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CONTRIBUTIONS TOWARD A BRYOFLORA OF CALIFORNIA III. KEYS AND ANNOTATED SPECIES CATALOGUE FOR LIVERWORTS AND HORNWORTS

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ABSTRACT

Keys are provided to 54 genera, 142 species, 6 infraspecific taxa, and 3 undescribed species of California liverworts and hornworts within 33 families. In addition, 3 genera and 16 species previously reported have been excluded from the California bryoflora. The keys emphasize gametophytic characters. Annotated comments for each species focus on what to look for and how to separate it from species with similar morphology. The worldwide and California distribution of each species is provided.

Key Words: California, flora, liverworts, hornworts, keys, species, distribution.

I like to look on plants as sentient beings, which live and enjoy their lives—which beautify the earth during life and after death may adorn my herbarium. When they are beaten to a pulp or powder in the apothecary's mortar, they lose most of their interest for me. It is true that the Hepaticae have hardly as yet yielded any substance to man capable of stupefying him or of forcing his stomach to empty its contents, nor are they good for food; but if man cannot torture them to his uses or abuses, they are infinitely useful where God has placed them, as I hope to live to show, and they are, at the least, useful to, and beautiful in themselves—surely the primary motive for every individual existence.

R. Spruce, *Notes of a Botanist on the Amazon and Andes* (ed. A.R. Wallace). London. 1908. Vol 1: xxxix.

Over 100 years has passed since the publication of *The Hepaticae and Anthocerotes of California* by M. A. Howe (1899) who recognized 36 genera and 86 species. Many additional species have since been added to our flora, taxonomic revisions have resulted in name changes, and distributional patterns are better understood. Now, 54 genera and 142 species are recognized and three new species await formal description. The liverwort and hornwort flora of California can be displayed and analyzed from different perspectives. There are 12 genera included in the complex thalloid liverwort group, three genera in the sphaerocarpoid group, seven genera in the simple thalloid group, 29 genera in the leafy liverwort group, and three genera in the hornworts (Table 1). Of the 54 genera in this catalogue, 26 genera are represented in the state by a single species. The largest liverwort genera in California include *Riccia* (13 species), *Lophozia* (11), *Scapania* (10), *Jungermannia* (9), *Cephaloziella* (6), and *Calypogeia*, *Frullania* and *Marsupella* (each with 5). These eight genera contain just under 50 percent of the liverwort flora of California.

This publication is a companion to the two publications on California mosses by Norris and Shevock (2004a, b). These three publications provide reference points for future research on the California bryoflora. Several regions of the state (e.g., Mojave and Sonoran Deserts, Sacramento and San Joaquin Valleys, and east side of the Sierra Nevada) and most counties still are in need of careful, intensive study. New additions (including new species) to the state's bryoflora are sure to be found with continued exploration and collection.

Although weedy or introduced liverworts and hornworts are uncommon in California, the potential of exotics becoming established is great in urbanized areas, especially in the coastal counties where a great diversity of introduced ornamental plants are grown coupled with a more moderate climate during the summer months. The threat is somewhat reduced by the summer drought typical of our Mediterranean climate. However, landscaped parks, convention grounds, and botanical gardens that use summer watering regimes can be sources for non-native bryophyte introductions.

The purpose of this publication is to help beginning students, public agency botanists, environmental consultants, and amateur and professional bryologists to accurately name liverworts

TABLE 1. SYNOPSIS OF FAMILIES AND GENERA OF LIVERWORTS AND HORNWORTS OCCURRING IN CALIFORNIA.

Liverworts		Hornworts
Aneuraceae	**Lepidoziaceae**	**Anthocerotaceae**
Aneura	*Bazzania*	*Anthoceros*
Riccardia	*Kurzia*	**Notothyladaceae**
Antheliaceae	*Lepidozia*	*Phaeoceros*
Anthelia	**Lunulariaceae**	*Phymatoceros*
Aytoniaceae	*Lunularia*	
Asterella	**Marchantiaceae**	
Cryptomitrium	*Marchantia*	
Mannia	*Preissia*	
Reboulia	**Metzgeriaceae**	
Blasiaceae	*Metzgeria*	
Blasia	**Pallaviciniaceae**	
Calypogeiaceae	*Pallavicinia*	
Calypogeia	**Pelliaceae**	
Cephaloziaceae	*Pellia*	
Cephalozia	**Plagiochilaceae**	
Cephaloziellaceae	*Plagiochila*	
Cephaloziella	**Porellaceae**	
Cleveaceae	*Porella*	
Athalamia	**Pseudolepicoleaceae**	
Conocephalaceae	*Blepharostoma*	
Conocephalum	**Ptilidiaceae**	
Fossombroniaceae	*Ptilidium*	
Fossombronia	**Radulaceae**	
Frullaniaceae	*Radula*	
Frullania	**Ricciaceae**	
Geocalycaceae	*Riccia*	
Chiloscyphus	*Ricciocarpos*	
Geocalyx	**Riellaceae**	
Lophocolea	*Riella*	
Gymnomitriaceae	**Scapaniaceae**	
Gymnomitrion	*Anastrophyllum*	
Marsupella	*Barbilophozia*	
Gyrothyraceae	*Diplophyllum*	
Gyrothyra	*Douinia*	
Jungermanniaceae	*Lophozia*	
Gymnocolea	*Scapania*	
Jungermannia	**Sphaerocarpaceae**	
Mylia	*Geothallus*	
Nardia	*Sphaerocarpos*	
	Targioniaceae	
	Targionia	

and hornworts, to document what and where they have been found, and to aid in the recognition of them as significant components of California's amazingly diverse flora. Not only is the search for and identification of liverworts and hornworts fulfilling in its own right, it also is an area in which beginners and amateurs can make significant contributions to the field of bryology and floristics (Kellman 2003). Liverworts and hornworts are small plants. Their study requires an innate appreciation of things small and a willingness to spend time to seek them out in their microhabitats in the field. With practice and experience, many genera and species can be recognized in the field with a high level of certainty. However, because of their small size, most liverworts and hornworts will need to be examined under a microscope to observe diagnostic features used for species recognition. Therefore, collecting samples for identification confirmation is necessary.

HOW TO DISTINGUISH LIVERWORTS AND HORNWORTS FROM MOSSES

Bryophytes (bryo- = moss; phyt- = plant). Historically, the term bryophytes collectively refers to mosses, liverworts and hornworts, which are land plants that lack lignified water-conducting tissue and reproduce by spores, rather than by seeds. They have similar life history strategies consisting of two distinct multicellular generations: 1) a free-living, longer-lived gamete-producing generation (called a gametophyte) and 2) a shorter-lived, spore-producing generation (called a sporophyte), which, during its development, remains attached to the gametophyte and produces a single capsule (sporangium).

In the field, mosses can be confused with leafy liverworts. With experience, however, the two groups usually are easily separated based on texture and growth characteristics that are easier to see than to describe.

The following features separate liverworts and hornworts from mosses:

Liverworts and Hornworts

- adult gametophytes leafy or thalloid, when leafy usually bilaterally symmetrical;
- leaves, when present, without a midrib (= costa);
- oil-bodies usually present in liverworts and absent in hornworts;
- leaves of many species lobed;
- rhizoids unicellular;
- sporophytes either lack a meristem (liverworts) or have one between the foot and capsule (hornworts).

Mosses

- adult gametophytes leafy and mostly radially symmetrical;
- leaves of most species with a distinct midrib (= costa);
- oil-bodies always absent;
- leaves not lobed;
- rhizoids uniseriate filaments;
- sporophytes with an apical meristem.

Serious students seeking to acquire a bryological library should obtain 1) the introductory bryophyte biology textbook by Schofield (1985), which provides detailed information about the major bryophyte groups, including helpful aids in the study of these plants, 2) the excellent reference book by Crum (2001), which is for more advanced students, and the six volume treatise by Schuster (1966–1992), which contains detailed descriptions of liverworts and hornworts of North America east of the hundredth meridian.

Specimen Collection, Preservation and Examination

What equipment is needed to bring voucher specimens back for identification? Basic needs include 1) a 10× to 20× hand lens, 2) a small knife or wood chisel, and a small spatula or putty knife to carefully extricate bryophytes from the substrate, 3) small flexible containers to hold individual specimens, and 4) pencil and paper to record field data. Recommended is an inexpensive, hand-held GPS to obtain elevation, latitude and longitude.

Your collection documents a species in a specific habitat and location at a point in time. Survey the population **before** making a collection. Is it a small, localized population or widely distributed in that habitat? A good rule of thumb: never take more than five percent of a colony or population. Make your collection an important research tool: 1) Except for rare species or small populations, collect more than a pinch. Collect enough plant material to show possible morphological variation; 2) Search populations for antheridia, archegonia, sporophytes, and gemmae because they can be significant aids in species identification; and 3) When a population occurs in a varying habitat (e.g., marshy areas with wet depressions and drier sides and tops of hummocks) include plants representing these different microhabitats. The color and form of plants of the same species can markedly vary when growing in wet, shaded, or drier microenvironments. Make good field notes and keep them with the specimens. The lasting value of the specimen is greatly enhanced with a detailed label that includes information on who collected it, when and where was it collected, what was it growing on, how common was it, and specific locational directions to the site.

It is essential that each collection be kept separate and separately labeled (except in inclement weather, when mixed collections should be sorted and labeled immediately upon return to a dry environment). Many bryologists use a numbered and folded paper specimen packet, or a paper #2 cargo or sandwich bag. Field collection data (including locality, habitat, substrate, and date) can be written in pencil directly on the bag or on a slip of paper and placed with the specimen. Some bryologists bring them back alive in plastic bags. Favored are the old-fashioned small plastic Baggies, which lack the zip-lock. Field data are placed in the Baggie with each voucher. At the end of the day, the live specimens can be placed in an ice chest (for a few days with no adverse effect) until return home.

Whichever collecting technique is used, it is really important to develop the habit of looking at the specimens under the microscope while they are still fresh. Doing so will expedite eventual identification. For microscope observations, clean plants of attached substrate so that rhizoids, scales and/or underleaves can be observed. In addition, oil-bodies in several genera (e.g., *Calypogeia, Lophozia, Nardia, Riccardia,* and *Scapania*) disappear in dry specimens and oil-body information is important for the identification of these genera. Even when oil-bodies are still visible in dry specimens, their form, number, and color can change in the drying process. For oil-bodies, record presence or absence, their distribution in a leaf or thallus, range and average number per (usually mid-leaf) cell, form, and their approximate size and color. Keep this information in the packets with the collections and develop the labels.

