Floristic Province dominated by sagebrush and pinyon pine-juniper woodlands that are well represented in Modoc and Mono counties. This last region includes the Colorado and Mojave deserts, and is dominated by creosote bush scrub in portions of Inyo, Imperial, Riverside, and San Bernardino counties. Therefore, it is fairly easy to describe the pattern of moss distributions in the state by reviewing the annual amount of precipitation each area receives.

In all of California's deserts rainfall is considerably reduced, and desiccation tolerance of mosses becomes a more important factor, along with growth form, in understanding species distribution patterns. Mosses in the families Pottiaceae and Grimmiaceae, with dense cushion growth forms (acrocarpous mosses), are dominant in arid environments, whereas mosses that have a matted, prostrate and highly branched growth form (pleurocarpous mosses) are indeed uncommon in the deserts.

Some of the desert mosses occurring in California also occur in other desert regions around the world. In many cases, it is the same species, or a sister species occupying the same basic ecological niche. As one would expect, there are fewer mosses in the dry interior of the state than in the coastal counties. [See articles in this issue by Lloyd Stark and Daniel Norris for more details.]

Climate and precipitation are the primary factors influencing species distributions. For mosses, the recurring interval pattern between cell saturation and desiccation sets the ecological tolerances for many moss species. Once cells are saturated, mosses have no ability to store additional water. Some mosses need to be wet or moist most of the year, such as species in springs and meadows or along rivers and creeks where they are seasonally submerged during peak flows.

Secondary factors influencing species distributions include substrate availability and elevation. Mosses occur in California from sea level to over 14,000 feet. Some species are relatively common such as *Bryum argenteum* and *Funaria hygrometrica* which have very wide habitat parameters and can be located throughout California. Others, however, are very specific to micro-environments. Some mosses prefer particular rock chemistry, such as acid rocks like granitics,

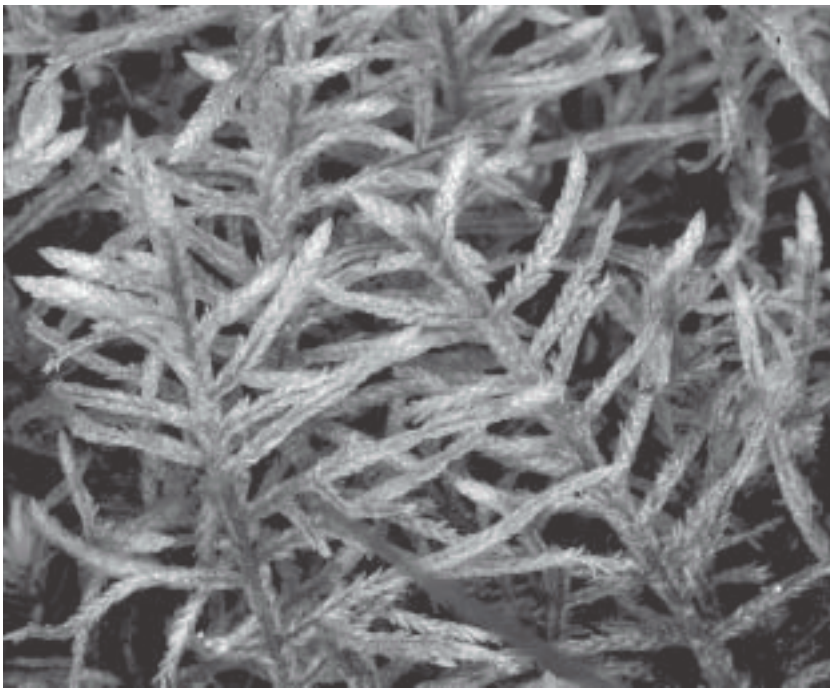
while other species prefer a higher pH like carbonate rock types including marbles and limestones.

Perhaps the mosses most restricted by substrate specificity are the "copper mosses." Both *Mielichhoferia elongata* and *Schizymenium shevockii* are restricted to rock types with high concentrations of metals like copper and are primarily located within the foothill woodland areas. *Scopelophila cataractae* in California has only been collected once in the Copperopolis area in Calaveras County. *Pseudoleskeella serpentinensis*, as the species name indicates, is restricted to serpentine areas in northern California.

Other mosses like to occur along rocky intermittent streamlets and rock slabs with little competition. Mosses preferring this type of habitat include *Didymodon norrisii* and *Schistidium* spp. Some mosses are nearly exclusively aquatic such as members of the genera *Fontinalis*, *Hygrohypnum*, and *Scouleria*, exposed only during low flows of unpolluted rivers and streams. Although there are no marine mosses, some species like *Schistidium maritimum* can tolerate salt spray. *Schistidium maritimum* occurs from Mendocino County northward. Only a handful of mosses can adapt to alkaline soils that contain a high accumulation of salts.

Within the California Floristic Province, the distribution pattern of many mosses follows a general pattern that is observed in the flowering plants. Common mosses in the coastal northwest portion of the state become increasingly uncommon southward, making their southern limit in the northern Sierra. Many mosses of the coastal counties such as *Alsia californica*, *Bryolawtonia vancouverensis*, and *Triquetrella californica* are not located inland, just as many of the mosses located in the alpine zone of the Sierra Nevada are not found elsewhere in the state.

Two regions of the state are



Schistostega pennata (top), commonly called the goblin moss. While not yet found in California, this very small (less than 1 cm) but distinctive moss should be found in areas with windthrow (exposed rootballs) and in openings of rock recesses, such as a cave. The nearest location is in southwestern Oregon. • *Pleurozium schreberi* (bottom), commonly called red-stem, is one of the most common feather mosses (i.e., pleurocarpous mosses) of North America. However it is yet to be found in northern California, where it should occur.

noteworthy for the amount of moss biomass occurring in the ecosystem. The first is the area dominated by the coast redwood forests. Epiphytic masses of *Isothecium myosuroides* and liverworts drape from the branches of trees, forming a tapestry of pastel greens while the forest floor is carpeted with mosses. The second area where moss cover is abundant is along the foothills of

the Sierra Nevada between the blue oak and black oak zone, especially along the river canyons. Here many species of mosses carpet tree trunks and boulders, such as *Antitrichia californica*, *Dendroalsia abietina*, and *Homalothecium* spp. In both cases, these areas are basically snow-free although snows may linger for a few days after major storms. Growth can occur once plants are hydrated

after the first rains in the fall and can continue to grow until the last rains in May.

The moss flora of California is also interesting when compared with the moss floras of adjacent states. Only about 50% of the mosses recorded for Arizona also occur in California. As with the flowering plants, water availability and climate play a key role in species distributions. The distribution of many moss species that occur in Arizona but not in California can be attributed to the availability of summer rain. In California, mosses are basically dormant in the summer, yet in much of Arizona, growth can occur in the summer due to that state's monsoon rainy season. Because of this climatic feature, the moss flora of Arizona has greater affinities with Mexico and the eastern United States than it has with neighboring California. For the most part, only the mosses of the Mojave and Colorado deserts have distributions which overlap both states.

The state of Nevada is less known bryologically, but it has many mosses in the high mountain ranges that have greater affinities to the moss flora of the Rocky Mountains. In the Great Basin Floristic Province, winter growth is limited due to snow, and the region does receive some summer precipitation and this in part accounts for these differences. Even Oregon, once beyond the northernmost section of the California Floristic Province, has a different moss flora. There are at least 70 species of mosses in Oregon which have not been documented to occur in California. These species are more aligned to taxa found in British Columbia and Alaska, and most are generally pleurocarpous mosses. Several of the large and dominant mosses on the forest floor in much of western North America such as *Pleurozium schreberi* have not been found in California. *Hylacomium splendens*, perhaps the most common pleurocarpous

moss species in North America, has only been recorded three times in California, and then only along the Oregon border.

Distributions of large moss genera are a fascinating study here in California too. The genus *Racomitrium* and *Sphagnum* offer two great examples on species distribution patterns. Mosses in the genus *Racomitrium*, with nearly 100 species worldwide, generally inhabit rocky substrates. This genus is well represented in North America. With 18 species of *Racomitrium* for California, we see a rapid decrease in the number of species as one leaves the northwest corner of California and the northern Sierra. By the time one arrives at the southern Sierra, over half of the *Racomitrium* species have dropped out. This genus is totally absent from mountain ranges in the Mojave Desert and is rare in southern California.

Peat mosses in the genus *Sphagnum* offer a different distribution pattern in California. There are about 200 species of *Sphagnum* in the world and they are common in higher latitudes, especially in the Northern Hemisphere. The 23 species of *Sphagnum* in California are restricted to bogs or perennially wet meadows and fens and are distributed in two distinct patterns. Species of *Sphagnum* from the first group are coastal, found along lagoons or in areas with poor water drainage among the coast redwood belt in northeast California, with the greatest species diversity occurring at the pygmy forest region near Fort Bragg in Mendocino County.

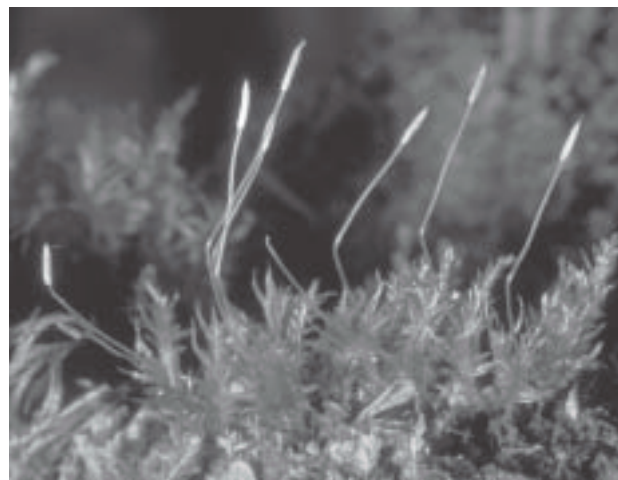
Sphagnum species from the other group are montane and are concentrated in the Sierra Nevada in meadows, fens, and lake shore habitats, from the lodgepole pine forests up to the alpine zone, generally in association with blueberry (*Vaccinium*), labrador tea (*Ledum*), *Kalmia*, and sundew (*Drosera*). By the time one gets to Tulare County, only a handful of *Sphagnum* species re-

main, and no *Sphagnum* have been documented from any of the mountain ranges of southern California. Perhaps the most remarkable station for *Sphagnum* in California is restricted to a small wet meadow surrounded by a pinyon pine woodland near Bodie, Mono County. Clearly this is a relictual occurrence, a holdover from the Pleistocene with no suitable habitat for miles in all directions. The nearest occurrence of a *Sphagnum* species to this site is nearly 4,000 feet higher up along the Sierran crest.

Because mosses generally have much larger geographical distributions than vascular plants, the number of mosses endemic to California is therefore reduced. What we have instead is a distribution pattern of widely-spaced disjunct occurrences. Many mosses are recorded from California from only five to ten occurrences. In some cases, this is merely a reflection of the number of herbarium specimens available for study and the collecting habits of botanists, yet other mosses are indeed very rare in California. Some mosses in California must now be viewed as relictual species—holdovers from a different cli-

matic era. *Atractylolcarpus flagellaceus* and *Campylopodia stenocarpa* are two such species that have recently been documented for California and

Tetraphis geniculata (below top), is named for the bent stalk (seta) of the sporophyte. Although reported for California, a specimen of this species has not been confirmed. Its sister species, *T. pellucida*, is fairly common in northwest California, especially in the northwest's redwood forest. This is the only moss in California with four peristome teeth. • *Tayloria* sp. (below bottom) is a member of the dung moss family (Splachnaceae). Currently this family has not been found in California, even though *Tayloria serrata* occurs as close as southern Oregon (near Crater Lake).





New species for California are being discovered all the time. Pictured here is Jim Shevock documenting the first California occurrence of *Helodium blandowii* from Kings Canyon National Park. Photograph by S. Haultain. • *Helodium blandowii* is a large pleurocarpous moss restricted in California to fen habitats. Photograph by J. Shevock.

are distant disjuncts from central Mexico.

The greatest threat to mosses in California is not species extinction, but rather, the loss of unique and highly isolated occurrences. These isolated and small populations are considerably more vulnerable to lo-

calized extirpations by alteration of habitat or loss of their specific micro-environments. In many cases, natural recolonization from such losses would be extremely unlikely because available spore or plant fragments are so far away. In nearly any study area for mosses in California, a suite of mosses will be "rare" for that location.

While California has nearly 600 mosses documented to date, they are not evenly distributed among the 58 counties in the state. Over 300 mosses have been recorded for the southern Sierra, and even our smallest county, San Francisco County, has a moss flora of over 130 species. Probably the county with the richest moss flora will turn out to be Siskiyou County, but a complete species list is not currently available. There are probably only about 100 mosses for the entire Mojave Desert, yet this is the least known area bryologically in California, so our knowledge of this portion of the state is bound to change once more bryophyte collections are made.

Therefore, the current picture of the mosses in California is one of a highly species-rich flora with numerous species yet to be documented. In addition, species of mosses new to science are also being discovered in the state.

CNPS members have a tradition of adding distribution records for our flora. For the first time, we have bryophytes listed in the CNPS *Inventory of Rare and Endangered Plants of California*. Much inventory and fieldwork remains in California. Current bryophyte workers like Colin Dillingham, Lawrence Janeway, Ken Kellman, Eve Laeger, Ronald Robertson, and David Toren are adding new species to the state and filling in the distribution range for many species. There are also opportunities for plant enthusiasts to learn more from either attending a Jepson Herbarium Workshop course on bryophytes or

the "SO BE FREE" bryology forays held annually during spring break (see "Workshops" on page 40). SO BE FREE is an ongoing series of West Coast forays organized by Brent Mishler at the University of California, Berkeley. For more details and a review of the past eight forays, visit the web at <http://ucjeps.berb.berkeley.edu/bryolab/trips/sobefree.html>.

It is hoped that many more CNPS members will find the world of bryophytes rewarding and stimulating. There is a whole new world of plant diversity just waiting for you to explore!

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Marchantia polymorpha is a common thallose liverwort of springs, seeps, creekbanks, and other wet areas. Pictured here with umbrella-like male branches bearing sperm-producing organs.