Note. Living plants kept too long, and plants dried too slowly can become etiolated or moldy. Specimens should be air-dried as soon as possible (do not use artificial heat), and plants never should be pressed flat. Once the specimens are dried and identified, then they can be transferred into archival quality packets. Use 100 percent cotton, acid-free paper for your permanent herbarium specimen packets. Duplicates of your collections can be made available to other researchers or for placement in a herbarim. Because most herbaria have their own curatorial procedures, these duplicates can be provided in standard photocopy paper, but enclose a label printed on at least 25 percent cotton fiber paper.

As with mosses, identification of liverworts and hornworts usually requires access to both a compound and a dissection microscope. The compound microscope should be fitted with an ocular micrometer in order to measure leaf, cell and spore sizes. Paton (1999) contains detailed data on measurements, including illustrations. Leaf Measurements. Occasionally, the length and width of a leaf must be compared (e.g., some species of *Jungermannia*). For leaf length, measure from the approximate middle of its insertion line on the stem to a) the apex of a pointed leaf, b) the midpoint of the leaf margin with a broadly rounded apex, or c) the midpoint of an imaginary line between the apices of a bilobed leaf or two longest lobes of a multilobed leaf. For leaf width, measure the widest part of the leaf at right angles to the leaf length. Cell Measurements. Cell length is measured along the axis generally parallel to the length of the leaf, leaf lobe or midrib (of thalloid plants). Cell width is measured at right angles to cell length. Exception. The direction of measurement of leaf and thallus marginal cells is an exception to cell length and width measurements described above. The width of marginal leaf and thallus cells is measured parallel to the margin of the leaf or thallus. In this publication, measurement of cell length and width includes the lumen and ½ the wall thickness on each side of the lumen. Spore Measurements. Spore diameter is measured on spores viewed from the distal or proximal face (See Appendix 1 for definition of terms). Measurement of spore diameter includes ornamentation of the spore coat. Measure fully mature, ready to discharge spores, because in some plants (e.g., *Fossombronia*), deposition of wall ornamentation material occasionally continues late during sporophyte maturation and seta elongation.

Occasionally, a thallus or stem requires cross-sectioning in order to examine details of internal structure. The senior author uses the following technique: 1) place a fresh or hydrated thallus or stem on a glass slide; 2) place your thumb gently but firmly on the specimen, parallel to the long axis of the specimen; 3) with a single-edge razor blade under a low power of the dissection microscope, use your thumb tip to guide the blade when cutting a section, the first section then is discarded; 4) with a slight chopping motion, begin to cut thin sections by slowly pushing the razor blade back against your thumb tip as sections are cut; 5) discard the remaining plant material and any sections that appear to be too thick; and 6) add a small drop of water and cover slip, and observe under the compound microscope. With experience and practice thin sections of thalli and stems are quickly produced.

Geographic Regions of California

The geologic history of California is complex and its geography varied—from the coast to the high Sierra Nevada, and from the temperate rain forests of the northwest to the southeastern deserts. This tremendous diversity in substrates, habitats, microenvironments and "higher" plant communities all serve to influence the distribution of liverworts and hornworts. (For detailed information about California's geology, plant life and natural history, see Oakeshott 1978; Ornduff et. al. 2003; and Schoenherr 1992). Figure 1 locates the 11 Geographic Regions used in this publication (modified from the 10 used by Norris and Shevock [2004a]; the Northwestern California Region used by them has been separated into the Klamath Ranges and the North Coast Region).

1. Klamath Ranges (KR). The KR rock types are similar to those of the Sierra Nevada, i.e., remnants of metamorphic and volcanic rocks intruded by granite (Oakeshott 1978), and include the Marble, Scott and Siskiyou Mountains, and Trinity Alps. The Klamath Ranges extend from Oregon south to the South Fork Mountain Fault Zone, essentially the line followed by the Klamath and

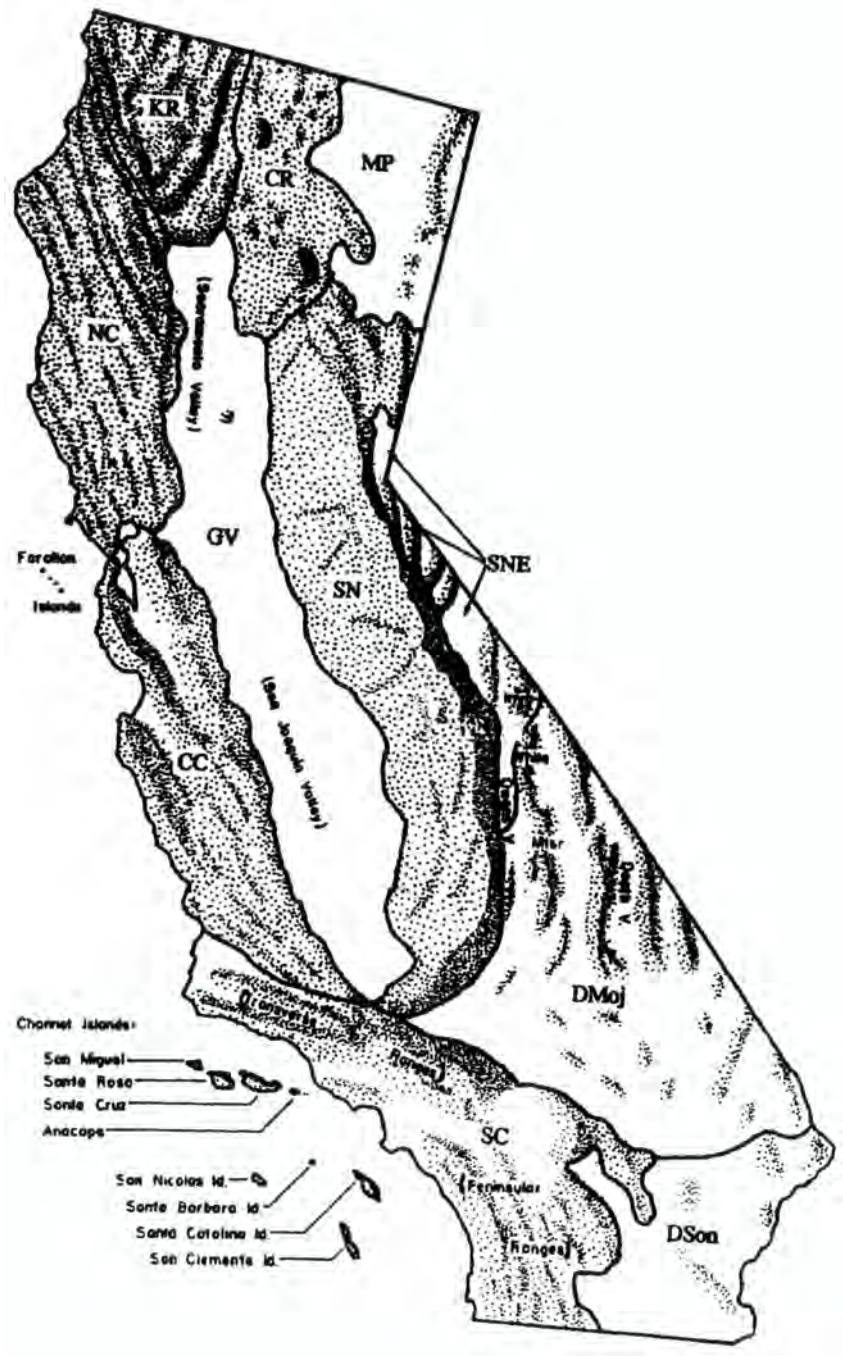

FIG. 1. California Geographic Regions. **CC**—Central Coast Region; **CR**—Cascade Range; **DMoj**—Mojave Desert; **DSon**—Sonoran Desert; **GV**—Great Valley; **KR**—Klamath Ranges; **MP**—Modoc Plateau; **NC**—North Coast Region; **SC**—South Coast Region; **SN**—Sierra Nevada; and **SNE**—Sierra Nevada East. (Modified from Munz, P. A. 1973. *A California Flora and Supplement*. UC Press, Berkeley, CA).

Trinity Rivers east to Douglas City, and then follow State Highway 299 from Douglas City east to Redding. The KR includes the area between the Del Norte County coast east to Interstate Highway 5 at Redding to the Oregon border.

2. North Coast Region (NC). The NC Region extends from South Fork Mountain Fault Zone-Redding south to the San Francisco Bay, and from the coast east to the Great Valley. Included are

Yolla Bolly, Snow Mountain, King Range, Mendocino Range, Mayacmas Mountains, Mount Tamalpais, and the Marin Peninsula.

3. Central Coast Region (CC). The CC Region extends from the San Francisco Bay south to State Highway 166 (on the north side of the Santa Ynez Mountains), and from the coast east to the Great Valley. Included are Diablo, Gabilan, Santa Lucia, and La Panza Ranges, and the Santa Cruz Mountains.

4. South Coast Region (SC). The SC Region extends from State Highway 166 south to Mexico, and from the coast east to the Mojave and Sonoran Deserts, and encompasses the Transverse and Peninsular Ranges. Included are the Santa Ynez, San Gabriel, Santa Monica, San Bernardino, San Jacinto, Santa Margarita, Santa Rosa, Laguna, Santa Ana, Agua Tibia, Cuyamaca, and In-Ko-Pah Mountains.

5. Cascade Range (CR). The CR region represents the southern end of a long north-south volcanic chain that extends from Southern British Columbia through Washington and Oregon into northern California. Included are Mount Shasta and Mount Lassen. Interstate Highway 5 north of Redding and the Great Valley form the western boundary. The southern boundary is complex, following an east to west line starting about where State Highway 44 joins State Highway 36 east of Susanville; it then follows State Highway 36 until it joins State Highway 32, and then follows Highway 32 until it reaches the Great Valley.

6. Sierra Nevada (SN). The SN Region represents a great block of granitic rock, with remnants of metamorphic and volcanic rocks. The Great Valley is its western border; the East of Sierra Nevada Region and the northwestern part of the Mojave Desert form the eastern border; the Klamath Range and Modoc Plateau form its northern border; and the Mojave Desert forms its southern border. The Sierra Nevada Region extends south to, and includes, the Tehachapi Mountains.

7. Great Valley (GV). The GV Region includes the Sacramento and San Joaquin Valleys.

8. Modoc Plateau (MP). The MP is an undulating volcanic landscape and is considered to be a small southwestern corner of the Columbia Plateau of eastern Oregon, Washington and southern Idaho. The boundaries of Modoc Plateau are Oregon on the north, Cascade Range on the west, Sierra Nevada on the south, and the State of Nevada on the east. The Warner Mountains are an uplifted section on the east side of the Modoc Plateau.

9. East of Sierra Nevada (SNE). The SNE Region includes the parts of Alpine and Mono Counties east of Sierra Nevada, and a part of Inyo County between Sierra Nevada and the Mojave Desert. The Sweetwater Mountains, Bodie Hills and Mono Lake are included in the East of Sierra Nevada Region.

10. Mojave Desert (DMoj). The DMoj Region includes the Inyo, White, Panamint, Funeral, New York, Clark, Last Chance, and Providence Mountains, Joshua Tree National Monument, and the Kingston Range. The Mojave Desert extends east into Nevada and Arizona.

11. Sonoran Desert (DSon). The DSon Region extends from the South Coast Region east into Arizona. The Pinto Basin is considered to be the western border of DSon. It includes Anza-Borrego Desert State Park, Palm Springs and the Chocolate Mountains. The California portion of the Sonoran Desert often is called the Colorado Desert.

Taxonomic Considerations

In early taxonomic treatments, hornworts were grouped with liverworts in the Hepaticae. Now it is recognized that liverworts and hornworts are not closely related and they are placed in separate phyla: Marchantiophyta (liverworts) and Anthocerotophyta (hornworts) (see Shaw and Goffinet [2000] for details). The informal names of liverworts and hornworts will be used here.

The genus and species names used, the citations of authors of species names, and the grouping of genera into families, are based on Stotler and Crandall-Stotler (1977), Grolle (1983), Crandall-Stotler and Stotler (2000), and Stotler and Crandall-Stotler (2005a), and updated as new information became available. Table 1 depicts the taxonomic grouping of genera within the families of California liverworts and hornworts.

Keys and Species Catalogue Overview

Key design. The following keys are hierarchical, organizing the bryoflora into smaller and smaller units. The first key separates liverworts from hornworts. Each group is treated separately in sections that follow. Liverworts are a large and diverse group. Because classification of the upper ranks of

liverworts presently remains unresolved, the first key under LIVERWORTS separates this large group into four informal sub-groups: 1) Complex Thalloid Liverworts, 2) Sphaerocarpoids, 3) Simple Thalloid Liverworts and 4) Leafy Liverworts. These categories are used for the convenience of ordering information for key purposes only and do not imply close phylogenetic relationships of all genera within a sub-group. When the sub-group to which your specimen belongs is known (e.g., Complex Thalloid Liverworts), then turn directly to the Genus Key of that sub-group in order to identify the genus. If you know the sub-group and genus, but not the species, turn to the Species Key under that genus. The genera are alphabetically listed under each sub-group.

Hornworts are a small group. Under HORNWORTS the keys by-pass sub-groups and go directly to genus and species (this section follows the liverworts).

Gametophytes of many species of liverworts and hornworts exhibit great morphological variability in response to local environmental conditions. In branching pattern and color, for example, a hornwort growing in a wet, reduced light habitat can look quite different from the same species growing in a drier, exposed habitat. Diseased individuals or plants collected early in its growing season (e.g., from November – February, following the variable onset of the California rains) can look different from healthy, mature (typical) shoots. Because a key character is not always present in all plants in a population, the cautionary words "sometimes," "usually," "mostly," "often," and "rarely" are used as reminders that variation does occur. It is important to select healthy, robust, mature parts of the plant for study, and to carefully read the keys.

Books with species illustrations are invaluable aids in identification. A must is Schofield (2002), *Field Guide to Liverwort Genera of Pacific North America.* (In this book, hornworts are included in the term liverwort). This useful book includes a full-page illustration of one species as a representation for each genus. Many species of California liverworts and hornworts are illustrated in this publication. Also recommended are the books by Paton (1999) and Damsholt (2002); although about British Isles and Nordic liverworts and hornworts they contain high quality and very detailed illustrations of many species that also occur in California. The six volume work by Schuster (1966–1992) on the liverworts and hornworts of North America east of the hundredth meridian also is an invaluable, but expensive resource; in addition, most of these volumes are out-of-print.

An effort throughout this work presented here has been made to keep scientific terminology to a minimum in order to focus on species identification, not on vocabulary. However, scientific terminology is more precise and provides a more accurate description. Appendix 1 contains a GLOSSARY of terms used in this publication.

Annotated species catalogue. A key is only a guide, a short-cut to plant identification. Annotation comments permit discussion about variation and potential problems in identification of each species. This publication is not designed as a manual, in which the same type of information is listed for each species. Instead, comments are crafted for individual species. The following categories enable us to share our experience in working with California liverworts and hornworts: **1) Distinctive features**—or what are the most important characteristics to look for in vegetative and reproductive plants. This section provides more detailed information about variation within a species than occurs in the key; **2) Separation**—how to descriminate a specimen from others that can look similar. For example, some dry plants of *Targionia hypophylla* can resemble some dry plants of *Asterella bolanderi*; a simple thallus cross-section can be used to separate these two plants; **3) Illustrations**—this publication does not provide illustrations. This section prresents references where high quality illustrations are available for visual comparison with your specimen; **4) Habitat**—often it is reassuring to know that your specimen was collected in the usual habitat. This section summarizes the types of habitats and at what elevations this species has been found previously; and 5) **Distribution**—this section summarizes the published worldwide distribution of the species, with particular reference to those California Geographic Regions in which it has been collected previously. A herbarium specimen is cited to document the regional distribution of each species.

Even with additional species information, be prepared for occasions when identification remains in doubt. Liverworts and hornworts are noted for the morphological variability of their gametophytes. Temporary changes in environmental conditions can produce dramatic changes in thallus and shoot color, leaf position, shape and size, leaf decurrency on the stem, development of cilia or trichomes, and cell wall thickness. In addition, juvenile growth forms of some species (of collections made too early in its growing season) often do not fit the key. Specimens that do not key to a known species can be a) a morphological variant of a known species, b) a species new to California, or c) an undescribed (new to science) species. Such collections often can be sent to a professional bryologist, along with full collection data and sufficient material for the bryologist to retain a portion of the collection to be placed in a herbarium so that the record is documented and is available to other researchers. **Important:** Write first. Communicate with any expert or professional before sending material.

There are times when research in progress requires use of caution in the circumscription of a species. In *Conocephalum conicum*, published preliminary research indicates that this taxon is comprised of more than one species (Szweykowski et al. 2005). Most of these new species cannot be morphologically separated. In *Marchantia polymorpha* research combining morphological studies and experimental techniques support the existence of three subspecies, but specimens can be assigned with certainty only when experimental data are available (Bischler-Causse and Boisselier-Dubayle 1991). In cases such as these examples, we use the species name in a broad sense (=*sensu lato* = *s. l.*), in contrast to a narrow sense (=*sensu stricto* = *s. str.*).

Liverwort and hornwort specimens at ABSH, CAS, CHSC, and UC, and in the personal herbarium of the senior author were the primary source for this study. We also examined specimens at COLO, DAV, MO, NY, SFSU, SFV, WTU, and YU. The Doyle herbarium is being transferred to UC.

Appendix I contains a glossary of terms as used in this publication. Appendix II is a list of synonyms of liverworts and hornworts reported for California.

Liverwort or Hornwort

1. Plants leafy or thalloid; cells of the apical region with many small chloroplasts per cell; capsules spherical to elongate, lacking stomata and a central columella. . . . . **Liverwort** p. 8.
1. Plants always thalloid; cells of the apical region with a single chloroplast per cell (some species have two or more chloroplasts in cells of other parts of the thallus); capsules elongate, long cylindrical (horn-like), with stomata and a central columella. . . . . **Hornwort** p. 97.

LIVERWORTS

Key to the Four Major Groups of Liverworts

1. Plants thalloid, with internal air chambers or vertical, finger-like air-channels; rhizoids of most species both pegged and smooth-walled. . . . . **Complex Thalloid Liverworts** p. 8.
1. Plants leafy or, if thalloid, without internal air chambers or vertical, finger-like air-channels; rhizoids always smooth-walled. . . . . **2.**
2. Plants leafy, only rarely dichotomously branched; archegonia and sporophytes terminal on the main axis or lateral branch. . . . . **Leafy Liverworts** p. 45.
2. Plants thalloid or, if leafy, dichotomously branched; archegonia and sporophytes on the dorsal surface of a main axis or lateral branch. . . . . **3.**
3. Plants **either** terrestrial with bottle- or flask-shaped involucres covering the dorsal surface, **or** ribbon-like submerged aquatics attached to the substrate. . . . . **Sphaerocarpoids** p. 31.
3. Plants terrestrial but never with bottle- or flask-shaped involucres on the dorsal surface. . . . . **Simple Thalloid Liverworts** p. 36.

Complex Thalloid Liverworts

Gametophytes of California species of complex thalloid liverworts are distinguished by a) a dorsiventral thallus with differentiated internal photosynthetic tissue consisting of air-chambers or vertical, finger-like air-channels, b) usually two kinds of rhizoids—pegged, with localized internal deposits of wall material and smooth-walled, lacking such deposits, and c) unistratose scales usually on the ventral thallus surface (these scales are obsolete or ephemeral in a few species).

The dorsiventral gametophytes of hornworts and simple thalloid liverworts a) lack differentiated internal photosynthetic tissue with air-spaces, b) have only smooth-walled rhizoids and c) usually lack unistratose scales.

In California, there are 12 genera, 28 described species, 1 species to be described in a subsequent publication, and 2 previously reported species excluded from the flora.

Genus Key (See Appendix I, Glossary, for definition of terms)

The first key is to be used for plants with sporophytes. Plants are more easily identified to genus when the key includes a combination of vegetative and sexual reproductive features. For this reason, try to plan field-work around the seasonal reproductive biology of the plants and search thoroughly for this year's or the previous year's reproductive structures before making a collection. In general, collections are best made from mid-March to late May in lower elevation, summer-dry habitats, and June to September in higher elevation, slow-to-dry or snow-melt areas.

The second key is to be used for plants that lack sporophytes. Because of vegetative thallus morphological and structural diversity within a genus, some species of the same genus will key at different places (e.g., species of *Riccia*). Moreover, the genera of *Mannia*, *Reboulia* and *Asterella* belong to the same family and, at times, can be very difficult to separate without the availability of reproductive structures; for these three genera the key goes directly to species.