THE ROLE OF THE AMATEUR IN BRYOLOGY: TALES OF AN AMATEUR BRYOLOGIST

by *Kenneth Kellman*

I am an amateur botanist. Like most members of the California Native Plant Society (CNPS), I enjoy hiking in a local meadow or along a creek, identifying the flowers and shrubs that I find along the way.

Each spring I run across old botanical friends, struggle to remember the names of the less common plants, and regularly find plants that I have never seen before. My process for identification involves keys and drawings in several references. Often enough, I have to call my mentor and describe the plant to him. Usually he makes a suggestion, or asks a question that points me in the right direction, and I continue my search. After I feel comfortable with an identification of a plant, I make a note in my local flora, or in my *Jepson Manual*, or perhaps add the name to a list I am

working on. I have been going on like this for perhaps 25 years, and I have never thought that I would find anything that someone else did not know about . . . until I started studying bryophytes.

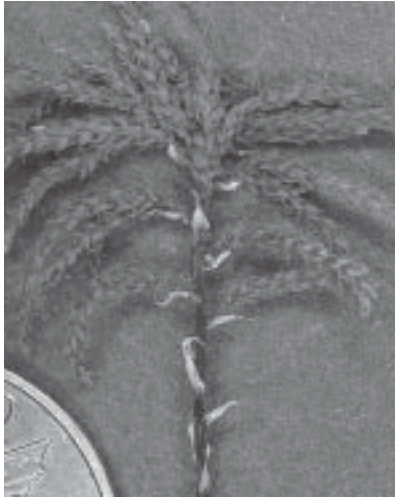
By trade I am a commercial air conditioning mechanic, and my formal training in botany has been minimal, consisting of one class in plant systematics and one in dendrology at the University of New Hampshire in the early 1970s. I have no degrees nor have I ever been close to getting one. The rest of my knowledge has come from a persistent curiosity, and the good will of more knowledgeable friends.

Sometime in 1992, I took on a project to compile a list of the plants in a local county park where I was a docent. It was a small park of 300 acres in Santa Cruz County, filled with microhabitats, and my list grew

to over 400 species. In an effort to make the list as complete as possible, I tried to reach every corner of the park. During one of those hikes, I came upon a colony of leathery looking plants growing in the middle of a sandy creek bottom. It

Kindbergia oregana, one of our most common feather mosses. It is especially prevalent on moist logs and soil banks on forest edges. Photograph by J. Shevock.





Overall aspect of *Leucolepis acanthoneura* (top), a moss found along moist stream-sides and shaded forest areas. • Individual plant of *Leucolepis acanthoneura* (bottom) showing “palm-tree-like” growth form. The bracts on the stem are white; *leucolepis* means “white scale.” Photographs by J. Game.

had spectacular little umbrellas springing up from the thallus, and little fringed cups, filled with “eggs.”

I had a vague memory from my systematics class that this was a liverwort, but I had no idea what species it was. I went home and started looking in my books, but none of my references even mentioned liverworts. I called my mentor, and asked him, but this time he was only able to give me someone’s name to call. Eventually I was referred to Bill Doyle at the University of California, Santa Cruz. I was delighted when he offered to meet me at the park and look at these liverworts.

I thought I would only show him this one colony, but inside of two hours, he had not only identified my plant (*Marchantia polymorpha* L.), but had also shown me ten other species of liverworts and hornworts! I had never heard of leafy liverworts, and had no idea that they were abundant on the bark of local rocks and trees. I thought I had been looking very closely at this park, yet I had been missing an entire suite of species and their habitat. That was the day I was bitten by the bryology bug. It was a dream come true for any naturalist . . . a whole new world to explore.

Bill very graciously taught me how to collect and then helped me identify my collections. He gave me keys, and allowed me to copy descriptions from antique books that he owned. He has continued to help me to this day.

Soon I bought my own microscopes. While my work with vascular plants continued, I was now recognizing the more common species of liverworts and hornworts on my hikes. After working on these plants for about nine months, I enrolled in the Jepson Herbarium weekend workshop on bryophytes. Two very important things happened as a result of that seminar. First, I was introduced to the study of mosses. Until that time I had purposely ignored mosses while I concentrated on the liverworts. Second, I met Dan Norris, who was teaching the bryophyte workshop.

Dan provided us with glossaries, keys, and bibliographies to get us started, and he encouraged us to collect. I was off and running. Three months later, I brought him a box of perhaps 150 packets of mosses. He patiently went through them and gave me tentative identifications. But in that box was one moss that had never before been collected south of Humboldt County. It was on that day I realized that an amateur bryologist could make a “contribution to science.”

I knew that I did not possess some special attraction to rare mosses; I was just collecting everything that I found. I also learned that day that the distribution of mosses was poorly understood in this most populous state in the nation, and that I could help correct that.

So I continued collecting and identifying my collections, but Dan Norris had moved to Washington State and I lost his expert assistance. As a neophyte, I did not feel confident in my keying decisions, and without Dan’s confirmations and corrections I floundered for a while. Then in the spring of 1998, Jim Shevock wrote an article on bryophytes (*Fremontia* Volume 26(2):1-8). I contacted him and within six months or so, my “research” rose to a new level.

Jim wanted to cite my collections in a paper he was writing with Dan on the distribution of California mosses. I had been working on a list of Santa Cruz County bryophytes, but never thought it would go beyond that. Jim encouraged me to start housing my collections in an herbarium, and told me that my work was significant enough to publish in a scientific journal. Taking Jim’s suggestions to heart, I decided to write a “Catalog of the Mosses of Santa Cruz County,” and to submit it for publication.

Eventually, Dan returned from Washington, and he, Jim, and I met every couple of months to review my collections and work. I combed through the collections in the three Bay Area herbaria, noting all of the collections from Santa Cruz County. This review of existing collections pointed out exactly how little was known about bryophyte distribution here.

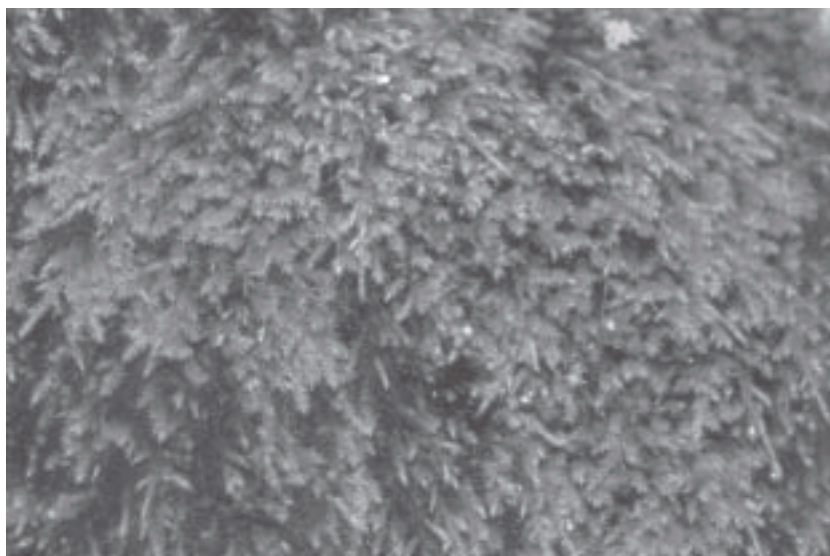
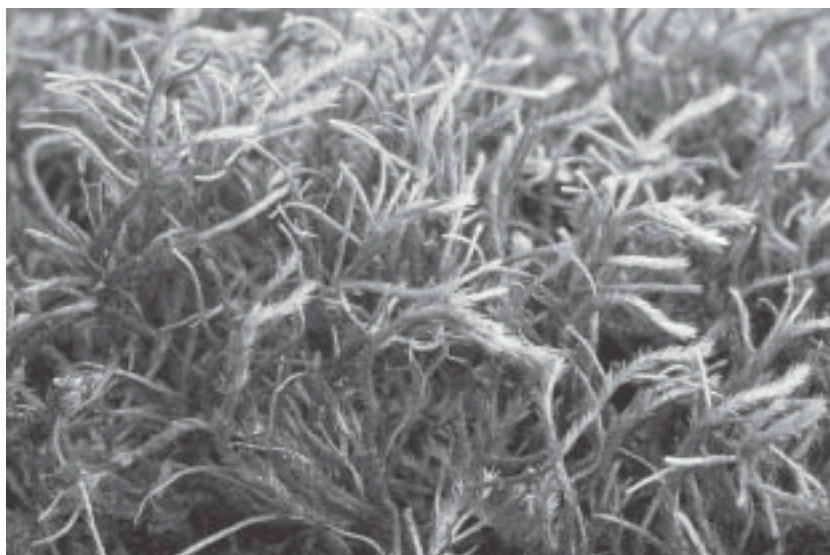
Of the approximately 190 species of mosses that I have documented in Santa Cruz County, well over half had never been collected from the county before. Fifteen of those have never even been col-

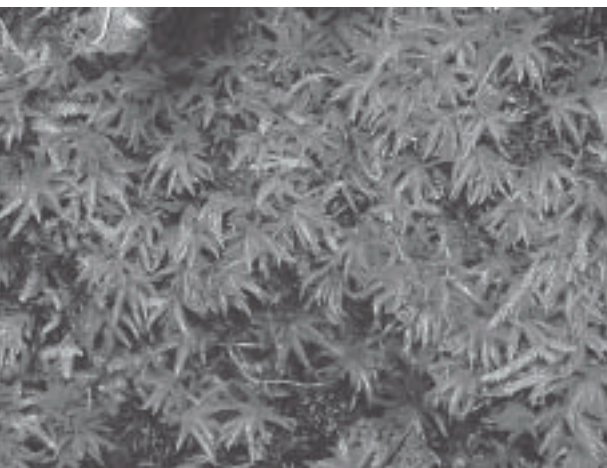
lected from the central coast of California. Seven of those 15 are still undescribed species, and local collections like mine add to the knowledge of range and morphological variation for each one. I still collect, and even after eight years, I am still finding new taxa to add to my list. My moss catalog has been published in *Madroño* (Volume 50:2), the journal of the California Botanical Society, and I am starting a formal catalog of the liverworts and hornworts of Santa Cruz County as well as starting collections in Monterey County for a bryophyte catalog there.

Collecting bryophytes is like a grand treasure hunt, and it is a great excuse to get outside and enjoy nature. Publishing a local catalog forced me to collect throughout the county, and so I have been to beautiful creeks and forests that I had never visited before. Another plus is that bryophytes (mosses in particular) grow everywhere—on dry rocks, in the water, on soil, on cement, even in the city—and they can be collected any time of the year.

They are very easy to collect and store. No pressing or mounting is allowed, much less required. Just put the plant into a packet, note the collection data, let it dry, and voila! This is nothing like the amount of work required for collecting a vascular plant. The packets are small enough that I can keep a hundred specimens in a bureau drawer. Since these plants desiccate in nature, a dry moss in a packet looks exactly like a dry moss on a rock, and because mosses preserve

Isothecium stoloniferum (top) is a common epiphytic moss in the temperate rainforests in northwest California. • *Antitrichia californica* (middle), a widespread species. Note the closely associated, concave leaves which give a wormlike (julaceous) appearance to the leafy plant. • *Pseudobraunia californica* (bottom), another julaceous moss. *Pseudobraunia* forms large bronze-hued mats on rocks. Photograph by J. Shevock.





Dicranum bowelli (top) is widespread in northwestern California, and is primarily found on forest litter. • *Atrichum selwynii* (bottom), common on mineral soils, is an acrocarpous moss readily recognized by its undulate leaves with prominent costa. Photograph by J. Shevock.

so beautifully, identification can be done the minute you get in from the field, or if that is inconvenient, in 25 years. All that is required is rehydration from a drop of warm water.

Studying bryophytes is not only exciting for the amateur, it is important. Most academicians have abandoned bryophyte floristics because it does not attract funding. Because of the discontinuous nature of bryophyte distribution (see Jim Shevock's article on page 12), bryologists aren't even sure what plants are rare in our state. It is difficult to accept that a group of plants this large can be so poorly

understood in the most populous state in the US, but it is true, and it will be true for some time to come. This provides the amateur naturalist with an opportunity to make a significant contribution to the existing body of botanical knowledge.

There are many opportunities for amateur bryologists to make a difference in our understanding of these plants. There is, of course, a floristic project like mine, which

Plagiomnium insignis has some of the largest leaves of any Californian moss. It is found on shaded and moist soil and humus along springs, streams, and waterlogged areas.



involves making a list of bryophytes in a park or even an entire county. Most of the counties in California represent giant holes in our knowledge, waiting for someone to make concentrated collections. Other county studies have revealed species new to California, and even species new to North America. Without extensive collection it is impossible to know what is rare and what is common. Creating a local catalog is an excellent way to learn bryophyte identification. If a catalog seems too ambitious a project, just making collections is a valuable contribution. Local herbaria are always hungry for properly identified, well-labeled specimens.

For those with a camera and a close-up lens, there is always a need for quality photodocumentation. Photographing bryophytes is notoriously difficult, and will become valuable as interest grows and field guides come into demand. Likewise, technical artists could draw bryophytes for articles describing new species, or for a small local flora.

Cataloging herbarium collections is an invaluable service that can be provided especially by those who enjoy working with computers. Very few herbaria in our nation are yet part of computer databases, so volunteers can make a huge difference here by entering data into computers. Once collections are part of computer databases, this wealth of information suddenly becomes accessible to people throughout the world via the Internet. A bryologist studying a particular taxon could then query a database and request loans from the herbarium, saving countless hours pouring over specimens.

Public education also offers the amateur additional opportunities to advance the field. Slide shows and hikes that focus on bryophytes are a great way of introducing people to these wonderful plants. Even if your knowledge is limited to recognizing the major bryological groups

and some of the basic bryophyte biology, people still love to see these tiny plants on a wildflower hike.

How do you get started? I heartily endorse attending the annual bryophyte weekend workshop sponsored by the Jepson Herbarium. This hands-on class provides a great foundation for your studies, and includes collection and dissection techniques, recognition of the various bryophyte groups, practice using keys, and an overview of bryophyte biology. (The next Jepson bryophyte workshop is February 21-22, 2004. For details see <http://ucjeps.berkeley.edu/jepwksbp.html>, or write to the Jepson Herbarium, University of California, 1001 Valley Life Sciences Building, #2465, Berkeley, CA, 94720-2465.)