I. Plants With Sporophytes

1. Archegonia and sporophyte capsules embedded in thallus tissue; sporophytes consisting of a capsule only (without a seta or foot); capsules containing spores but not sterile cells (elaters). . . . . **2.**
1. Archegonia and sporophyte capsules associated with an archegoniophore or involucre, but never embedded in thallus tissue; sporophytes consisting of a capsule, seta and foot; the capsules containing spores and sterile cells (elaters). . . . . **3.**
2. Plants floating like a canoe or raft on the water surface, ventral scales conspicuous, purplish, pendant and lanceolate, or plants stranded with ventral scales smaller, inconspicuous, and purplish to hyaline; oil-cells scattered in the dorsal epidermis and ventral scales; thalli of male plants with elongate antheridial receptacles in the dorsal grooves. . . . . **Ricciocarpos**
2. Plants terrestrial, or if aquatic, floating at or just below the water surface; ventral scales minute, vistigial or larger and projecting beyond the thallus margins; oil-cells absent in the dorsal epidermis and ventral scales; antheridia scattered in the dorsal thallus tissue, but never in a differentiated receptacle. . . . . **Riccia**
3. Sporophytes sessile, displaced to the ventral surface at a branch apex and enveloped by a conspicuous, shiny, purplish-black involucre. . . . . **Targionia**
3. Sporophytes elevated on an archegoniophore above the thallus surface, not enveloped by a conspicuous, shiny, purplish-black involucre. . . . . **4.**
4. Thallus dorsal epidermis with compound pores; antheridia elevated on antheridiophores above the thallus. . . . . **5.**
4. Thallus dorsal epidermis with simple pores; antheridia in receptacles or scattered on the dorsal thallus surface, not elevated on antheridiophores. . . . . **6.**
5. Carpocephalum with 7–11 finger-like rays (resembling spokes of an umbrella); thalli often with dorsal cup-shaped gemma-receptacles; ventral scales in 4–6 rows (2–3 rows on each side of the midrib), with oil-cells. . . . . **Marchantia**
5. Carpocephalum without finger-like rays; thalli without gemma-receptacles; ventral scales in 2 rows (1 row on each side of the midrib), without oil-cells. . . . . **Preissia**
6. Thallus air-chambers in a single layer, with uniseriate chlorophyllose filaments attached to the chamber floor; ventral scales each with a single, semicircular appendage. . . . . **7.**
6. Thallus air-chambers in more than one layer, empty of filaments, but often subdivided by cell-plates or secondary walls (the photosynthetic tissue often appearing spongy); ventral scales each with 1–4 slender appendages. . . . . **8.**
7. Thalli large, to 25 cm long and 17 mm wide; fresh thalli generally fragrant when crushed; terminal cells of photosynthetic filaments under pores markedly elongate and somewhat pyriform in shape; carpocephalum conical at maturity; gemma-receptacles absent. . . . . **Conocephalum**
7. Thalli smaller, 1.5–4 cm long and 5–10 mm wide; fresh thalli not or only little fragrant when crushed; terminal cells of photosynthetic filaments under pores not elongate and pyriform, but rounded on the free end; carpocephalum cruciate at maturity; gemma-receptacles crescent-shaped, usually present on some thalli of a population. . . . . **Lunularia**
8. Archegoniophores arising from the dorsal thallus surface behind the apex; antheridia scattered (not in a defined receptacle) in an elongate band on the dorsal thallus surface, with conspicuously elongate ostioles; ventral scales without marginal slime-hairs. . . . . **Athalamia**
8. Archegoniophore arising from the apex of a main or short lateral branch; antheridia developing in a usually well-defined receptacle on the dorsal thallus surface, without conspicuously elongate ostioles; ventral scales with marginal slime-hairs. . . . . **9.**
9. Carpocephalum with a conspicuous whitish or purplish pseudoperianth, which is longitudinally split into 6 or more linear segments. . . . . **Asterella**
9. Carpocephalum without or with an inconspicuous pseudoperianth, but when present not split into segments. . . . . **10.**

10. Carpocephalum nearly circular in circumference when mature, slightly convex on the upper surface, and nearly flat below; thallus very thin when dry; air-chambers large and empty; ventral scales small or rudimentary. . . . . **Cryptomitrium**
10. Carpocephalum hemispherical or subconical when mature; thallus thin or thick when dry; air-chambers usually with many secondary partitions; ventral scales conspicuous. . . . . **11.**
11. Carpocephalum distinctly lobed; lids of mature capsules falling away in fragments; pores in the dorsal epidermis surrounded by 3–5 concentric circles of cells. . . . . **Reboulia**
11. Carpocephalum not or little lobed; lids of mature capsules falling away intact; pores in the dorsal epidermis surrounded by 2–3 (seldom more) concentric circles of cells. . . . . **Mannia**

II. Plants Lacking Sporophytes

1. Thalli with gemma-receptacles. . . . . **2.**
1. Thalli without gemma-receptacles. . . . . **3.**
2. Gemma-receptacles cup-shaped; dorsal epidermis with compound pores. . . . . **Marchantia**
2. Gemma-receptacles crescent-shaped; dorsal epidermis with simple pores. . . . . **Lunularia**
3. Plants aquatic that float on or below the water surface, or become stranded on soil at the water's edge. . . . . **4.**
3. Plants clearly terrestrial. . . . . **5.**
4. Plants aquatic and **either** a) floating on the water surface with several rows of conspicuous, large, purplish ventral scales that are pendent in the water column; oil-cells present in the dorsal epidermis and ventral scales of both aquatic and stranded thalli; **or** b) plants stranded, large and grayish-green, thin and usually with a shiny dorsal surface when dry; ventral scales hyaline and usually difficult to locate because of the numerous rhizoids. . . . . **Ricciocarpos**
4. Plants aquatic and suspended in the water column; ventral scales of both aquatic and stranded thalli vestigial or inconspicuous and in a single median row (but can appear to be in two rows when bifid); oil-cells absent in the dorsal epidermis and ventral scales.. . . . . (some species of) **Riccia**
5. Photosynthetic tissue with narrow, vertical, finger-like air-channels. . (some species of) **Riccia**
5. Photosynthetic tissue with air-chambers in one or more layers. . . . . **6.**
6. Dorsal epidermis with compound pores (cut thallus cross-sections to determine). . . . . **7.**
6. Dorsal epidermis with simple pores (cut thallus cross-sections to determine). . . . . **8.**
7. Ventral scales hyaline to slightly purplish, in 4–6 rows (2–3 rows on each side of the midrib), with scattered oil-cells; gemma-receptacles usually present. . . . . **Marchantia**
7. Ventral scales deep purplish-black, in 2 rows (1 row on each side of the midrib), without oil-cells; gemma-receptacles always absent. . . . . **Preissia**
8. Air-chambers in a single layer (view in thallus cross-section), photosynthetic filaments attached to the chamber floor. . . . . **9.**
8. Air-chambers in more than one layer (view in thallus cross-section), photosynthetic filaments absent from the air-chambers (the chambers may be subdivided by cell-plates or secondary walls). . . . . **11.**
9. Thalli mostly 1–2.5 cm long × 2–5 mm wide; ventral scales dark blackish-purple, with a lanceolate appendage. . . . . **Targionia**
9. Thalli 1.5–25 cm long × 5–22 mm wide; ventral scales hyaline to purplish, with semi-circular or reniform appendages. . . . . **10.**
10. Thalli large, 5–25 cm long × 5–22 mm wide; ventral thallus tissue with slime-canals; freshly collected plants usually fragrant when crushed; terminal cells of filaments under pores elongate, somewhat pyriform at their free-ends; gemma-receptacles lacking. . . . **Conocephalum**
10. Thalli medium sized, 1.5–4 cm long × 5–10 mm wide; ventral tissue without slime-canals; freshly collected plants not, or only little fragrant when crushed; terminal cells of filaments under pores rounded at their free-ends: crescent-shaped gemma-receptacles usually present. . . . . **Lunularia**
11. Epidermal pores poorly developed, inconspicuous; dorsal epidermis often disintegrating in older thallus parts, especially upon drying, giving the thallus a frothy or spongy appearance. . . . . (some species of) **Riccia**
11. Epidermal pores well-developed and conspicuous; dorsal epidermis remaining intact in older thallus parts and upon drying. . . . . **12.**
12. Thallus wing with a thin, often undulating surface; dorsal epidermal cells with many chloroplasts; ventral scales small and inconspicuous or fragile and lacking; oil-cells lacking in the dorsal epidermis. . . . . **Cryptomitrium**

12. Thallus wing thin or thick, often firm and somewhat leathery, but not undulating; dorsal epidermal cells not richly chlorophyllose; ventral scales conspicuous and persistent; oil-cells usually present in the dorsal epidermis. . . . . **13.**
13. Thallus sparingly dichotomously branched, often appearing long and strap-shaped, branching generally lateral, of ventral origin; antheridia and/or archegonia on short lateral branches of ventral origin (look for short lateral branches on dry plants). (Dry thalli of *Targionia* occasionally fit this description, but key out earlier because they have air-chambers in a single narrow layer with photosynthetic filaments attached to the floor.) . . . . . **14.**
13. Thallus frequently dichotomously branched, seldom appearing long and strap-shaped; antheridia and archegonia on main thallus branches. . . . . **16.**
14. Ventral scales with 2–3 hyaline appendages visible at the thallus apex; female branches with a conspicuous apical tuft of hyaline scale appendages; living plants of some populations fragrant, other populations not fragrant; plants of higher elevations, mostly above 1450 m. . . . . **Mannia fragrans**
14. Ventral scales with 1–2 purple or reddish-purple appendages usually not visible at the thallus apex; female branches without an apical tuft of scale appendages; living plants of most species not aromatic; plants of lower elevations, mostly below 1400 m. . . . . **15.**
15. Ventral scales with 1 (occasionally 2) appendages that usually do not extend beyond the thallus margin; archegonia and antheridia on short lateral branches of ventral origin; oil cells of ventral scales reddish in color. . . . . **Asterella bolanderi**
15. Ventral scales with 1–2 appendages that often extend beyond the thallus margin, but never forming an apical tuft at the thallus apex; archegonia on short lateral branches of ventral origin and antheridia on the dorsal surface of main branches; oil-cells of ventral scales hyaline. . . . . **Mannia californica**
16. Ventral scales in 2 or more irregular rows with the scale apex conspicuous and appendage-like (not constricted at the base from the main scale body), and the scale appendages usually conspicuously projecting apically and laterally beyond the thallus margin; ventral scales without oil-cells and 1-celled marginal slime-hairs. . . . . **Athalamia**
16. Ventral scales in 2 definite rows with the scale apex bearing 2 or more appendages that extend only little beyond the thallus margin; ventral scales with oil-cells and 1-celled marginal slime-hairs. . . . . **17.**
17. Ventral scales each with 2–4 appendages (look at several scales before deciding). . . . . **18.**
17. Ventral scales each with 1–2 appendages (look at several scales before deciding). . . . . **19.**
18. Dorsal epidermis roughened with elevated distinct pores and visible underlying areolation; thallus lateral margins entire (not scalloped or crenulate); ventral scales each with 2–4 appendages (look at several scales). . . . . **Asterella californica**
18. Dorsal epidermis smooth with only slightly elevated indistinct pores and indistinct underlying areolation; thallus lateral margins usually distinctly scalloped to crenulate; ventral scales each with 2 (seldom 3) appendages (look at several scales). . . . . **Reboulia hemisphaerica**
19. Dorsal epidermis with a few, scattered oil-cells; ventral scales with 1 (rarely 2) appendages; plants of higher elevations, mostly above 1000 m. . . . . **Asterellagracilis**
19. Dorsal epidermis without oil-cells; ventral scales with 1–2 appendages; plants of lower elevation, mostly below 950 m. . . . . **Asterella palmeri**

Asterella P. Beauv. 1805
(Aytoniaceae)

This genus is separated from the other genera of complex thalloid liverworts by a) the presence of conspicuous pseudoperianths pendent from the lower surface of carpocephala, and b) pseudoperianths that are longitudinally divided into 6–14 narrow lanceolate segments.