Another source of good information and contacts is the bryophyte listserve on the Internet. To join, send an e-mail, with the single word "subscribe" in the body of the message to bryonet-l@mtu.edu. The annual bryophyte foray "SO BE FREE" sponsored by Brent Mishler's laboratory at UC Berkeley is a great event for amateurs to meet other bryologists of all skill levels. Information on the event is posted at <http://ucjeps.berkeley.edu/bryolab/trips/sobefree.html>.

As your interest and commitment grows, you will need access to microscopes and a good reference library. Used microscopes can be obtained from local microscope technicians for a reasonable price, and investing in a personal library is well worth the expense. Currently, there is no "*Jepson Manual*" for California bryophytes, so a number of floras from North America and beyond must be used for identification. I am the first to admit that this work involves a long learning curve, so finding yourself a mentor is almost imperative. But the bryologists I have met have proven to be a friendly and generous lot, and will be more than happy



Top photograph: Dan Norris (left) and Jim Shevock (right) during a Jepson workshop in the Sierra National Forest, near Minarets pack station. Photograph by S. Markos, courtesy of the Jepson Herbarium, UC Berkeley. • Bottom photograph: Dan Norris (left) and Jim Shevock (right) working in the University Herbarium bryophyte collection, UC Berkeley. Photograph by B. Ertter.

to help you if they sense a commitment to learn.

I encourage you to polish your hand lens, and then open your eyes to the tiny world that you have been walking by every day of your life.

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MOSES IN THE DESERT?

by Lloyd R. Stark

When I first came to the Mojave Desert as a student intern in botany, it was so hot and dry that I was amazed that plants, least of all mosses, could survive the heat and scarcity of rainfall. After all, mosses require a moist environment to grow and reproduce, and the Mojave Desert is the hottest and driest region on the continent. Nevertheless, my instructor in botany at Humboldt State University, Daniel Norris, had convinced me that mosses did indeed inhabit the desert, and he had

briefed me on what to look for based upon the northeastern California “high desert” region.

Many years passed before I took up a permanent residence in the Mojave, and at this point I had distanced myself from a study of mosses. Although I had spent some time in the Chihuahuan Desert of southern New Mexico, when I came out to the Mojave Desert of southern Nevada and California, I honestly did not expect to encounter much in the way of mosses in the lower elevation desert terrain. I re-

call very distinctly when the passion to study mosses returned. A short trip into a desert canyon near Lake Mead allowed me to survey the area for mosses, fully expecting to find very little in the way of these plants. After all, generations of bryologists had routinely avoided the desert with the preconceived notion that it represented a vast void harboring few if any species able to tolerate the heat, lack of water, wind, and general severity of weather.

Botanical collectors of flowering plants in the desert often restrict themselves to a few weeks of collecting in order to avoid the heat. After spending nearly 15 years in the eastern temperate forests where mosses and liverworts are abundant, and then relocating near Las Vegas, I can comment on this prevailing viewpoint of mosses being generally absent in deserts: it is utterly false. To my surprise, this short hike revealed several species of mosses, at which point my interest in these little plants was rekindled. So struck was I with this discovery that my career path actually changed at that moment, and I was drawn back into the field of bryology. This was about nine years ago, and I have never looked back. The mosses of the Mojave Desert have offered an outdoor laboratory heretofore untapped, and have yielded some of the most fascinating patterns of reproduction and survival among plants.

Now, strictly from the standpoint of diversity (the number of species in a given area), it is true that there are fewer species in the Mojave Desert than surrounding areas; Jim Shevock is estimating about 125 species as of this writing. While this number represents a small proportion of the estimated 600 species of mosses in California,

Typical Mojave Desert habitat for *Crossidium* species. A wash runs through the center of the photograph (covered with green vegetation), and *Crossidium* is found at the base of the small rocks on the north-facing side of this wash. Photograph by L. Stark.



the desert species are perhaps more interesting because: 1) several globally rare endemics occur in deserts, even a new liverwort awaiting description that will be named after the Mojave Desert; and 2) the species inhabiting the desert exhibit some amazing survival strategies of desiccation tolerance and reproduction found nowhere else in the world.

Although qualifying definitions of deserts vary widely in the literature, the boundary between desert and semidesert can be recognized as occurring below the 120–150 mm isohyet of annual precipitation. By this definition, only the western edge of North America's deserts conforms to a true desert, namely the Mojave and western Sonoran deserts (inclusive of the Colorado Desert of Southern California). Compared to other deserts of the world, North American deserts are not only small in area, but youthful in age. As judged by paleobotanical evidence using packrat middens, present floristic compositions extend only to circa 8,000 years ago. The boundary of the Mojave Desert can generally be said to follow the distribution of creosote bush (*Larrea tridentata*) and also the Joshua tree (*Yucca brevifolia*).

The desert biological crust of the Mojave Desert. Black patches on the soil surface are composed of mosses and lichens, with the dominant moss *Syntrichia caninervis*. Photograph by L. Stark.

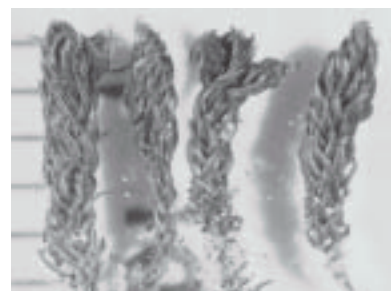


THE WAITING GAME

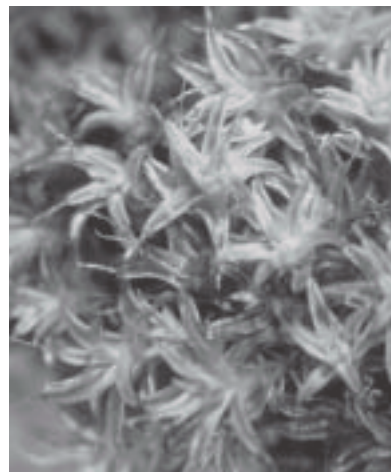
How are these rootless plants that have no water storage capacity able to survive the rigors of the desert, where rainfall is not only on the order of millimeters per year, but is more sporadic and unpredictable than any region on earth? Mosses have no roots, no water storage organs, few protective pigments to diffuse the sun's rays, and occupy only the surface of the substrate on which they grow. Therefore, they dry out as rapidly as the soil dries out, which can range from a few days following a winter rain, to a few hours following a summer rain. In the Mojave, most of the rainfall is during the cooler winter months, so herein lies a major irony insofar as desert mosses are concerned: they are shade-adapted plants that do best when temperatures are cool and moisture is readily available.

Optimal growth conditions for desert mosses surprised everyone. They prefer it to be 60–70°F under very dim light (full shade). I struggled for years trying to grow desert mosses in a growth chamber until an undergraduate student discovered the plants have to be shielded even from the direct light of a grow light! From April through November, mosses in the desert *tolerate* the heat and desiccation in a dormant state. During this period of blistering heat, the cells do not die, but remain physiologically alive yet totally inert (respiration is undetectable!).

Going nine months without water is a trick that not even the most heat tolerant Mojave Desert flowering plant can carry out. However, this feat is relatively easy for a desert moss, most species of which are able to tolerate several years of total desiccation and then spring to life when wetted. After eight years in dry storage in the dark (in an herbarium), one specimen, to our amazement, showed 100% viability among its stems, and we still do not

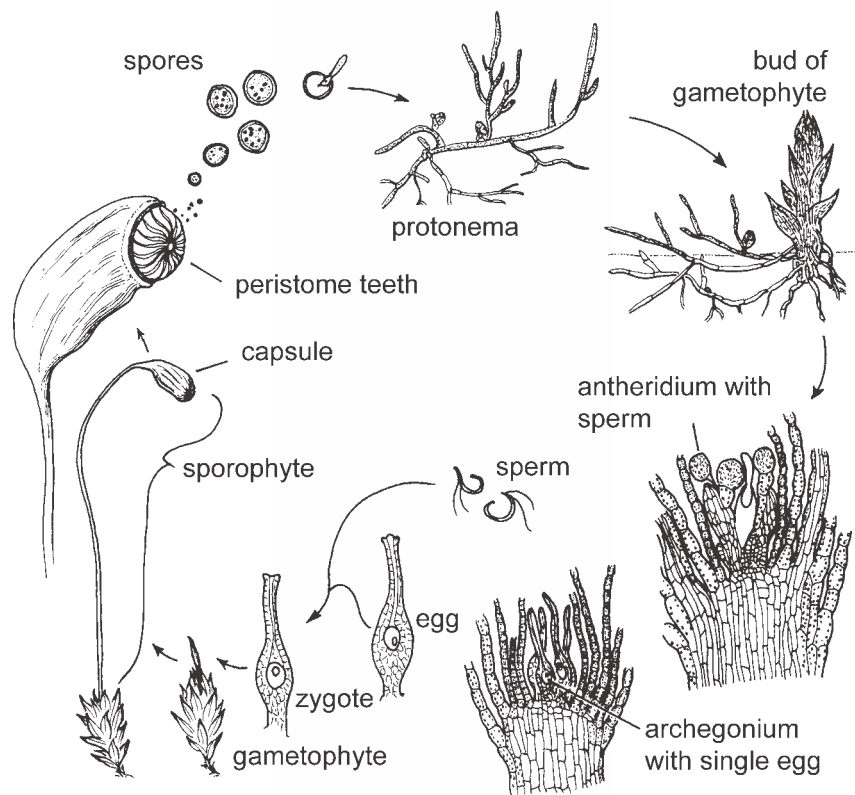


Four desiccated plants of *Pseudocrossidium crinitum* (top) from the Mojave Desert. Leaves of desert mosses often show a characteristic spiral twisting of the leaves about the stem. • A wetted patch of *Pseudocrossidium crinitum* (bottom) from the Mojave Desert. This hydrated condition is evident only a few days following a rain-storm. Photographs by L. Stark.



know just how long a desert moss can survive in a dried state. Desert mosses are photosynthetic opportunists: they capitalize on the window of opportunity, from about December to March, when a sufficiently hydrating winter rain occurs. Within hours of a rain they are carrying out positive net photosynthetic gain—making sugars.

Thus the life of a desert moss is really a waiting game, where the plants patiently await a winter storm that may only occur every few years. Recently I followed a few populations of the most desiccation-tolerant moss in the Mojave Desert, a species in the genus *Crossidium*, for a period of one year in order to determine the duration of the hydrated versus the dormant dry state.



Typical moss life cycle, showing diploid stages (zygote and sporophyte) and haploid stages (spores, protonema, gametophyte, and gametes). Illustration by L. Vorobik.

During this year (2001), the area around Las Vegas received slightly more (120 mm) than its normal annual rainfall (104 mm). These plants were fully hydrated for a total of 31 days in 2001, partially hydrated (in the process of drying down) for a total of 35 days, and entirely desiccated for the remaining 299 days. During one stretch these plants tolerated 147 consecutive days of desiccation. Fully wetting these plants required about 4 mm of precipitation, as rain.

The mosses, then, “wait” for a good winter rain, after which, due to the lower temperatures of winter, they can remain hydrated for several days. The first day of hydration is spent repairing their tissues from the damage of the wet/drying cycle of events (primarily membrane damage). From the second day onward, they can grow and reproduce. It is in their patterns of reproduction that many an interesting tale can be told. If a summer thunderstorm hits, it is very bad news to the mosses. Tem-

peratures following a summer storm may be 90–110°F, and the moss finds its metabolism accelerated and unbalanced, outside of its optimum range. Photosynthesis is difficult and substantial damage can occur that is unrepairable. Many plants and all reproductive structures can die in a matter of hours. Fortunately, summer thunderstorms are sporadic in the Southwest US, occurring about once per year.

BIZARRE REPRODUCTION IN THE DESERT

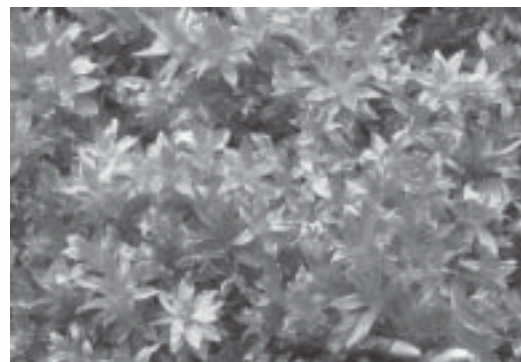
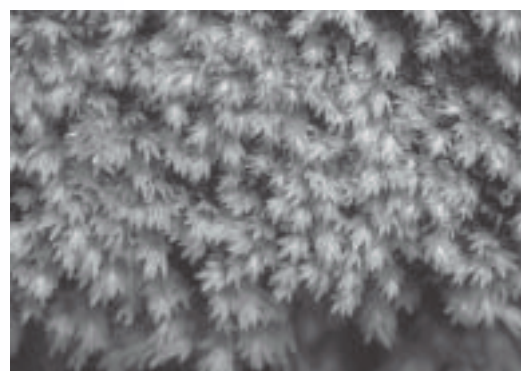
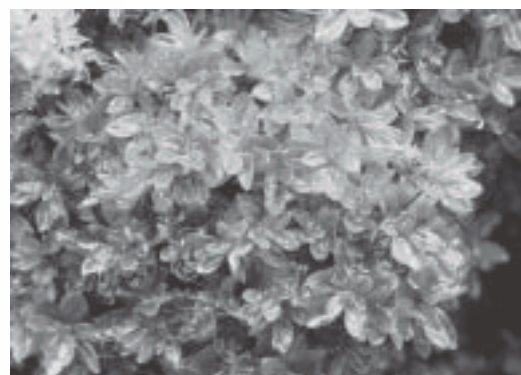
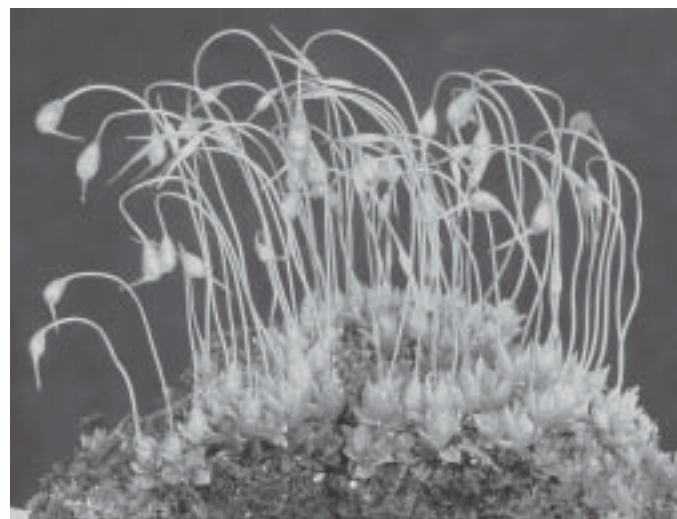
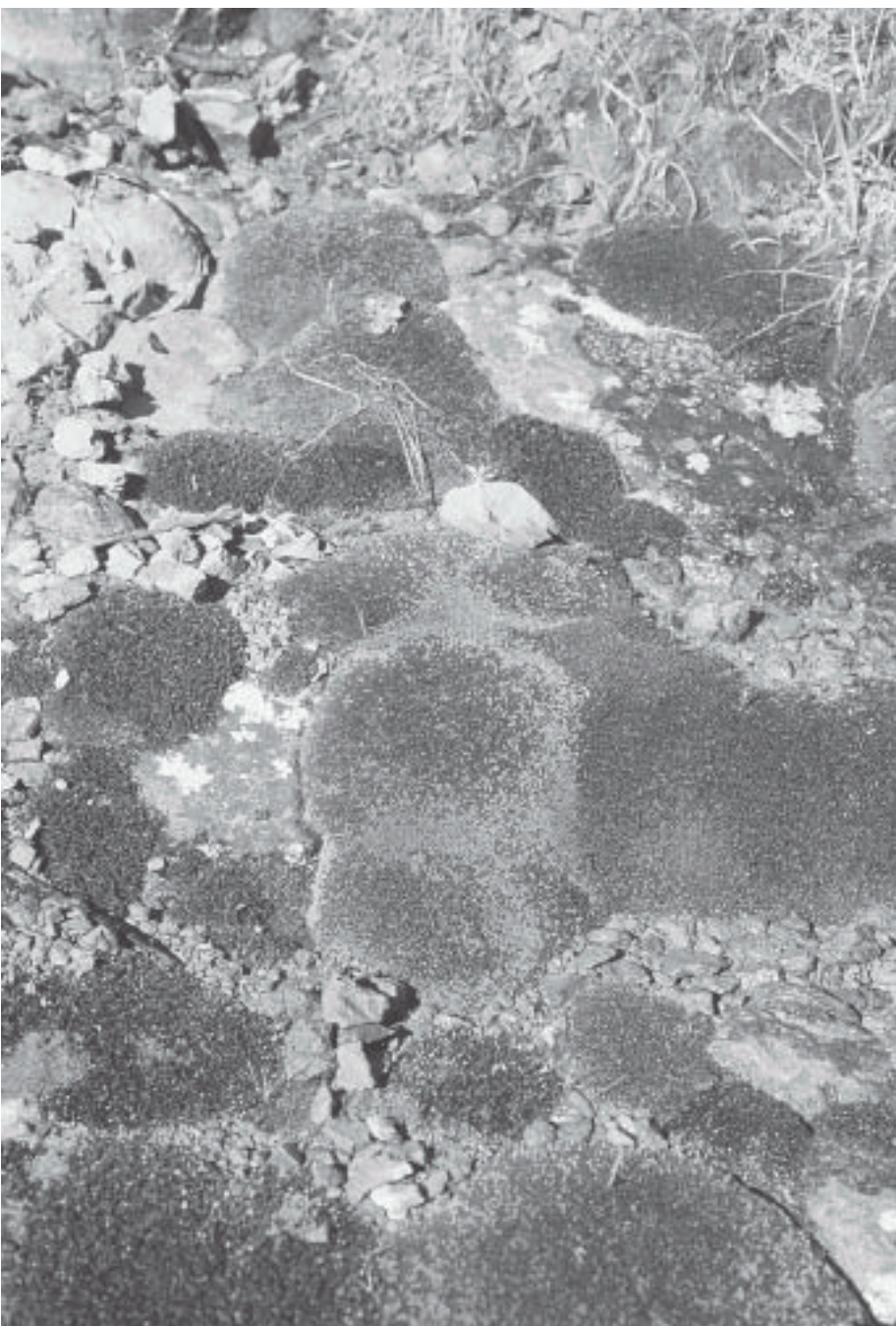
I was fortunate enough to be exposed to an unexplored frontier, to be the first one to really take a look at how desert mosses reproduce. It is an ongoing privilege that has consumed many pleasurable hours of my time. One thing that became very noticeable was that many desert mosses were bisexual, more than expected in true desert

habitats. About 80% of moss species are bisexual in true desert habitat, compared to an expectation of 40–50% of mosses at large. Bisexuality allows the male and female reproductive structures to be in close proximity, allowing self-fertilization to occur, and thus the plants reproduce sexually by producing large quantities of airborne spores.

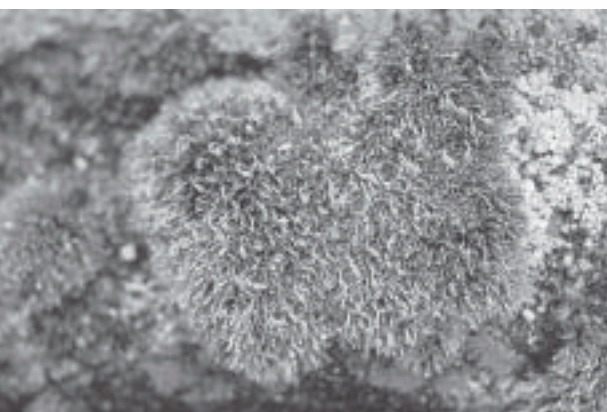
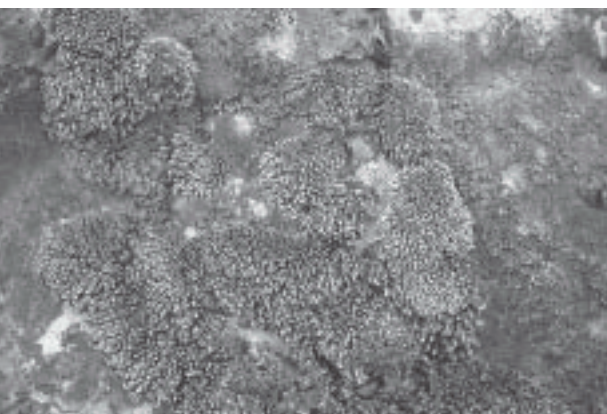
In mosses—as described by Daniel Norris in his article on page 5—sperm is transferred from male to female reproductive structures by droplets of rain. The sperm is carried to the egg in a rather haptenance manner, having no directed vectors of dispersal (unlike pollen, which can be transported effectively by insects and even wind). Therefore, for a dioecious species, in which the male and female sexes occur on separate plants, the male and female plants have to be immediately adjacent to one another (within a centimeter), which seldom occurs; thus the selective advantage of bisexuality.

The second most noticeable circumstance regarding reproduction in desert mosses is that in dioecious species the sex ratio is exceedingly skewed in favor of females. Further investigation revealed that this ratio represented the most biased sex ratio of any plant, flowering or otherwise. How biased you might ask? How about: on the order of one male for every 100 females, or even the total absence of the male, i.e., entirely female populations. There are even a handful of species in the American Southwest in which male plants are unknown to science. On the contrary, there are no male-only species in this region.

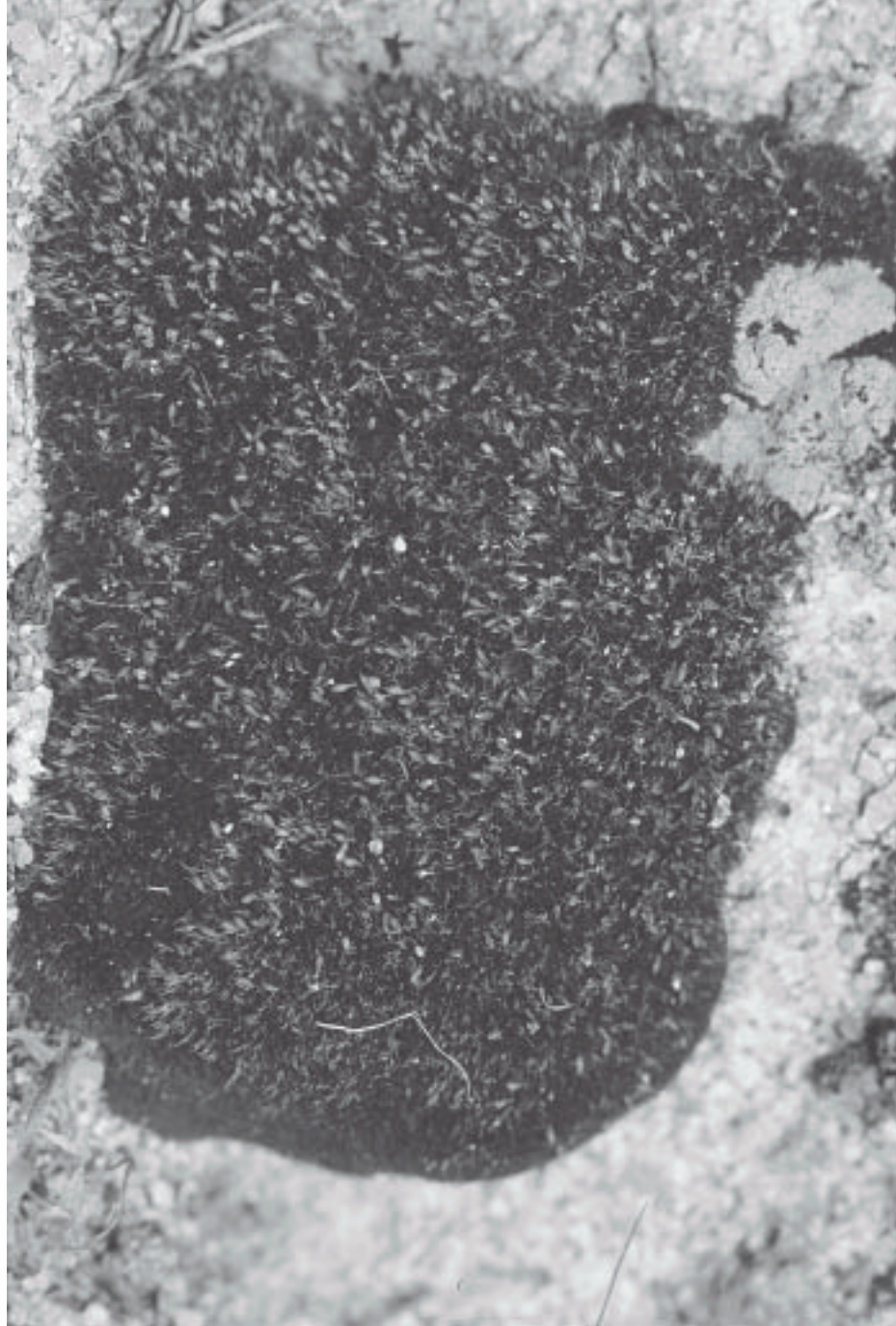
Finding such skewed sex ratios in desert mosses was most unusual, because the expected sex ratio is 1:1. Sex is chromosomally determined, with the male plant carrying a single y-chromosome, and the female plant carrying a single x-chromosome. Equal numbers of



Mosses of watercourses (clockwise from top left): *Didymodon brachyphyllus* is seen here in a watercourse. This species is a member of one of the more difficult genera of mosses. Here it intercepts water and sand brought down in this stream channel during occasional storms. Photograph by J. Shevock. • *Funaria hygrometrica*. This may be the moss most frequently used in physiological experiments. It is abundant throughout the world, but is especially abundant on the ash of old burn piles. • *Crumia latifolia* is seen here in another watercourse. It belongs to the same family as *Didymodon*. *Crumia* has thickened leaf margins that may resist tearing during floods. • *Fissidens bryoides*. *Fissidens* is a very large genus primarily found in tropical areas. The flattened leafy stems (as indicated by the leaf arrangement) may remind one of a leafy liverwort, but the presence of a midrib in the leaves defines it as a moss. This moss often grows in wet seeps. • *Bryum capillare* is one of our most widespread mosses in deserts and in mesic areas outside of desert regions. It is a member of the largest genus of mosses in the world. In deserts, it is found in seeps that have little or no salt accumulation.



Mosses of sunny rock outcrops: (this page, clockwise from top) *Grimmia laevigata* is like most species of the genus in having hyaline awns (transparent leaf tips). These may give a frosted appearance to the colony, and thus insulate the plants from the heat of the desert sun. Photograph by J. Shevock. • *Grimmia pulvinata* is one of our most widespread members of its genus. It is especially common on cement blocks or walls in urban environments. It is found not only in deserts, but also in humid areas of the coast. Photograph by J. Shevock. • *Grimmia moxleyi* is the most desert-adapted member of this genus. It is restricted to the very hot and dry rocks of California's southeastern deserts. Photograph by J. Shevock. • Opposite page, top to bottom: closeup of *Grimmia moxleyi*. This moss has hyaline awns restricted to the leaves which surround the sporophytes. When dry, the living material of *G. moxleyi* plant cells is protected by black, opaque cell walls that shield cell contents from the sun. Photograph by J. Shevock. • *Coscinodon calyptratus* is another member of the Grimmiaceae, separated from *Grimmia* by the large and basally-lobed calyptrae (sporophyte caps). This moss, in California, is restricted to the desert or desert fringes. Photograph by J. Game.

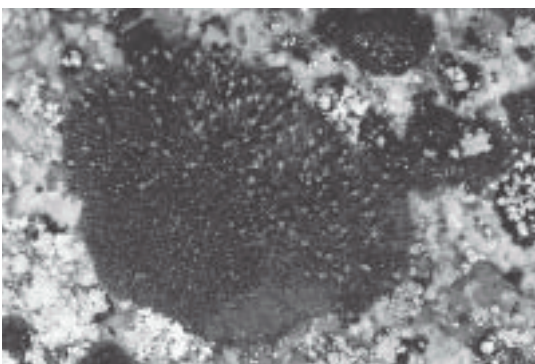


male and female spores are produced, and one expects to find males and females in equivalent numbers in the field. In all desert dioecious species examined, the pattern of female-bias is easily observed. Determining the reasons why males should be so much rarer than females has occupied the time of several scientists over the last few years.