Four species are confirmed for California.

Species Key

1. Thallus mostly with lateral branching of ventral origin; antheridia developing on the dorsal surface of a short lateral branch of ventral origin; archegoniophore developing at the apex of a short lateral branch of ventral origin. . . . . **A. bolanderi**
1. Thallus usually dichotomously branched; antheridia developing on the dorsal surface of a main branch; archegoniophore developing at the apex of a main branch (**note:** In *A.*

californica, the archegoniophore can appear to be lateral because of the continued growth of non-reproductive branches). . . . . **2.**

2. Plants dioicous; carpocephalum strongly lobed; filiform scales present at the apex of the archegoniophore; thallus air-chambers subdivided by secondary wall partitions; spore coat with fine areolation giving the spore a frothy appearance under the compound microscope. . . . . **A. californica**

2. Plants paroicous; carpocephalum little or not lobed; filiform scales absent at the apex of the archegoniophore; thallus air-chambers not, or only incompletely, subdivided by secondary wall partitions; spore coat without fine areolation and without a frothy appearance under the compound microscope. . . . . **3.**

3. Carpocephalum hemispherical evenly rounded in side view; pseudoperianth segment tips usually free at maturity; spores yellow to yellow-brown, 58–82 μm in diameter. . . . **A. gracilis**

3. Carpocephalum conspicuously conic in side view; pseudoperianth segment tips remain attached at maturity; spores dark brown to nearly black, 65–93 μm in diameter. . . . **A. palmeri**

Asterella bolanderi, A. californica and *A. palmeri* usually occur in summer-dry habitats of lower elevation and can occur in close proximity. *Asterella gracilis* generally occurs in damper, slower-to-dry habitats of higher elevation.

Excluded. Asterella saccata (Wahlenb.) A. Evans. Based on *Howell 704* (CAS), Sutliffe (1947) reported the presence of this species from the high Sierra Nevada of Inyo County. Examination of the *Howell 704* during this study, however, located the presence of a female thallus with archegonia in a pit-like depression on the dorsal surface of the thallus midrib, behind the apex. In addition, the morphology and structure of plants in *Howell 704* are consistent with *Athalamia hyalina*. No herbarium collection examined in the present study confirmed the presence of *A. saccata* in California.

Asterella bolanderi (Austin) Underw.

Distinctive features. With reproductive plants, look for a) on the same thallus, antheridia and archegonia on separate short lateral branches of ventral origin, b) archegoniophore with a few filiform scales on the stalk and at the apex, but none at the base, c) a strongly lobed carpocephalum in both living and dry plants, d) 10–16 whitish to purplish pseudoperianth segments that remain attached at sporophyte maturity, and e) yellowish-brown spores, 75–105 μm in diameter with a coarsely areolate distal face, the areolae 12–20 μm wide. Sporophytes mature late March through mid-June.

With vegetative plants, look for a) relatively long, sparingly dichotomously branched, strap-shaped thalli, b) mainly lateral branching of ventral origin, c) living thalli 1.5–4.5 mm wide, with a green dorsal surface and margins that turn purplish with age, d) dorsal epidermal cells with no or small trigones, e) margins of dry thalli usually very strongly incurved and nearly tubular, exposing the blackish-purple ventral surface, f) usually reddish-purple ventral scales, mostly with 1 hyaline to purplish appendage that usually does not extend beyond the thallus margin or apex, and g) oil-cells of ventral scales reddish in color.

Separation. The a) sparingly dichotomously branched, relatively long, strap-shaped main branches, b) location of both antheridia and archegonia on separate lateral branches of ventral origin, and c) spore markings, readily separate this species from others in the genus and most other complex thalloid liverworts. Vegetative plants can be confused with *Mannia californica* and *Targionia*. However, as seen in a thallus cross-section, *Targionia* has the photosynthetic tissue in a single thin layer with photosynthetic filaments attached to the chamber floor, unlike both *A. bolanderi* and *M. californica*. The latter two genera are in the same family (Aytoniaceae) and both have generally similar vegetative morphology and anatomy. See *M. californica* for separation from that species.

Illustrations. Frye and Clark 1937; Howe 1899; Schuster 1992b.

Habitat. Exposed to lightly-shaded summer-dry areas. Soil of meadows, and of creek-, road- and ravine-banks, soil around rock outcrops, open areas in chaparral and woodlands. Elevation usually below 1300 m, but occasionally up to 1550 m.

Distribution. Asterella bolanderi is endemic to southwestern Oregon and California. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 11354* (UC), **CR**: Tehama Co. *Doyle 8594* (UC), **KR**: Shasta Co. *Doyle 9125* (UC), **NC**: Mendocino Co. *Doyle 10416* (UC), **SC**: Riverside Co. *Doyle 7326* (UC), **SN**: Nevada Co. *Doyle 8498* (UC).

Asterella californica (Hampe) Underw.

Caution. This is the most common and widespread species of *Asterella* in California. Non-reproductive, vegetative plants can be variable in color and growth characteristics, and occasionally are challenging to identify. The dorsal surface of plants collected early following the onset of winter rains, or from dimly-lit and/or wet habitats (e.g., wet shaded underhangs of cliff faces and boulders, and shaded streambanks and seepages), can be nearly uniformly green with little or no yellowish-brown to brown to purplish-black coloration of the lateral margins, and with little or no purplish-black coloration of the ventral thallus surface or scales. Moreover, the lateral margins of these plants often do not incurve when dry. The appearance of these plants contrasts markedly with plants collected later in the year from the same area, or from plants that grow in more exposed habitats; these plants generally have yellowish-brown to brown to purplish-black lateral margins and purplish-black ventral surfaces and scales. When dry, the margins of these "typical" plants usually are strongly incurved over the photosynthetic tissue, often with only the dark ventral surface and scales exposed to the environment.

Distinctive features. This is the only dioicous species of this genus in California. With reproductive plants, look for a) separate female and male plants, b) antheridia clustered in distinctive non-stalked receptacles on the dorsal thallus surface of main branches (mature receptacles of plants in exposed habitats usually are purplish and slightly elevated above the thallus surface, and often have small scales around the receptacle margin; plants from wet or dimly-lit habitats often have antheridia in a slightly raised single or double row that lacks purplish coloration and scales), c) a cluster of filiform hyaline scales at the archegoniophore apex and none at the base, d) a strongly 3–4 (occasionally 5) lobed carpocephalum, with pseudoperianths directed obliquely to nearly horizontally outward, e) hyaline pseudoperianths with 12 or more segments, the segment tips remain attached at sporophyte maturity, f) distinctive yellow spores, 95–125 μm in diameter, the distal face usually with broad, rounded folds/ridges that occasionally form one or more large areolae, and g) finely areolate surface texture of both distal and proximal faces, which give the spore a frothy appearance with the compound microscope. Sporophytes mature early February through late May.

With vegetative plants, look for a) frequently dichotomously branched thalli, the branches 0.9–2.3 cm long and 5–10 mm wide and b) hyaline ventral scales usually with 2–4 appendages.

Separation. This species is readily separated from others of the genus by its yellow, frothy-appearing spores. Occasionally, however, non-reproductive plants of *A. californica* occuring in damp shaded habitats have lateral margins that are yellowish-brown to brown and remain flat when dried. Vegetative plants of this species have been confused with the related species, *Reboulia hemisphaerica*. The two species can be separated by a) lateral thallus margins entire in *A. californica* (vs. distinctly scalloped to crenulate lateral margins in *R. hemispherica*) and b) *A. californica* has 2–4 scale appendages that are subulate with acute apices (vs. usually only 2 scale appendages that are linear with acute apices).

Male plants of *A. californica* from exposed habitats and with mature antheridial receptacles are distinctive and should not be confused with male plants of other complex thalloid liverworts. However, male plants from wet or dimly lit habitats occasionally have antheridia in only one or two rows and only slightly elevated on poorly differentiated receptacles. These plants superficially can be confused with male plants of *Athalamia hyalina*. Look at the ventral scales: the ventral scale of *Asterella californica* has 2–4 appendages that are sharply differentiated from the main scale, whereas the ventral scale of *Athalamia hyalina* has a single, long triangular "appendage" that is not constricted at the base or sharply differentiated from the main scale.

Illustrations. Frye and Clark 1937; Howe 1899.

Habitat. Diverse exposed to lightly shaded areas that dry soon after cessation of spring rains, such as open areas in chaparral and oak woodlands, and on rock and sandstone outcrops, ravine banks, and cliffs. Elevation mostly from near sea-level to 1200 m, but occasionally up to 2000 m.

Distribution. Asterella californica occurs in southwest Oregon, California, Arizona and Mexico (incl. Guadalupe Island). Calif. Geographic Regions: **CC**: San Mateo Co. *Whittemore 4407* (CAS), **CR**: Tehama Co. *Doyle 8624* (UC), **DSon**: San Diego Co. *Doyle 11274* (UC), **KR**: Trinity Co. *Doyle 5821* (UC), **NC**: Colusa Co. *Kellman 2731* (CAS), **SC**: San Diego Co. *Doyle 9902* (UC), **SN**: Tulare Co. *Shevock 12983* (CAS).

Asterella gracilis (F. Weber) Underw.

Because of a taxonomic mixup, this species is listed as *A. ludwigii* (Schwaegr.) Underw. in older publications (e.g., Frye and Clark 1937).