One of the puzzles is that sexual reproduction, with all of its supposed advantages to a species (i.e., enhancing genetic variation, repairing the DNA, and producing a nice

dispersal unit—a seed or spore) is very rare among dioecious desert mosses. One such species, *Syntrichia caninervis*, dominates the soil in zones of blackbrush, *Coleogyne ramosissima*. Acres upon acres of females occur, with but a male here and there, if the male is present at all. In fact, we have yet to find a population that is exclusively male, while exclusively female populations are commonplace.

Successful sexual reproduction is hindered by several factors, among them: 1) male rarity, 2) low



sex expression, 3) the highest known abortion rate among mosses, and 4) local weather variation that causes reproductive cycles to skip years. Low sex expression is characteristic of dioecious species of mosses in general, and desert species in particular. By that is meant that, if one collects a few stems of this *Syntrichia*, hydrates the stems on a microscope slide, examines them under a dissecting microscope, and probes around the leaves and at branch junctions in search of sex organs, in all likelihood the stem will be found to be a “nonexpresser” (of undetermined sex).

On average, less than 10% of all stems have expressed sex (produced sex organs) *over their entire lifetime*. The average age of an individual stem is about 15 years in the Mojave, although clones can be much older. Even on the rare occasion when sex is achieved, the odds are that the offspring generation resulting from sex (called the sporophyte, a spore-bearing structure) will abort. In fact, about 60–70% of all fertilizations abort. Why is this the case? Appar-

ently resources are so limiting (especially water and secondly nitrogen in deserts) that the maternal plant does not have sufficient resources to dedicate to her offspring. So, instead of sacrificing her own potential to survive, she jettisons her offspring in order to preserve the possibility of future reproduction for herself. After all, if she should die while nurturing her offspring, she will not be able to reproduce in the future. However, if she aborts the offspring due to a shortage of resources that she can provide, she lives to reproduce another day, perhaps more than once.

A “decision” is made early on in order to conserve resources. As a result, nearly all abortions occur in the embryonic phase. One nice thing about studying reproduction in mosses is that a person can examine a female stem under a dissecting microscope and see what happened in each of the last three to four years of reproduction—reproductive structures (sex organs and abortions) usually remain intact along the stem.

Rainfall in the Mojave Desert is one of the most erratic and unpredictable events on the continent. Weather forecasters are not to be relied upon. In the winter of early 2002, rain was predicted in the Las Vegas Valley on five occasions, and nary a drop fell. This is a typical scenario. Since the mosses depend upon external water from rain showers for their growth and reproduction, and really have a “window of opportunity” that extends from about December through March, should insufficient rains fall during this period, the entire reproductive cycle will be skipped. This exact thing happened across the Mojave Desert for three consecutive years in the late 1990s. A few years ago, we had a stretch in the eastern Mojave of over 200 consecutive days without a drop of rain. The mosses lived on, but no sexual reproduction was possible.

WHY ARE MALES SO RARE?

Male rarity is the primary reason why sexual reproduction is so infrequent in dioecious desert mosses, but why are there so few males to start with? Some low-elevation desert mosses are entirely female, with the male of the species only occurring at higher elevations where conditions are moister. Although this sex ratio may sound like a great situation to be in for the males, this is really *not* the case at all. The vast majority of males never father any progeny, and >99.9% of females are virgins for life, i.e., a sort of chaste society if you will. The female-biased sex ratio in mosses is quite opposed to the often male-biased sex ratio in seed plants.

How can this be? In seed plants, it is the male that is more common, more vigorous, and more tolerant of xeric conditions. The prevailing hypothesis for male dominance among seed plants states that it boils down to energy budgeting: since the female has to nurture an energetically expensive fruit, she then has less energy and resources to fight infection, survive environmental stresses, and to devote to growth. The male, on the other hand, produces pollen, which is cheap compared to fruit. He can afford to devote more resources to surviving the rigors of the desert.

With the mosses, however, the tables are turned, and the male devotes more energy to reproduction. The cost of a sperm packet far exceeds the cost of a single egg. A male will produce hundreds of sperm while a female produces only a few eggs. Because fertilization requires both sexes to be side by side in the presence of external water, fertilization is so rare that females do not experience their full cost of reproduction, producing only unfertilized eggs and no offspring to nurture (clearly, sex in the rain is

not what it is cracked up to be). Meanwhile, males always experience their full cost of reproduction (sperm) regardless of the presence of a female.

Females, then, have a surplus of resources to devote to desiccation stress, survival, growth, and maintenance, whereas males are compromised in these activities. As a result, the male has fewer resources to devote to survival, desiccation tolerance, and growth. The female, then, is expected to grow faster, exhibit greater clonality, and to occupy more desiccated habitats than is the male. True enough, one rarely finds males of desert mosses in true desert habitats (lower elevations) in the Mojave Desert.

WHERE TO FIND DESERT MOSSES

It takes “an eye to the ground” to perceive these little plants, but with a hand lens you can find mosses in nearly every corner of the desert. In the desert, mosses appear much like the color of the sand and rocks they inhabit, even blackish brown. However, upon wetting, these dark mosses turn brilliant shades of green. At lower elevations, mosses are restricted to the north-facing sides of outcrops and shrubs, where they enjoy the shaded shadows and remain hydrated for hours longer than adjoining exposed sites. In desert canyons, it is possible to come across carpets of mosses hugging the rock faces where the winter sun seldom reaches.

The best place to start is to locate a canyon that runs east/west, and has steep slopes. This canyon should be at about 3,000 feet or higher for best results. One of these slopes will offer a north-facing aspect, and here is where you want to concentrate your efforts. Along a north-facing slope during the winter and early spring months, a day or so after a good hydrating rain-

storm, you should be able to locate healthy populations of mosses that appear a beautiful green. The scent of creosote bush from the surrounding lower elevations should be sufficiently intoxicating at this time, and that should be your cue. Look for places at the bases of boulders and shrubs that receive no direct sunlight, even at high noon. The soil here remains moist for longer periods, and is conducive for mosses to grow. Once you get the idea of what to look for, you may want to venture into lower elevation desert canyons and try your luck.

A sharp contrast exists between north-facing and south-facing slope aspects: bryophytes may be absent entirely from surfaces along a south-facing aspect that exceeds 20 degrees, whereas rich moss communities can occur on north-facing sloping soils or, more commonly, rock outcrops. The reasons for their absence from south-facing aspects is called the “carbon balance hypothesis”: mosses on south-facing slopes dry out quicker than mosses on the other side of the canyon due to warmer temperatures and greater light exposure. Mosses must be wet to photosynthesize, and need to be moist for at least a full day after each rainstorm to make sufficient sugars for growth and reproduction. Therefore, those plants on the south-facing side of the canyon cannot reach a positive carbon balance needed for survival because they dry out too rapidly.

Avoid areas where cattle are allowed to graze. Personal observations in the Mojave Desert in California and Nevada indicate that where livestock grazing is presently occurring or has recently occurred, soil moss communities are severely damaged or absent entirely, and the bryophytes are restricted to boulder and rock outcrops. Recent research indicates that mosses take over a century to reestablish in ar-

reas of heavy grazing, even after the grazing has stopped.

The presence of high mountain ranges in deserts creates ecological elevation gradients over which plant assemblages change drastically within short distances. The lower tree line is encountered as one enters pinyon-juniper woodland, and the “desert” is left behind. Above this point, at least five well-defined vegetation zones occur, including a mesic evergreen forest at the highest elevations. Thus the southwestern deserts contain a variety of nondesert communities. Across these seed plant communities, the moss communities change too, and you can find a completely different set of mosses at high elevation than just a few miles down the road at lower elevations. The higher in elevation you go in deserts, the greater the diversity and prominence of mosses.

Mosses can also be found in spring/seepage areas depending on water availability, water chemistry, and surrounding vegetation. Here, too, cattle and burros have impacted the bryophyte community. The desert offers the botanist or botanical enthusiast the opportunity to view a variety of habitats all within a few miles of one another. By driving a road from a lowland desert region up into a mountain range, one encounters a range of plant communities, from creosote bush to ponderosa pine.

As you might expect, the changes in vegetation extend also to the communities of mosses. In going from low to high elevation, the “structure” of moss populations changes markedly: species diversity increases (more species per unit area), density of populations increases (mosses become easier to see because they are more dense), and the frequency of acrocarpous (having the reproductive parts at the tip of a stem) populations decreases (the mosses with creeping stems tend to predominate).

RARE SPECIES FROM THE MOJAVE

Perhaps oddly enough, the Mojave Desert is home to several globally rare or endemic species of mosses and liverworts. One liverwort grows throughout the Mojave Desert, from Joshua Tree National Park to southwestern Utah, and is still undescribed to science. The Nevada didymodon, *Didymodon nevadensis*, was recently described from the southern Nevada Mojave, and is restricted to gypsum formations. Its distribution probably spans into the eastern Mojave in California. Despite a few reports from outside deserts, *Crossidium seriatum* remains a globally rare species that is sporadically distributed across the Mojave, Sonoran, and Chihuahuan deserts. It also occurs on gypsum and calcareous soils.

Trichostomum sweetii appears to be a southwestern endemic, known

only from seven populations worldwide. *Phascum hyalinotrichum* is reported from the southern California Mojave Desert, the southern California chaparral, the Sonoran Desert of southern Baja California, and disjunct to the Chihuahuan Desert of Mexico. This species exhibits an unusual life history for desert mosses: it is an annual species. Because of its small size, it may be overlooked in the field. *Entosthodon planoconvexus* is known from only three populations worldwide, one of which is in the Mojave Desert of southern Utah, one in the Sonoran Desert of Arizona (Pima County), and a recent collection from the Isthmic Desert of northern Egypt.

Grimmia americana is known from only two populations worldwide, one in west Texas and the other in the eastern Mojave. In the Mojave Desert, *Pseudocrossidium crinitum* is known from only one

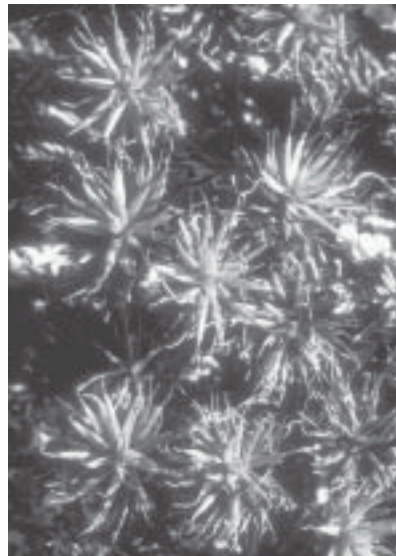
locality in the eastern Mojave Desert and another locality in southern Utah. This species, and at least four others (*Syntrichia bartramii*, *S. chisosa*, *S. pagorum*, and *Didymodon nevadensis*) are of interest in that males are entirely unknown.

NOTABLE CHARACTERISTICS OF DESERT MOSSES

The blackish, superficial, crusty covering often observed atop desert soils, while inconspicuous, has great ecological value to the community. It consists of not only mosses, but elements from as many as four different kingdoms. Lichens with cyanobacterial symbionts fix atmospheric nitrogen. In addition to providing the primary source of nitrogen for the ecosystem, the desert crust functions in preventing soil erosion, retaining soil water, and enhancing seedling germination. Desert mosses are highly vulnerable to disturbance. If crushed by human or animal agent (hiker, vehicle, horse), current estimates based on Utah communities indicate that it will take close to two centuries for them to fully reestablish. In the Mojave Desert, where it is drier, time to full reestablishment is probably longer.

If you find yourself inspired by this article to learn some desert mosses, be encouraged: identification, while sometimes trying due to their small size, is easier because nearly all of the desert mosses (except those found in high mountains) fall into only two families. The dominance of the Pottiaceae and Grimmiaceae is evident to both the amateur and professional. These mosses have upright stems, grow on soil and rocks, and often have twisted leaves when dry.

Mosses of shallow soil over rocks (clockwise from top left): *Syntrichia ruralis* shows hyaline awns reminiscent of those seen in *Grimmia*. In *Syntrichia*, however, the awns function as a water-repellant device: the leaves will be hydrated only in heavy rainstorms, and not in light sprinkles. Moss tissue will die if both wet and hot. This adaptation ensures wetting of moss leaves only if there is enough precipitation to maintain a period of photosynthesis. Photograph by J. Game. • *Polytrichum piliferum*. Note the water repellent hyaline awns. Photograph by J. Shevock. • *Polytrichum piliferum* is found throughout California wherever a layer of shallow soil covers rock outcrops. In desert regions, it is a plant restricted to higher elevations. The leaves of *Polytrichum* are very thick, unlike most other mosses, which most typically have leaves one cell layer in thickness. The primary photosynthetic area is a group of photosynthetic filaments internal to the leaf.



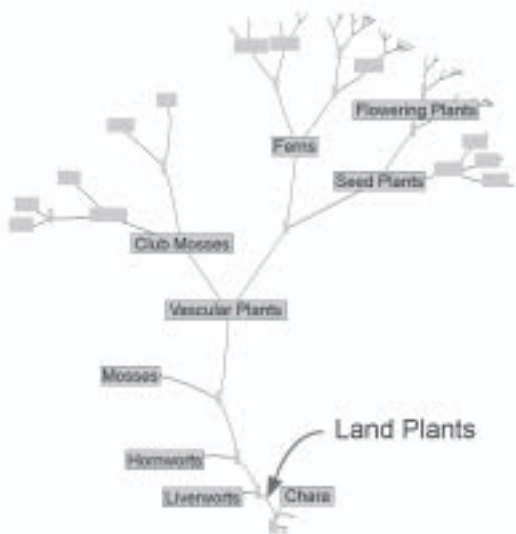
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THE BIOLOGY OF BRYOPHYTES, WITH SPECIAL REFERENCE TO WATER

by Brent D. Mishler

The bryophytes, with more than 20,000 named species worldwide, are the most diverse group of land plants (embryophytes) except for the flowering plants. The group includes three quite distinct lineages (i.e., mosses, liverworts, and hornworts) of familiar species frequently encountered in mesic forests and along streams, as well as a number of less familiar species of tropical rain forests, arctic tundra, and desert boulders. The three main bryophyte lineages, plus a fourth, the vascular plants (tracheophytes), comprise the entirety of the monophyletic land plants (embryophytes, see figure below), arguably one of the most important lineages to have arisen in earth's history. They made possible

Phylogenetic (evolutionary) tree of plants showing early divergence of bryophytes, with each group (liverworts, hornworts, and mosses) as a separate lineage. This is modified from a hyperbolic tree of green plant relationships presented on the web (<http://ucjeps.berkeley.edu/TreesofLife/hyperbolic.php>). The tree can be navigated online through its thousands of branches by clicking and dragging with a mouse—try it!



the colonization of the land by animals, and evolved an unparalleled diversity of size, structure, chemistry, and function.

Bryophytes contribute much to the “background” impressions of lushness and diversity that one experiences in many habitats in California. But what are they, exactly, and what about them deserves to be brought to the “foreground” in our appreciation of plants? There are several avenues pursued in the articles in this issue; the direction I’ll emphasize here is *water*. One of the very most important requirements for land plants is finding enough water to get established, metabolize, and reproduce. How do the bryophytes manage, and why? What general lessons can we learn from them about how plants manage on dry land?

First, it is necessary to go way back in time, because the three lineages of bryophytes are modern-day survivors of the most ancient branching events in the phylogeny of the land plants. Fortunately, these plants remain with us today, all the way from the spectacular radiation of the embryophytes in the Devonian Period, some 400 million years ago. As three-fourths of early land plant diversity, retaining as they do many of the primitive characteristics of the first land plants, bryophytes are a key to understanding how the embryophytes got started. They are also the key to deciphering how plants conquered the hostile land environment from their primitive home in fresh water—habitats still occupied by relatives of the land plants, certain green algae such as *Chara* and *Coleochaete* (Mishler and Churchill 1984, 1985; Graham 1993; Kendrick and Crane 1997).

Despite their diversity, phylogenetic importance, and key roles in the ecosystems of the world, study of many aspects of the biology of bryophytes has lagged behind that of the larger land plants, perhaps because of their small size and the few scientists specializing on the group. This is unfortunate because of the intrinsic scientific value of these plants. They have several biological features making them particularly suited to serve as study organisms in macroevolutionary, population genetic, and ecological research (Mishler 1988; Shaw 1991).

The plants are complicated enough in development and mature structure to serve as model systems for studying land plant evolution in general. However, they are simple enough morphologically (constructed as they are from easily traceable cell lineages derived from single apical cells) and genetically (given the haploid vegetative plant body) to be readily studied with current techniques. They are in the great majority of cases (except for some ephemeral species) observable throughout the year; they are also small in size, easily regenerated from fragments, and thus easy to study in culture.

In a recent review (Mishler 2001), I asked the question: In what ways is bryophyte biology different from that of the larger tracheophytes? The short answer was—in almost every way possible! Many aspects need much more study, but what is known suggests that in general the bryophytes differ in most ways in their biology, ecology, and evolution from tracheophytes. Consider, for example, the following unusual features:

Haploid dominance. The green,

vegetative part of the life-cycle in bryophytes (the “gametophyte” or gamete-bearing plant) is haploid (i.e., it has only one set of chromosomes, like a human gamete). Without the genetic benefits of dominance—the masking effect of having two copies of each gene in a diploid organism like our own bodies—genes acting in the gametophyte are presumably subject to relatively severe selection.

Extensive phenotypic plasticity. Studies have shown that bryophytes

tend to have very high amounts of morphological and physiological plasticity. This may compensate for their demonstrated low levels of genetically-based ecotypic differentiation (perhaps due to haploidy).

Relatively slow evolutionary rates in morphology. The fossil record of bryophytes indicates that ancient forms are very similar to modern ones, unlike the flowering plants which originated and diversified greatly in relatively recent times. Biogeographically, bryophytes tend

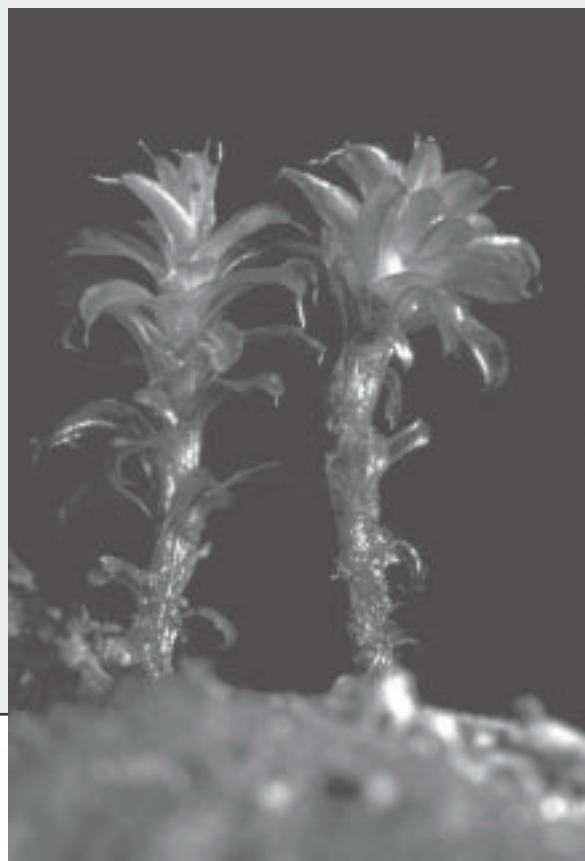
to follow the same historical patterns of disjunction as tracheophytes, but at a lower taxonomic level.

Small stature and the occupation of microhabitats. Because of their small size and lack of roots, bryophytes are in close relationship with their immediate microenvironment. Over geological time, they may be less influenced by climatic change, and linger in refugial habitats.

The clump as a “super-organism.” Many mosses and some liverworts

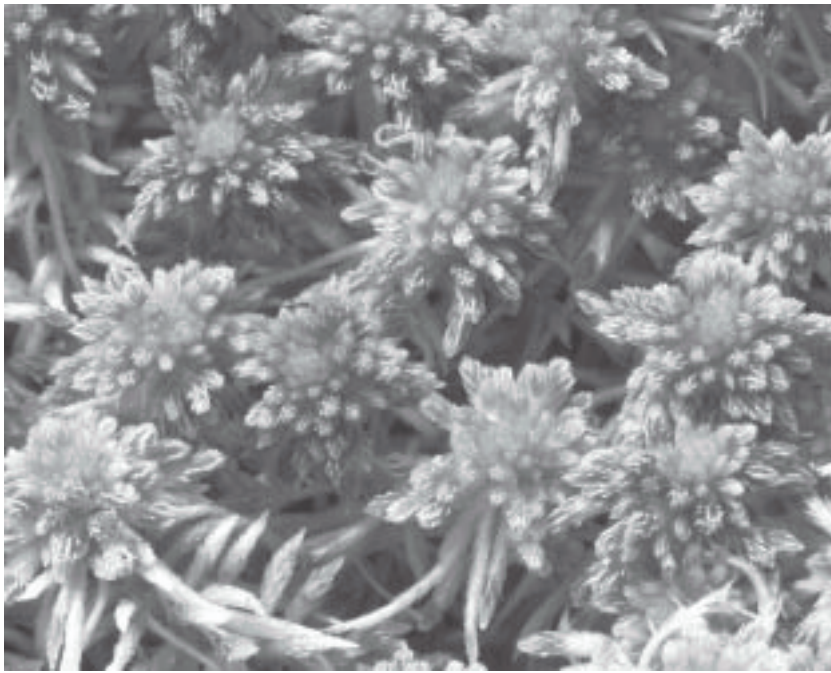
POIKILOHYDRY AND DESICCATION TOLERANCE: SURVIVAL STRATEGIES

The rapid equilibration of internal water content to the external environment is called “poikilohydry” (analogous to the term “poikilothermic” used for lizards and snakes, the so-called “cold-blooded” animals that rapidly equilibrate their internal temperature to the environment). Poikilohydry usually requires desiccation-tolerance for survival, but not necessarily. Poikilohydry is the rapid equilibration of the plant’s water content to that of the surrounding environment, while desiccation tolerance is the



ability of a plant to recover after being air-dry at the cellular level. All bryophytes have these abilities to some extent, unlike the larger, more complex, and endohydric tracheophytes, none of which are poikilohydric and very few of which (such as the resurrection ferns) are desiccation-tolerant.

Syntrichia ruralis (top), contrasting wet (left of twig) and dry (right of twig) plants. Photograph by B. Mishler. • Individual plants of *Syntrichia ruralis* (bottom), showing the widespread tendency of mosses to grow at the apex, while dying and decaying at the base. Thus most mosses live essentially forever.

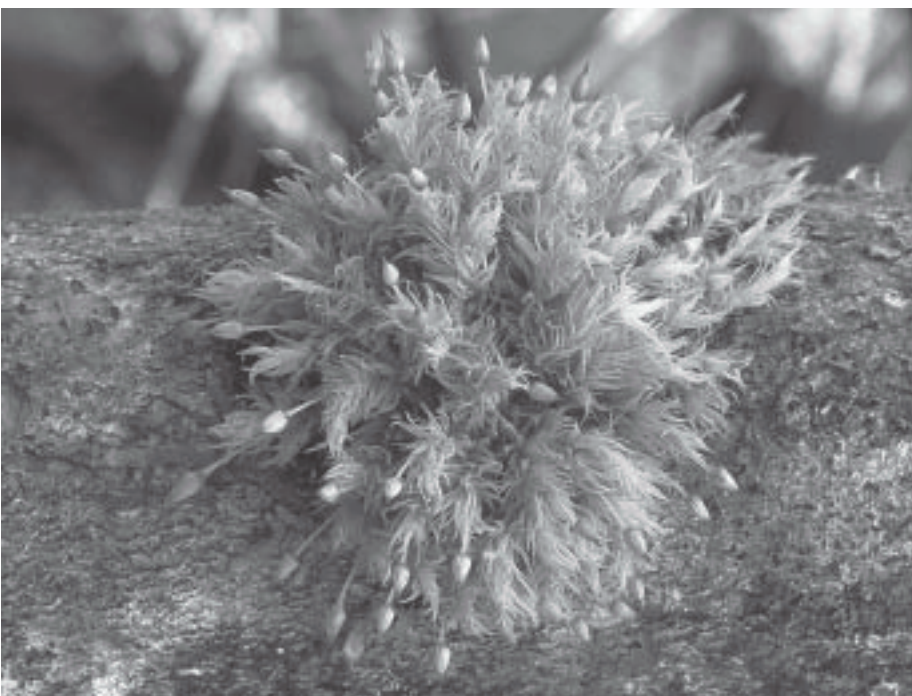
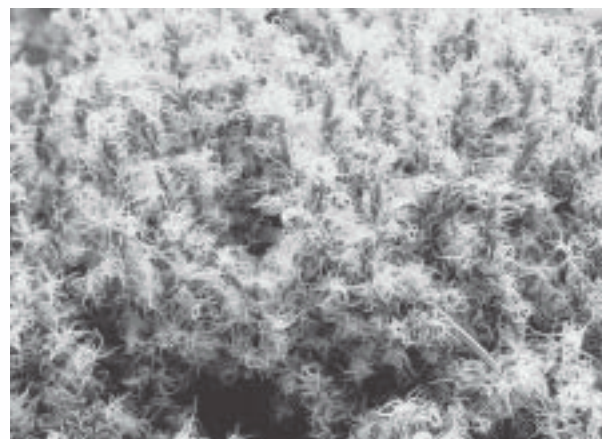
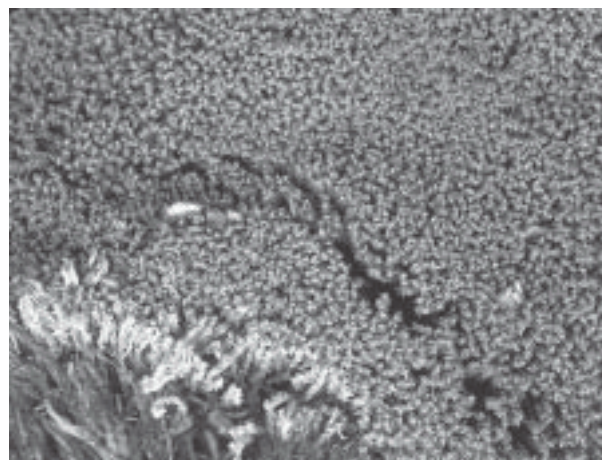
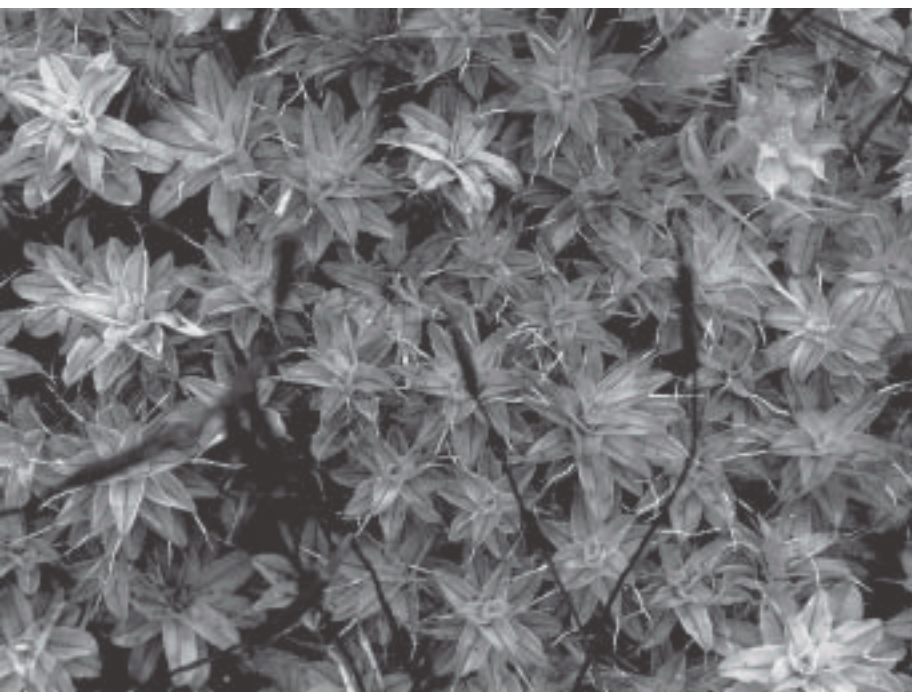


Sphagnum sp. (top). Note the very closely spaced branches on an elongated main axis. The closeness of the branching creates capillary spaces along which water moves up the stem, an efficient alternative to the internal conducting mechanisms of the tracheophytes. • The MossCam Project (bottom). Digital video monitoring, combined with micro-environmental sensors, provide an automated way to continuously monitor the hydration status and phenology of *Tortula princeps* at the James Reserve. The clump can be observed live at: www.jamesreserve.edu/mosscam/index.html along with microclimate data, a movie, and image archive. The camera has been gathering data for a year and a half, summer and winter (when the mosses are most active). Photograph by S. Lubin.

are essentially social organisms like a beehive. This results from the combination of clonal growth and external water conduction. The plants in a clump are subject to natural selection as a group. Intimate contact of each vegetative cell with the environment (due to poikilohydry—described in the sidebar on page 35), lends itself to interplant chemical communication via pheromones (Newton and Mishler 1994).