Distinctive features. With reproductive plants, look for a) archegoniophores, often reddish near the base, at the apices of main branches, b) antheridial receptacles sessile in a small, often poorly defined, purplish cluster either (1) posterior to the archegoniophore or (2) on a separate branch, c) archegoniophore lacking an apical tuft of scales and scales inconspicuous or absent at the base, d) carpocephala of living plants nearly hemispherical and little lobed (the lobing is more pronounced in dry carpocephala), and with pseudoperianths directed obliquely or nearly vertically downward, e) hyaline or slightly reddish-purple pseudoperianths, each usually with 6–8 segments; the segment tips usually are free at sporophyte maturity, f) yellow to yellowish-brown spores, 58–82 μm in diameter, the distal spore face with rounded sinuous ridges that intersect and usually form shallow areolae 8–16 μm wide. Sporophytes mature late April through August.

With vegetative plants, look for a) often slightly fragrant living plants, b) usually dichotomously branched thalli, 0.5–1.5 cm long and 1–3 mm wide, c) green dorsal thallus surface, often with reddish lateral margins, and (usually) shiny reddish-purple ventral surface and scales, d) dorsal epidermis with a few, scattered oil-cells, and e) ventral scales mostly with a single appendage.

Separation. Details of spore markings (yellow to yellowish-brown and non-frothy) easily separate this species from others in the genus. In addition, the combination of a) slight fragrance of living plants, b) frequently dichotomously branched, c) usual reddish coloration of thallus margins, d) shiny reddish-purple of the ventral surface and scales, and e) a plant of higher elevation can be used to separate vegetative plants of *A. gracilis* from the other species in the genus.

Illustrations. Damsholt 2002; Frye and Clark 1937 (as *A. ludwigii*); Schofield 2002; Schuster, 1992b.

Habitat. A species of slow-to-dry, higher elevations. Damp soil of seepages, creek and lake banks, cliff recesses, and rock outcrops; splash of cascades and waterfalls. Elevation usually above 1500 m, but down to 550 m in Plumas Co.

Distribution. Asterella gracilis occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 9887* (UC), **KR**: Trinity Co. *Doyle 4627* (UC), **MP**: Modoc Co. *Doyle 2889* (UC), **NC**: Humboldt Co. *Norris 50159* (UC), **SN**: Mariposa Co. *Shevock 18491* (CAS).

Asterella palmeri (Austin) Underw.

This species, like the others in the genus, has spores with species-specific markings. Study immature spores of *A. palmeri*, because mature spores are opaque and the markings can be difficult to discern.

Distinctive features. With reproductive plants, look for a) antheridia in a small irregular receptacle usually posterior to the archegoniophore, b) at the apex of a main branch, an archegoniophore that lacks basal and apical scales, c) in living plants, a carpocephalum nearly conical and scarcely lobed with the pseudoperianths directed nearly vertically downward; in dry plants, the top of the carpocephalum shrinks considerably and the pseudoperianths usually are directed obliquely outward, d) pseudoperianths with 8–12 hyaline segments, the tips of which remain attached at maturity, e) dark-brown to nearly black mature spores 65–93 μm in diameter; the distal spore face usually with short, rounded and tightly spaced ridges. Sporophytes mature late February through early May.

With vegetative plants, look for a) usually dichotomously branched thalli, 0.5–1 cm long and 2–5 mm wide, b) brownish-black to purplish thallus margins usually strongly incurved in dry plants, c) absence of oil-cells in the dorsal epidermis, and d) ventral scales with 1–2 appendages.

Separation. The dark brown, nearly opaque spores separate this species from others in the genus. Also distinctive in living plants is the conical carpocephalum with pseudoperianths directed nearly vertically downward.

Illustrations. Frye and Clark 1937; Howe 1899.

Habitat. Exposed to lightly shaded summer-dry soil; usually on gentle to steep slopes around chaparral, *Quercus* and *Pinus*. Elevation usually below 950 m, but up to 1250 m in the southern Sierra Nevada.

Distribution. Asterella palmeri is restricted in distribution to California and northern Baja California, Mexico. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8115* (UC), **NC**: Sonoma Co. *Baker 2* (UC), **SC**: Riverside Co. *Doyle 7256* (UC), **SN**: Kern Co. *Laeger 2553* (CAS).

Athalamia Falc. 1851
(Cleveaceae)

The presence of pit-like depressions in the midrib tissue of the dorsal thallus surface of female plants is a distinctive feature of this genus. These depressions contain archegonia, and, following fertilization, the archegoniophore develops in these depressions.

A single species in California.

Athalamia hyalina (Sommerf.) S. Hatt.

Distinctive features. With reproductive plants, look for a) antheridia, with conspicuous, elongate hyaline ostioles, in an elongate band on the dorsal midrib region of male plants, b) one or more circular or elongate pit-like depressions with projecting white lanceolate scales on the dorsal midrib region of female plants; post-fertilization, the scales are elevated at the apex of the archegoniophore, c) the archegoniophore arising from the midrib dorsal surface well behind the thallus apex, and d) distinctive orange- to reddish-brown spores, 45–64 μm in diameter, with numerous, prominent hemispherical bumps or blisters on the distal spore face. Sporophytes of plants below 1820 m generally mature mid-March through May; above 1820 m from late May through September.

With vegetative plants, look for a) dull- to gray-green thalli 0.5–1.5 cm long and 2.5–5.5 mm wide, b) hyaline or purplish appendage-like apices of ventral scales that often form conspicuous apical clusters and also usually extend beyond the lateral thallus margins, c) simple epidermal pores with a single (sometimes indistinct) circle of cells that sometimes appear stellate in surface view because of wall thickening on the radial cell walls (**note**: cells around the pores of plants collected early in the growing season or from moist habitats can lack the thickened radial walls), and d) ventral scales in 2 to several irregular rows and which lack oil-cells and 1-celled slime filaments.

Separation. Pit-like chambers in the midrib region of the dorsal surface of female thalli separate *A. hyalina* from other California complex thalloid liverworts. Search field populations for thalli with young or last year's pit-like depressions. Male plants also are distinctive—antheridia a) are in an elongate band in the midrib region of the dorsal surface, b) have conspicuous, elongate hyaline ostioles, and c) are not in a well-defined receptacle. See *Asterella californica* for separation of male plants of that species from *Athalamia hyalina*.

Vegetative plants can be separated by the combination of a) presence of conspicuous hyaline or purplish ventral scale appendages that usually extend beyond the thallus apex and lateral margin and b) pores of air-chambers surrounded by a single circle of cells.

Illustrations. Damsholt 2002; Frye and Clark 1937; Schofield 2002; Schuster 1992b.

Habitat. Damp and slow-to-dry soil around granite rocks, and limestone, sandstone, granitic and metamorphic outcrops; margin of drainages and steep hillsides. Elevation from near sea-level to 3820 m.

Distribution. Athalamia hyalina occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 10910* (UC), **DSon**: San Diego Co. *Doyle 7078* (UC), **KR**: Trinity Co. *Doyle 6621* (UC), **MP**: Modoc Co. *Doyle 7492* (UC), **SC**: Los Angeles Co. *Doyle 10366* (UC), **SN**: Inyo Co. *Doyle 6650* (UC).

Conocephalum Hill 1780
(Conocephalaceae)

The following combination of characteristics separates this genus from other complex thalloid liverworts: a) large size of the thallus (6 to 25 cm long), b) air-chambers in a single layer and with simple pores, c) elongate (beaked) terminal cells of photosynthetic filaments under the pores, d) male receptacles terminal on very short branches, and e) spores germinate and become multicellular prior to discharge from the capsule.

The number of species in the genus and the name of the species in California is uncertain. Until recently, *Conocephalum conicum* was considered to be the name of the species in California. However, Szweykowski et al. (2005) restricted *C. conicum* to Europe and placed collections from the U.S.A. and India in a new species, *C. salebrosum* Szweyk. et al. They also reported that there are six cryptic species in *C. conicum*. The morphology of California specimens examined in this study fit *C. salebrosum*. However, Forrest et al (2006) have determined that although Illinois specimens are morphologically like *C. salebrosum*, they are very distinct from this species in molecular sequence data. They recommend that the cryptic species diversity within *C. conicum* s.l. needs further investigation. In the

present publication, we use *C. conicum* s.l. and look forward to the resolution of this taxonomic question.

Conocephalum conicum (L.) Dumort. *s. l.*

Distinctive features. Most populations will be vegetative or without sporophytes. The simplest way to identify *C. conicum* s. l. in the field is to crush a small bit of the fresh thallus—released will be a strong to weak musty or mushroomy aroma. With dry plants, look for a) large thalli, 6–25 cm long and 6–22 mm wide, b) simple pores and air-chambers in a single, thin layer with photosynthetic filaments attached to the chamber floor, c) terminal cells of filaments immediately below the pores conspicuously elongate (beaked) and with few or no chloroplasts, d) mucilage cells in the ventral thallus tissue, e) male plants with violet to purple oval, circular or crescentic antheridial receptacles sessile on the dorsal surface of very short lateral branches, f) archegoniophores at the apices of main branches, g) a strongly conical carpocephalum with 6–9 very short lobes, and h) spores 72–93 μm in diameter, with thin light-brown walls; the spores become multicellular through cell divisions prior to spore discharge. Sporophytes mature late January through April.

Separation. Conocephalum conicum s. l. occasionally grows in proximity to *Marchantia* and *Lunularia*. It is separated from *Marchantia* by the presence of simple dorsal epidermal pores (vs. compound pores), and from both *Marchantia* and *Lunularia* by the absence of gemma-receptacles.

Illustrations. Damsholt 2002; Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. Shaded sites; compacted soil, rocks and walls of ditches, creeks, rivers, and seepages. Usually close to water where it is seasonally inundated and there is elevated humidity during summer months. Elevation from near sea-level to 2520 m.

Distribution. Conocephalum conicum s. l. occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 6147* (sporophytes) (UC), **KR**: Trinity Co. *Doyle 5810* (UC), **MP**: Modoc Co. *Doyle 6692* (UC), **NC**: Humboldt Co. *Doyle 7683* (UC), **SN**: Mono Co. *Doyle 6724* (UC).

Cryptomitrium Austin ex Underw. 1883
(Aytoniaceae)

Distinctive features of this complex thalloid liverworts are: a) an unlobed, nearly circular carpocephalum that is only slightly convex on the upper surface and nearly flat on the lower, b) a thin thallus with a somewhat shiny dorsal surface (especially on dry plants), and c) thin-walled dorsal epidermal cells that contain numerous chloroplasts.

A monotypic genus.

Cryptomitrium tenerum (Hook.) Austin ex Underw.

Distinctive features. With reproductive plants, look for a) sessile antheridia, in 1–2 rows immediately behind the archegoniophore on the dorsal thallus surface, b) archegoniophores at the apex of main branches, c) when mature, a carpocephalum that is circular to discoidal in outline, and bears 3–7 sporophytes, d) in side view, the upper surface of the carpocephalum is slightly convex, and the lower surface is nearly flat, and e) light to dark brown spores, 45–60 μm in diameter, the distal spore face with irregular areolae. Sporophytes mature late February through March.

With vegetative plants, look for a) a thin thallus; the dorsal surface of dry plants often appears fragile (not firm or leathery), b) often somewhat undulate, but not crenulate, lateral thallus margins that do not or only little incurve when dry, c) yellowish-brown older thallus areas, d) dorsal epidermal cells with numerous chloroplasts and without oil-cells, e) large air-chambers sparingly divided by supplementary wall partitions, and f) small ventral scales in 2 rows, each with 2 filiform appendages; the scales sometimes fragmentary.

Separation. This species should easily be separated from other complex thalloid liverworts by a) the unlobed carpocephalum with a low, rounded dome on the upper surface and a flat lower surface, b) the relatively thin vegetative thallus often with an undulate lateral wing that usually does not incurve when dry and c) the large number of chloroplasts in cells of the dorsal epidermis.

Illustrations. Frye and Clark 1937; Howe 1899; Schofield 2002.

Habitat. Usually calcareous substrates. Damp, mostly dimly-lit and somewhat humid habitats. Soil of rock outcrops, steep hillsides, recesses in cliffs and creek banks; usually shaded by chaparral, oaks, rock overhangs or narrow canyon walls. Elevation from 45 to 1200 m; mostly below 800 m.

Distribution. Cryptomitrium tenerum occurs in southwest Oregon (David Wagner, personal communication), south to Central and South America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 6105* (UC), **CR**: Tehama Co. *Doyle 5767* (UC), **NC**: Napa Co. *Howell 476* (CAS), **SC**: Santa Barbara Co. *Doyle 10345* (UC), **SN**: Tulare Co. *Shevock 17022* (CAS).

Lunularia Adans. 1763
(Lunulariaceae)

The occurrence of crescent-shaped gemma-receptacles on the dorsal thallus surface is a definitive feature of this genus.

A monotypic genus.

Lunularia cruciata (L.) Lindb.

Distinctive features. Distinctive are crescent-shaped gemma-receptacles on the thallus dorsal surface. These receptacles generally are present on at least a few thalli in most populations. Also look for a) light- to gray- to yellow-green thalli, sometimes browning with age, 1.5–4 cm long and 5–10 mm wide; the thallus margins often incurve when dry, b) air-chambers with simple pores and in a thin single layer, c) photosynthetic filaments 3–4 cells long, the terminal cells under the pores densely chlorophyllose and about the same size as the subtending cells, and d) hyaline to light-brown ventral scales in two rows, each scale with 1 semicircular appendage.

Sporophytes are rare in this dioicous species, and, in California, known only from Marin County (*Proskauer s.n.* [dated 1953 and 1962] [UC]). From November to June, look for a) antheridia in a clearly defined, slightly raised purplish receptacle with raised margins on the dorsal thallus surface of very short branches, b) female plants with conspicuous apical clusters of hyaline scales at the apices of short, lateral branches that bear archegonia, c) a carpocephalum with (usually) 4 finger-like, nearly horizontal (cruciate) lobes and capsules that dehisce by 4 valves.

Separation. Lunularia is a distinctive plant and easily separated from other complex thalloid liverworts when crescent-shaped gemma-receptacles are present. Plants without gemma-receptacles have been confused with small, non-gemmiferous thalli of *Marchantia*, with small thalli of *Conocephalum* and with *Reboulia*. *Lunularia* is separated a) from *Marchantia* by the presence of simple thallus pores (vs. compound pores), b) from *Conocephalum* by its smaller thallus size (1.5–4 cm long × 5–10 mm wide vs. 6–25 cm long and 6–22 mm wide) and the lack of a distinctive aroma from crushed living thalli, and c) from *Reboulia* by air-chambers in a single layer (vs. in more than one layer).

Illustrations. Damsholt 2002; Frye and Clark 1937; Schofield 2002; Schuster 1992b.

Habitat. Soil of shaded drainages, and creek and river banks; usually occurs higher on banks than does *Marchantia* and *Conocephalum*. It also occurs under and near chaparral of gentle-sloping hills (e.g., off the Edwards Trail, of the Joseph D. Grant Santa Clara County Park). Elevation from 20 to 1800 m; mostly below 650 m.

Distribution. Lunularia (like *Marchantia*) is a greenhouse, nursery-yard, and garden weed, where it reproduces asexually and disperses by means of multicellular gemmae. Most researchers consider *Lunularia cruciata* to be a native of the Mediterranean region; it occurs in Europe, Asia, Africa, North, Central, and South America, New Zealand, and Australia. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 9931* (UC), **CR**: Tehama Co. *Doyle 8588* (UC), **NC**: Marin Co. *Proskauer s.n.* (1 Dec. 1953 & 10 Jan. 1962, both collections with sporophytes) (UC), **SC**: San Diego Co. *C. Wagner 932* (UC), **SN**: Inyo *Shevock 15283* (CAS).

Mannia Opiz 1829
(Aytoniaceae)

Species in this genus have a) a thallus dorsal epidermis with simple pores, each surrounded by 1–3 concentric circles of cells, b) air-chambers in more than one layer, the chambers sparingly divided by supplementary wall partitions, c) oil-cells present in both the dorsal epidermis and ventral parenchyma

tissue, d) antheridia sessile on the dorsal thallus surface, e) sporophytes elevated on archegoniophores, and f) no pseudoperianth around each sporophyte.

Two species in California.

Species Key

1. Ventral scales with 2–3 hyaline appendages usually forming a conspicuous cluster at the apex of female branches; archegoniophores developing at the apex of a main branch or large ventral branch, with a conspicuous basal and apical cluster of hyaline scales; spores yellow to yellow-brown. . . . . **M. fragrans**
1. Ventral scales with 1–2 usually purplish appendages never forming a conspicuous apical cluster; archegoniophores usually developing at the apex of a short branch of ventral origin, without a basal or apical cluster of scales; spores reddish- to dark purple. . . . **M. californica**

Mannia californica (Gottsche ex Underw.) L. C. Wheeler

Distinctive features. With reproductive plants, look for a) antheridia in an ill-defined group on a main branch, b) archegoniophores at apices of short, lateral branches of ventral origin and lacking basal and apical clusters of scales, c) hemispherical, obscurely lobed carpocephala, d) reddish- to dark-purple spores, 69–82 μm in diameter; the distal spore face with irregular large bumps, folds and ridges that do not intersect and form areolae, e) a flattened proximal spore face with facets between arms of the triradiate ridge with small, low bumps and thin ridges, with the ridges often intersecting to form small areolae, and f) the surface texture of both distal and proximal faces roughened by very small, rounded papillae and granules. Sporophytes mostly mature from March through May.

With vegetative plants, look for a) plants with a grayish-green dorsal surface and brownish lateral margins, b) strongly incurved (sometimes tubular) thallus margins in dry plants, c) air-chambers subdivided by many supplementary walls, d) medium to large, concave-sided trigones in dorsal epidermal cells, e) purplish black ventral surface and scales, f) ventral scales with 1–2 accuminate, usually purplish appendages that do not form a dense apical cluster, and g) ventral scales with hyaline oil-cells.

Separation. Mature, dry vegetative plants of *M. californica* and *Asterella bolanderi* often have strongly incurved margins that appear tubular and blackish. For easy separation, cut a thin section with a razor blade parallel to the dorsal epidermis; epidermal cells of *M. californica* have medium to large trigones (vs. none or small trigones in *A. bolanderi*). Occasionally, robust dry thalli of *Targionia* (especially from southern California) also are tubular and blackish. Cut a thallus cross-section with a razor blade. *M. californica* has an air-chamber system with many supplementary wall partitions but no photosynthetic filaments (vs. air-chambers in a thin single layer with photosynthetic filaments in *Targionia*).

Illustrations. Howe 1899; Schuster 1992b.

Habitat. Not common, but occasionally it forms large local populations. Exposed or shaded, somewhat slow to dry, summer-dry soil around rocks of hillsides and cliffs; and often under chaparral and *Quercus*. Elevation from 130 to 1800 m, but generally below 1300 m.

Distribution. Mannia californica is known only from two widely disjunct areas in the United States: 1) Arkansas and North Carolina (Ozarks and Appalachian Mts.) and 2) Arizona and California. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 192* (UC), **DMoj**: San Bernardino Co. *Laeger 2479* (CAS), **NC**: Solano Co. *Doyle 860* (UC), **SC**: San Diego Co. *Doyle 7171* (UC), **SN**: Tulare Co. *Shevock 17021* (CAS).

Mannia fragrans (Balb.) Frye and L. Clark

The species name *fragrans* refers to the fragrant aroma of fresh thalli. In the field, occasionally the nose can lead the eye to a nearby population. **However, do not use aroma alone as the only clue to the presence or identification of this species because not all populations are fragrant.**

Distinctive features. Sporophytes usually mature soon after liberation from snow cover. With reproductive plants, look for a) antheridia in a defined receptacle on the dorsal thallus surface, b) a cluster of hyaline scales at the apices of branches with archegonia, c) clusters of white scales at both the base and apex of archegoniophores (occasionally the archegoniophore elongates very little

before spore discharge), d) yellowish- to light-brown spores, mostly 58–84 μm in diameter; however, spores of plants along the trail to Long Gulch Lake, Siskiyou Co., *Doyle 5976* (UC), are smaller, ranging from 47–65 μm, e) prominent, thick rounded ridges that often intersect to form areolae on the distal face, and f) thinner ridges and smaller areolae on the proximal face. Sporophytes generally from mid-April to July.

With vegetative plants, look for a) plants often forming dense populations, b) green or whitish-green thallus dorsal surface and purplish lateral margins, c) deep purplish-black ventral surface and scales, d) cells of the dorsal epidermis with thick walls and large to bulging trigones, e) dark colored ventral scales usually with 2–3 hyaline appendages, and f) dry plants that appear blackish and tubular, with strongly incurved margins and conspicuous hyaline scale appendages.

Separation. With the archegoniophore at the thallus apex, and conspicuous clusters of hyaline scales at both its base and apex, reproductive plants of *M. fragrans* can hardly be confused with any other California liverwort. At times, however, vegetative plants can be confused with *Reboulia hemisphaerica* and *Asterella gracilis*. Dried plants of California populations of *R. hemisphaerica*, however, seldom are blackish or as tightly tubular, and they lack hyaline scale appendages. *Asterella gracilis* is separated from *M. fragrans* by its a) thin-walled epidermal cells with small or no trigones (vs. thick-walled epidermal cells with large to bulging trigones in *M. fragrans*), b) ventral scales usually with only one appendage (vs. usually 2–3 ventral scales in *M. fragrans*) and c) thallus lateral margins and ventral scales reddish (vs. purplish-black thallus margins and ventral scales). Tubular and blackish dried vegetative thalli of *M. fragrans* also can be confused with dry plants of both *Asterella bolanderi* and *Mannia californica*. However, *M. californica* and *A. bolanderi* do not have hyaline scale appendages that extend beyond the thallus margins and apices of female plants, and they are plants of lower elevations.