In particular, let's examine in more detail the unusual ways in which bryophytes relate to water in their environment, leftovers from the primitive past of all the early land plants. An ancestral feature of the early land plants is the constraint imposed by the swimming sperm; there remains a need for free water for sexual reproduction to be achieved. Swimming gametes, quite feasible in the aquatic ancestral environment, are a very clumsy mechanism for land organisms (and thus were superseded in seed plants with the advent of pollen, and in land animals by internal fertilization). The fact that swimming gametes have short dispersal distances leads to frequent inbreeding in species where both sexes are borne on one plant, and leads to lack of sporophyte production in species where the sexes are borne on separate plants. Due to the difficulty of achieving fertilization, many bryophytes have evolutionarily lost functional sexuality. Unusually heavy reliance on asexual reproduction has cascading effects on ecology and population genetics (Newton and Mishler 1994).

Vegetative water relationships of bryophytes are even stranger by comparison to the plants you are used to thinking about. Unlike the tracheophytes, they have no well-developed structural mechanisms for drawing water from the soil (no roots), for moving water internally (poorly developed conducting tissue), or for holding water inside (leaves are only one to two cells thick



Examples of some desiccation-tolerant mosses (clockwise from top left): *Syntrichia ruralis* often goes through several cycles of drying and wetting, even in a single day, without apparent damage to the plant. • *Grimmia torquata*. In a genus especially adapted to growth on dry rocks, *G. torquata* is an exception. Its dense cushions are found on rock overhangs where protected from direct rainfall. While it has hyaline awns, like most of the rest of the genus, those awns are very reduced in size. It is also a unique member of the genus in having leaves that dry in a disorderly manner (crispate). • *Racomitrium lanuginosum* is another member of the Grimmiaceae, but members of this genus grow primarily on very sunny rocks in humid coastal areas. In Alaska and high arctic, *R. lanuginosum* often grows in such large colonies as to be identified from as far as one mile away. • *Racomitrium heterostichum* is our most common member of the genus *Racomitrium*, and is often found covering cliffs and roadcuts, especially in northwestern California. In its typical habitat it may be dry and dormant for ninety percent of the year. • *Orthotrichum consimile* belongs to one of the largest genera of mosses in California. Members of this genus are found growing on both rocks and trees, and obtain essentially all of their water from rapid absorption of droplets on the above-ground plant. Like all mosses, species of *Orthotrichum* have no root system penetrating the substratum.

with thin cuticles). Instead, bryophytes have about the same water relationships as a piece of paper sitting on a rock—if it rains it gets wet fast, if it stops raining it gets dry fast.

In a recent study, Oliver, Tuba, and Mishler (2000) showed that vegetative desiccation tolerance was primitively present in the land plants (as seen today in all bryophytes), but was then lost in the evolution of tracheophytes. The initial evolution of vegetative desiccation-tolerance was a crucial step required for the colonization of the land, but that tolerance came at a cost, since metabolic rates are lower in tolerant plants as compared to plants that don't maintain costly mechanisms for tolerance. Thus, the loss of tolerance might have been favored along with the internalization of water relationships that happened as the vascular plants became more complex and able to control their internal water balance.

However, at least two independent evolutions (or re-evolutions) of desiccation-tolerance occurred in *Selaginella* and in some ferns. Within the flowering plants, at least eight independent cases of evolution (or re-evolution) of vegetative desiccation-tolerance occurred. The time scale and mechanisms of desiccation and rehydration are different each time the general phenotype was re-evolved. Deciphering the physiological mechanisms and genes behind these complex phenotypes is an exciting area of current research with both intellectual and economic applications (for more information see the "Plants Without Water" website at: <http://ucjeps.berb.berkeley.edu/bryolab/pww>).

Poikilohydry defines many aspects of bryophyte ecology. Since water is moving back and forth directly across the membrane of the photosynthetic cell, these membranes are in unusually intimate contact with their immediate microenvironment. They are famous for ion exchange, most notably the

genus *Sphagnum*, which acidifies its environment by trading hydrogen ions for other cations. Mosses (along with lichens which are also poikilohydric) are quite sensitive to water and air quality and thus are important bioindicators. They can also be quite choosy about their habitats, each species growing on particular bark, rock, or soil types.

We know little about the actual water budget of these poikilohydric plants, i.e., how often they are wet, for how long, and at what frequency. To know this would require constant monitoring of populations over years, which is impossible for someone to do first-hand. To begin to approach this question, Mike Hamilton and Sheri Lubin (of the James Reserve in the San Jacinto Mountains in Southern California) and I initiated a remote-sensing project using video cameras hard-wired to the Internet (dubbed the "MossCam" project; see photograph on page 36 and www.jamesreserve.edu/mosscam/). We are monitoring clumps of the diverse moss genus *Syntrichia*, looking at periodicity of hydration, and seasonality of reproduction. In addition to its serious scientific side, this project also provides an exciting website where one can watch moss grow in real time!

Many other aspects of the biology of bryophytes are in need of study and could yield important results. Many of the observations needed are very low-tech, and could be carried out by any general botanist. We need to know much more about simple demography (i.e., how new plants are established and how they die), phenology (the annual timing of production of gametangia and sporophytes, the diploid phase), distribution patterns (both geographic and ecological), use by animals, and many other topics that are accessible and would lend themselves to simple field research. Like the other authors in this special issue, I urge you to find out more

about these remarkable little plants. We need your help to understand them better.

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FROM THE ARCHIVES: BRYOPHYTES & LICHENS

This is not the first *Fremontia* issue with articles on non-vascular plants. As mentioned on page 12, Jim Shevock wrote an article about bryophytes that appeared in the April 1998 issue of *Fremontia* (Volume 26(2): 3–8). You may wish to read this article as an introduction to the current issue, as Jim describes the basic characteristics of bryophytes in general, followed by a more in-depth discussion of mosses in particular, including distributions and notes on collecting them. The section on field guides in this article is somewhat dated; see this issue's Notes and Comments (page 40) for Jim's current comments under "Building a Bryophyte Library."

The California Native Plant Society is also interested in lichens, which are not technically plants, but rather are organisms consisting of a

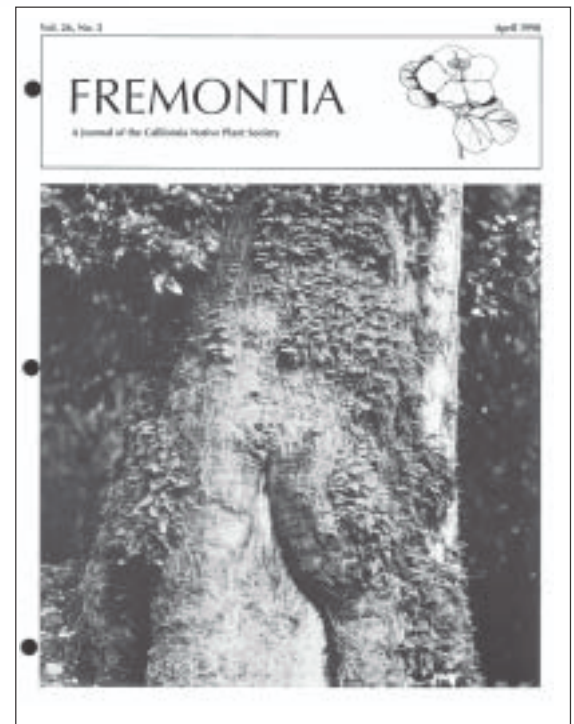
Cover of the July 1999 issue of *Fremontia*, with pixie-cup lichen (*Cladonia asabinae*), shown growing on the base of a tree in Carmel (the original photograph by S. Sharnoff).



fungus (not a plant; provides the scientific name for the lichen) associated with an alga (photosynthesizes within the structure formed by the fungus and provides energy to the organism). See the July 1984 issue of *Fremontia* (Volume 12(2): 21–22) for an article by Janet H. Wood (then studying lichens for her Master's thesis) on how lace lichen (*Ramalina menziesii*) is used to indicate air pollution levels. Lace lichen is often found draping from oak trees.

The April 1993 issue (Volume 22(2):3–12) has an excellent article on lichens written by Wayne P. Armstrong (then biology professor at Palomar College in San Marcos) and Jamie L. Platt (then student at California State University, San Marcos), where the authors fully describe the relationship between the fungus and alga that together form the lichen. The authors also discuss the structure of a lichen and the three growth forms (with lovely photographs), along with the role of lichens in succession, uses of lichens by natives and explorers, and the diminished range of lichens due to air pollution.

Stephen Sharnoff's "Lichens: A Different Window on California's Diversity" appears in the July 1999 issue (Volume 27(3):10–13). This article is graced with Steve's and his



Cover of the April 1998 issue of *Fremontia*, showing the trunk of a large interior live oak (*Quercus wislizenii*) covered with the mosses *Dendroalsia abietina* and *Homalothecium* sp. (the original photograph by M. Bourell).

late wife Sylvia D. Sharnoff's spectacular lichen photography, and was a prelude to their book (with I.M. Brodo, lichenologist), *Lichens of North America*. A book review of this volume appears on page 41 along with two examples of Sharnoff lichen photography.

COMPLETE YOUR SET

Back issues of *Fremontia* are available for sale from the CNPS Office, 2707 K Street, Suite 1, Sacramento, CA 95816; phone (916) 447-2677. Issues for Volume 28 and later (2000–present): \$5 each or \$10 for three. Issues before Volume 28: \$2.50 each or \$6 for three. Double issues priced as two single issues; shipping costs determined upon order placement.

BUILDING A BASIC BRYOPHYTE LIBRARY

The bryological literature is widespread, residing among numerous journals and other books. Some bryofloras and identification manuals are currently out of print. However, there are several key works that are available and quite useful to begin a study of California bryophytes. These publications are organized under the titles of bryofloras, field guides, and textbooks.

Bryofloras

Flowers, Seville 1973. *Mosses: Utah and the West*. Brigham Young University. Provo, UT.

This book contains excellent illustrations and has recently been reprinted by Blackburn Press [www.blackburnpress.com]. It is very useful for the identification of mosses from the more arid regions of California, especially the deserts and southern California.

Lawton, Elva 1971. *Mosses of the Pacific Northwest*. Hattori Botanical Laboratory. Miyazaki-ken, Japan.

This book is available in a paperback edition from the Hattori Botanical Laboratory [hattoril@pastel.ocn.ne.jp]. It is very useful for the coastal counties of northern California and mountainous portions of the state. Illustrations are provided but not as detailed nor of the same quality as those from *Mosses: Utah and the West*.

Field guides

Malcolm, B. and N. Malcolm, 2000. *Mosses and Other Bryophytes: An Illustrated Glossary*. Micro-optics Press. New Zealand.

While not a field guide, this illustrated glossary contains 970 color images to provide a visual aid to definition of bryophyte features and terminology. This book is essential when using bryophyte keys for identification purposes and is highly recommended.

Schofield, W.B. 1969 (reprinted). *Some Common Mosses of British Colum-*

bia. Royal British Columbia Press. Victoria, BC.

A nice paperback guide with black and white illustrations. Useful for moss identifications along the coast redwood belt of northwest California.

Schofield, W.B. 2002. *Field Guide to Liverwort Genera of Pacific North America*. Global Forest Society, San Francisco and University of Washington Press. Seattle, WA.

A really nice paperback with full-page illustrations of each genus. Available through Washington University Press [www.washington.edu/press].

Textbooks

Crum, Howard H. 2001. *Structural Diversity of Bryophytes*. University of Michigan Herbarium [phone order 734-764-2407].

This is the last work of the late Howard Crum and it is a gem. It is well written and illustrated.

Schofield, W.B. 1985 (reprinted 2001). *Introduction to Bryology*. Blackburn Press. Caldwell, NJ.

This is an excellent textbook (suitable too for college courses) that is also well illustrated.

Shaw, J. and B. Goffinet 2000. *Bryophyte biology*. Cambridge University Press. Oxford, UK.

This paperback edited by Shaw and Goffinet contains 13 chapters written by leaders in their bryological field of expertise. It is a bit more technical than either Crum or Schofield. There-

fore, it can be viewed as a reference for someone that has already had a general bryophyte course or desires more information after reading either Crum (2001) or Schofield (1985).

BRYOLOGICAL INTERNET RESOURCES

The following is a brief list of useful Internet sites for both the beginning and professional bryologist.

American Bryological and Lichenological Society (ABLS), www.unomaha.edu/~abls.

The ABLS publishes two quarterly bryological journals. The more technical of the two is *The Bryologist* and the other is *Evansia*. The ABLS home page provides numerous links to other bryological websites around the world. Other bryological societies and journals can be accessed through this site.

Missouri Botanical Garden—Bryology Lab (MO), www.mobot.org/MOBOT/research/links5.shtml.

This page provides links to a wide variety of bryological institutions throughout the world. Bryology at MO has several floristic projects underway and the herbarium has over 300,000 bryophyte collections. In addition, a complete list of bryophyte names can be accessed electronically at this site.

New York Botanical Garden (NY), www.nybg.org/bsci/bcol/bryo/bryology-center.html.

The NY site provides access to many bryological sites and useful information. The North American bryophyte specimens at NY (the Nation's largest herbarium) can be searched on line.

IUCN World Red List of Bryophytes, www.artdata.slu.se/guest/SSBryo/Bryolist.htm.

This section of the IUCN is working to save the world's most endangered mosses, liverworts, and hornworts. Two California liverworts (*Geothallus tuberosus* and *Sphaerocarpus drewei*) are on the World Red List.

BRYOPHYTE WORKSHOPS

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BOOK REVIEWS

Moss Gardening: Including Lichens, Liverworts, and Other Miniatures, by George Schenk. 1997. 262 pages, with 97 color photos. Timber Press (www.timberpress.com). Portland, OR. Price \$34.95, hardcover.

Appearing in fossils 400 million years old and totaling 15,000 species from the Arctic to the Antarctic, mosses tell an ancient success story of longevity and dispersion. North America alone supports 1,200 of them. George Schenk's beautiful book is perhaps the first to cover the whole gamut of moss gardening. *Moss Gardening* is sure to become a classic, not only because it covers "almost as much about the mechanics of moss gardening as the *Kama Sutra* does about dancing," but also for the author's entertaining writing style.

The book covers primitive miniatures (or cryptogams) which reproduce by spores: mosses, lichens, liverworts, lycopodiums, and selaginellas. The information on propagating, cultivating, and transplanting is applicable to gardens of practically any climate. Landscaping recommendations are offered for use in alpine and rock gardens, with flowering plants in borders, as a lawn substitute, and for use in miniature gardens.

George Schenk retired from his landscape and nursery business and now designs and maintains gardens for friends in Seattle, North Vancouver, Auckland, and Manila. He authored of three other horticultural books.

Anonymous
Timber Press

Gathering Moss, A Natural and Cultural History of the Mosses, by Robin Wall Kimmerer. 2003. Oregon State University Press. Corvallis, OR. Orders processed through collaboration with University of Arizona Press. Tucson, AZ. 168 pages. Price \$17.95, hardcover.

The mosses (and other bryophytes) are a remarkable group of plants, and many botanists and plant enthusiasts have yet to be exposed to their diminutive beauty. Many people have asked

me how to get started in learning about bryophytes and what books to buy. A popular, non-technical, easy-to-read yet scientifically accurate book has finally crossed my desk.

Robin Kimmerer's book is a great place to start for those unfamiliar with mosses. Kimmerer is a biologist (associate professor) and a Native American woman who shares her experiences of how the mosses speak to us

and of their importance. She clearly has a cultural kinship to the mosses which, in many ways, makes this book unique. It reads like a natural history, but one with a considerably more personal tone to it. Despite its non-technical approach, however, the book provides information about general ecology as well as examples of scientific principles.

Each of the book's short essays pre-

The lichen *Cladonia carneola* on a rotting log. Photograph by S.D. Sharnoff.



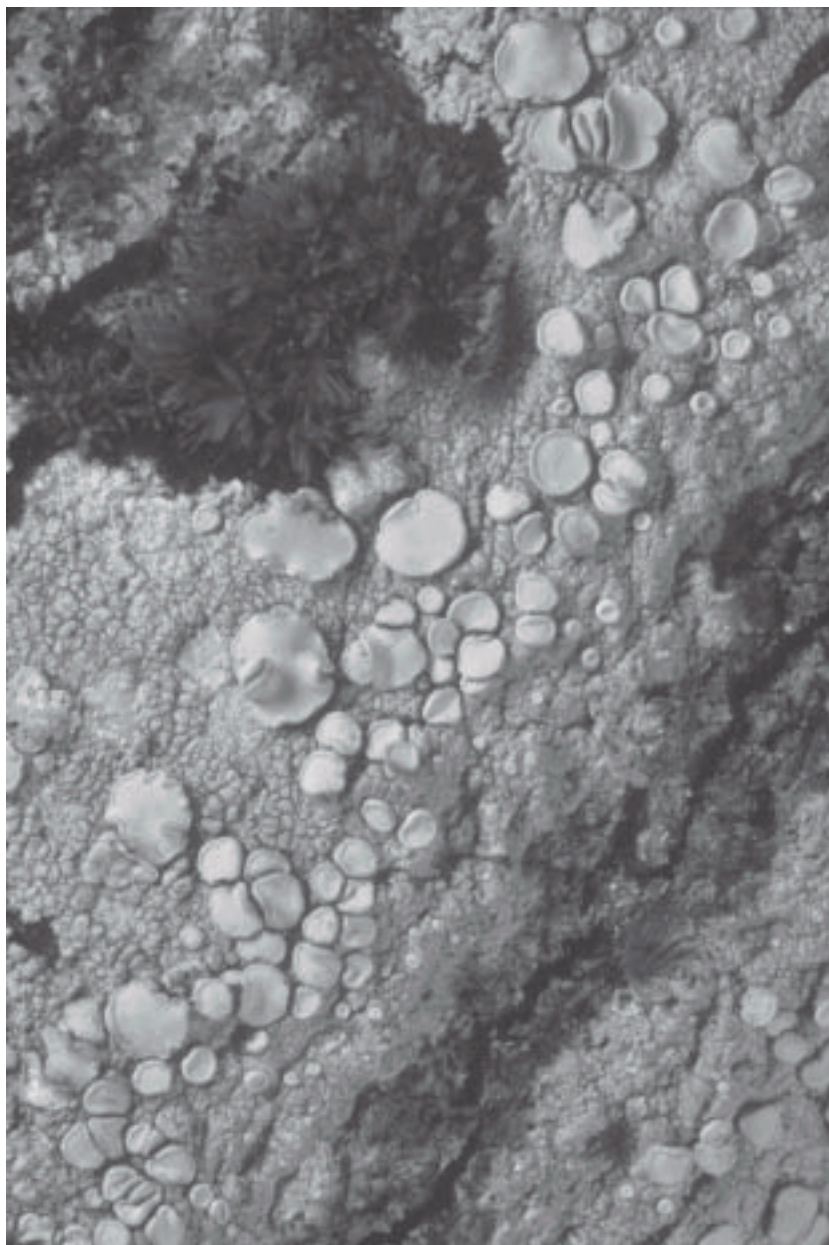
sents a particular story and lesson about the role mosses play in our world. Here are a few passages to give you the flavor of Kimmerer's prose and how she brings us into the world of mosses.

"... *Learning to see mosses is more like listening than looking. A cursory glance will not do it. Straining to hear a far-away voice or catch a nuance in the quiet subtext of a conversation requires attentiveness, a filtering of all the noise, to catch the music. Mosses are not elevator music; they are the intertwined threads of a Beethoven quartet. You can look at the mosses the way you listen deeply to running water over rocks. The soothing sound of a stream has many voices, the soothing green of mosses likewise.*"

"... *At the scale of a moss, walking through the woods as a six-foot human is a lot like flying over the continent at 32,000 feet. So far above the ground, and on our way to somewhere else, we run the risk of missing an entire realm which lies at our feet. Every day we pass over them without seeing. Mosses and other small beings issue an invitation to dwell for a time right at the limits of ordinary perception. All it requires of us is attentiveness. Look in a certain way and a whole new world can be revealed.*"

The closing passage of the Preface sets the stage for all of the essays that follow. "... *In indigenous ways of knowing, we say that a thing can not be understood until it is known by all four aspects of our being; mind, body, emotion, and spirit. The scientific way of knowing relies only on the empirical information from the world, gathered by the body and interpreted by the mind. In order to tell the mosses' story I need both approaches, objective and subjective. These essays intentionally give voice to both ways of knowing, letting matter and spirit walk companionably side by side. And sometimes even dance.*"

As an ecologist, Kimmerer has studied mosses in the field for countless hours and through this association their secrets have been revealed to her. She now shares them freely with the reader. It is a rare event for me to read a botany book from cover to cover without jumping between chapters. This is just such a book—unlike anything I have read in a long time. I found it to be a delight and I suspect you will too. And once you've com-



The lichen *Lecanora caesiiorubella* on oak bark. Photograph by S.D. Sharnoff.

pleted it, your next walk in a forest may very well seem like your first!

James R. Shevock
Department of Botany
California Academy of Sciences

Lichens of North America, by I.M. Brodo, S.D. Sharnoff, and S. Sharnoff. 2001. Yale University Press, New Haven and London. 795 pp. Price \$ 69.95, hardcover.

With *Die Flechten Baden-Württembergs*, fifteen years ago Volkmär Wirth set the standard for what would ever since have been the dream for a lichen monographer: a book in high print quality, filled with first class color pho-

tographs of several hundreds of lichen species, useful to the specialist, the amateur, and the natural historian with general interests. The second edition of this opus, published as two volumes in 1995, also included the well-elaborated keys known from Wirth's *Flechtenflora*, and additional photographs of more species.

None, including myself, would have believed it possible to match or surpass the superb quality of Volkmär Wirth's books. Yet, here we are with another book for which it is difficult, if not impossible, to find superlatives, and which not only matches, but surpasses any other similar book pub-

lished in this area: Brodo et al's *Lichens of North America*. When I first saw this book, I simply couldn't believe that something as wonderful as this really existed. But it does, and it is not only affordable, in fact, the price of this book is quiet incredible [but note that at time of publication of this *Fremontia* issue, less than 300 copies remained], considering that it features nearly 1,000 color photographs of absolutely superb quality.

One could certainly criticize a few minor weak points of this opus. For example, many line drawings are not originals but reproduced from other books. Or, compared to Wirth's books, comparatively few crustose lichen species are represented. Also, in most genera, the keys to species are not complete but rather represent a selection of common North American taxa.

However, this is not the moment to criticize. In fact, this book is beyond criticism, because its primary goal is not to be a complete lichen flora of North America. This book is different. This book is probably the most important work ever published on lichens, because it addresses the widest audience possible and will, without doubt, attract hundreds, if not thousands of students and nature lovers to this fascinating and important group of organisms. And, there are two significant advantages over Wirth's books. First, the introductory part of *Lichens of North America* is much more extensive, covering all aspects of lichen biology and their potential uses, and second (trivial but not less important!), this book is in English, and hence it is accessible to anybody with a basic knowledge of that language.

I have already experienced the impact of *Lichens of North America* on several occasions, most recently during a visit to an herbarium (UNAM) in Mexico, where Marusa Herrera Campos has successfully established a lichenological working group, and all the students, regardless of whether they could possibly afford it or not, unanimously stated: "I want that book!" It is certainly no overstatement to say that the *Lichens of North America*, from now on, will be the bible for lichenologists and a treasure for every nature lover. It is also not hard to pre-

dict that this book will have a significant impact on, and raise the numbers of, students of lichenology. And if there is one most important achievement of any scientific book, it is the attraction of students to the subject. Irwin Brodo has marked lichenology in North America and beyond for decades. The Sharnoffs [S.D. Sharnoff

is the late Sylvia Sharnoff, S. Sharnoff is Stephen Sharnoff] range among the best nature and plant photographers in the world. *Lichens of North America* is definitely their masterpiece.

Robert Lücking
Lichen Collection Manager
Field Museum of Natural History
Chicago

CONTRIBUTORS (Cont'd from back cover)

both in western North America and in neo- and paleotropical regions. His bryophyte collection, at over 106,000 specimens, is one of the largest in the world, and forms the nucleus of the University Herbarium bryophyte collection.

James R. Shevock, research associate with the Department of Botany, California Academy of Sciences, and the University Herbarium, UC Berkeley, is one of the foremost authorities on both bryophytes and vascular

plants in the Sierra Nevada. He is research coordinator for the National Park Service at the Californian Cooperative Ecosystem Studies Unit.

Lloyd Stark, PhD, is an assistant professor at the University of Nevada, Las Vegas, Department of Biological Sciences. His research explores how male and female desert mosses respond to stresses of extreme temperatures and desiccation, and also tracks the distributions of rare aridland species of mosses.

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FROM THE EDITOR

Are you ready to appreciate the small and wonderful? Prepare yourself to spend some field time on your knees, or pressed against tree trunk or rock, after reading this issue and becoming enthused to learn more about mosses, liverworts, and hornworts.

The issue begins conversationally: Dan Norris provides general information about these small green plants in a series of questions that he has heard throughout his career as bryology professor. How better to learn about a group than to read the answers to the most frequently asked questions?

Next, Jim Shevock provides an overview of the mosses that occur in California, where they might be found, and some of their characteristics. He then teases us with names of several mosses that should be in California, but that have yet to be discovered, combined with the information that new species of mosses are found in our state every year!

If you quake with the trepidation of a novice, read Ken Kellman's article. He, like most bryologists, started with the vascular plants (wildflowers, in fact), but once he learned a bit about mosses he was irretrievably hooked

into collecting and cataloguing those from the environs of his Santa Cruz home.

Think mosses are only from wet areas? Wonder how mosses survive continual wetting and drying, without real roots? Consider the paper by Lloyd Stark, who studies mosses of desert regions, or that of Brent Mishler, who is very interested in how mosses utilize the water in their environment. Read, enjoy, research more, but do get down on your knees to glory in the greatness of these tiny green plants.

Linda Ann Vorobik
Editor

CONTRIBUTORS

John Game works in molecular genetics for the Lawrence Berkeley National Laboratory, with degrees in botany from Oxford, England. He is a research associate at the UC/Jepson Herbaria, an active California Native Plant Society member, as well as an enthusiastic plant photographer with many images published in books, magazines, and on the internet.

Martin Hutten received a graduate degree in forest science at Oregon State University studying relationships between mycorrhizae and trees, and has spent several years conducting an inventory of lichens, mosses, and liverworts for Olympic National Park. His excellent photographs populate this entire issue of *Fremontia*.

Kenneth Kellman is an amateur botanist who has been studying bryophytes since 1995. He is currently working on "A Catalog of the Liverworts and Hornworts of Santa Cruz County", and is starting collections for a bryophyte flora of Monterey County.

Brent Mishler, PhD, is director of the Jepson and University Herbaria at UC Berkeley, as well as a professor in the Department of Integrative Biology, where he teaches systematics and plant diversity. His research interests are the systematics, evolution, and ecology of bryophytes, as well as the phylogeny of green plants and the theory of systematics.

Daniel Norris, PhD, is research botanist at the University California, Berkeley, with extensive bryological experience
(*Cont'd on page 43*)

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