Illustrations. Damsholt 2002; Frye and Clark 1937; Schofield 2002; Schuster 1992b.

Habitat. Gravelly soil around rocks and outcrops; hillsides and banks of ephemeral creeks; often in exposed areas that dry soon after snow-melt. Elevation range from 1450 to 3650 m.

Distribution. Mannia fragrans occurs at higher elevations in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Siskiyou Co. *Shevock 25869* (CAS), **MP**: Modoc Co. *Doyle 7491* (UC), **SN**: Inyo Co. *Doyle 5899* (UC).

Marchantia L. 1753
(Marchantiaceae)

The presence of cup-shaped gemma-receptacles on the dorsal thallus surface is a definitive feature of this genus. Also look for a) compound pores in the dorsal epidermis, b) antheridiophores and archegoniophores, and c) carpocephala with finger-like rays.

A single species in California—*Marchantia polymorpha*. The high morphological variability of this species has resulted in description of some 50 species and infraspecific taxa (subspecies, varieties, forms, subforms). Schuster (1992b) and Damsholt (2002) separate *M. polymorpha* into three species; Paton (1999) uses three subspecies. In research that combined morphological studies and electrophoretic techniques, Bischler-Causse and Boisselier-Dubayle (1991) reported that electrophoretic patterns indicated the existence of three major and clearly distinct groups, which they considered to be subspecies. However, they reported difficulting in assigning individual samples to a subspecies based on morphological features alone. We also have found that many California specimens also are not assignable to a subspecies (or species of Damsholt and Schuster) only on morphological characters. Without experimental work (which is not practical), it is not possible to be totally sure to which subspecies your specimen belongs. Therefore, in this publication the species *M. polymorpha* is circumscribed in a broad sense (*sensu lato* or *s. l.*).

Marchantia polymorpha L. *s. l.*

Distinctive features. This dioicous species has large pale- to dark-green thalli, 5–10 mm wide and up to 10 cm or more long. Thalli usually are prostrate, but are ascending when growing among other bryophytes. The dorsal surface of some thalli have a strong, weak, interrupted or continuous dark line that extends over the midrib. Look for a) cup-shaped gemma-receptacles with lobed, fringed margins and which contain multicellular gemmae, that occur on the dorsal surface of at least some plants in most populations, b) compound dorsal epidermal pores that lead into air-chambers, c) air-chambers in a single thin layer that contain photosynthetic filaments, d) 4–6 rows (2 to 3 rows on each side of the midrib) of purple or hyaline ventral scales with oil-cells.

Sporophytes are not common although antheridiophores and archegoniophores occur from May to September. Look for a) the upper surface of the antheridiophore nearly circular in outline and with an upturned membranous margin, b) carpocephala usually with 7–11 prominent finger-like rays (resembling spokes of an umbrella), and c) small yellowish spores, 10–14 μm in diameter.

Separation. This is the only genus with circular, cup-shaped gemma-receptacles. Although *Marchantia* and *Preissia* both have compound pores in the gametophyte, *Preissia* lacks gemma-receptacles. Young or non-gemmiferous thalli of *Marchantia* are separated from *Preissia* by the presence of ventral scales in 4–6 rows (vs. ventral scales in only 2 rows in *Preissia*).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. This species often forms very large populations and occurs in diverse habitats: damp and wet places, occasionally submerged; on soil, rocks and organic matter near creeks, rivers, seepages, gardens (where it can be invasive), and burned-over areas (where it can be a pioneer species). Elevation from near sea-level to over 3600 m.

Distribution. Marchantia polymorpha is nearly world-wide in distribution. Like *Lunularia*, it often is a greenhouse, nursery-yard and garden weed. In California, it is a native plant, but its distribution is considered to have increased due to human activity. Calif. Geographic Regions: **CC**: Monterey Co. *Kellman 3356* (CAS), **CR**: Siskiyou Co. *Shevock 25877* (CAS), **KR**: Del Norte Co. *Doyle 7746* (UC), **MP**: Modoc Co. *Norris 108483* (UC), **NC**: Glenn Co. *Shevock 15878* (female plants) (UC), **SC**: San Diego Co. *Wiggins 2850* (UC), **SN**: Mono Co. *Doyle 10114* (female and male plants) (UC).

Preissia Corda 1829
(Marchantiaceae)

Preissia has compound pores in the dorsal epidermis that lead into air-chambers, and antheridia and sporophytes elevated on antheridiophores and archegoniophores, respectively. In addition, a) it lacks gemma-receptacles and gemma development, b) it has ventral scales in only two rows and each scale has a single subulate appendage, and c) its carpocephalum is lobed, but lacks finger-like rays.

A monotypic genus.

Preissia quadrata (Scop.) Nees

Distinctive features. With vegetative plants, look for a) dull- to gray-green thalli, 0.6–15 mm wide and 0.5–3 cm long, with lateral margins often becoming brownish- or reddish-purple with age, b) thallus margins of dry plants usually not or only little incurved, c) thin-walled dorsal epidermal cells without trigones, d) air-chambers with compound pores, in a thin single layer and with branched photosynthetic filaments, and e) purplish-black ventral scales in two rows, without oil-cells, and each scale with a single, subulate appendage.

California plants appear to be dioicous. From July thorugh September, look for a) male plants with antheridiophores and female plants with archegoniophores, b) a (usually) 4-lobed carpocephalum with quadrate low ridges on the upper surface, and c) angular brown spores 55–80 μm in diameter, with numerous wavy lamellae that occasionally form coarse areolae on the distal face.

Separation. Thalli of *Preissia* are about the same size and have similar secondary coloration as *Reboulia hemisphaerica*. *Preissia* is separated by a) compound thallus pores (vs. simple pores in *R. hemisphaerica*), b) ventral scales with a single appendage (vs. scales with 2–3 appendages), and c) antheridiophores (vs. sessile antheridia). *Preissia* might also be confused with young plants of *Marchantia polymorpha*—both have gametophytes with compound pores. *Preissia* can be separated by a) absence of gemma-receptacles (vs. gemma-receptacles present in *M. polymorpha*), b) ventral scales in 2 rows (vs. ventral scales in 4–6 rows), and c) a carpocephalum without finger-like rays (vs. a carpocephalum with finger-like rays).

Illustrations. Damsholt 2002; Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. Damp soil and rocks of shaded creek banks and seepages; splash of creeks and cascades; often under willow; places that remain damp for long periods of time following snow-melt. It occurs between 2600 to 3550 m in the central and southern Sierra Nevada, and above 1500 m in the Klamath Ranges.

Distribution. Preissia quadrata occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Trinity Co. *Duell 1740.11-1g.* (ABSH), **SN**: Tulare Co. *Doyle 7849A* (female) & *7849B* (male) (UC).

Reboulia Raddi 1818
(Aytoniaceae)

Distinctive characteristics of this genus include a) simple pores of the dorsal epidermis surrounded by 4–6 concentric circles of cells b) ventral scale appendages with 2–3 filiform appendages and b) conspicuous filiform scales at the base and apex of the archegoniophore.

A single species in California.

Reboulia hemisphaerica (L.) Raddi

Distinctive features. The firm, somewhat leathery, dull light-green thallus is 4–9 mm wide × 1.5–4 cm long. With vegetative plants, look for a) thalli usually with scalloped to crenulate lateral margins that are brownish to brownish-purple, b) often thin and somewhat parchment-like dry thallus margins, c) bulging trigones in mature dorsal epidermal cells, d) simple pores in the dorsal epidermis with 4–6 concentric circles of cells, the pores only slightly elevated, and e) purplish ventral scales, often with whitish margins, and with scattered hyaline oil-cells, marginal 1-celled slime-hairs, and usually 2–3 filiform appendages on each scale.

With reproductive plants, look for a) antheridia in sessile, mostly reniform, receptacles bordered by small purplish scales, b) archegoniophores with basal and apical filiform scales, and c) yellow to yellowish-brown spores 65–80 μm in diameter; the distal spore face with a few large areolae, 16–20 μm wide. Sporophytes mature late March through May.

Separation. Vegetative plants of *R. hemisphaerica* have a superficial resemblance to *Preissia quadrata*. *Reboulia hemisphaerica* is separated from *P. quadrata* by a) vegetative thallus with simple thallus pores (vs. compound pores *P. quadrata*), b) dorsal epidermal cells with bulging trigones (vs. dorsal epidermal cells with no trigones) and c) ventral scales with 2–3 filiform appendages (vs. ventral scales with only 1 subulate appendage). For separation from *Asterella californica*, see discussion under that species.

Illustrations. Damsholt 2002; Frye and Clark 1937; Schofield 2002; Schuster 1992b.

Habitat. Soil on small ledges and in channels of steep metamorphic rock outcrops; soil of hillsides. Elevation below 900 m.

Distribution. Reboulia hemisphaerica is widespread in the temperate and warmer regions of both the Northern and Southern Hemisphere. Its known distribution in California consists of three disjunct populations: two sites on the western slope of the Sierra Nevada and one in the City of San Francisco (at Laguna de la Puerca, now known as Pine Lake, near the western edge of Stern Grove). Calif. Geographic Regions: **CC**: San Francisco Co. *Brandegee 1* (CAS), **SN**: Plumas Co. *Janeway 5468* (MO) and Sacramento Co. *Brandegee 25* (UC).

Riccia L. 1753
(Ricciaceae)

In number of species, this is the largest liverwort genus in California. The genus is distinguished by a) antheridia and archegonia that develop within dorsal thallus tissue, b) a sporophyte that consists of a capsule only (lacking a seta and foot), and c) a capsule that lacks sterile cells (i.e., elaters) intermixed with spores remains fully embedded in thallus tissue. Two groups or subgenera are recognized within this genus in California: (1) subgenus *Riccia*, in which the photosynthetic tissue has vertical, narrow, finger-like air-channels, and (2) subgenus *Ricciella*, in which the photosynthetic tissue has somewhat polygonal air-chambers.

Care must be taken during specimen collection and species identification, because species of *Riccia* often grow intermixed. Care also must be taken in deciding the presence or absence of cilia, because cilia development in some species appears to be facultative; i.e., normally ciliate plants may have no or only sparsely developed cilia when growing in wet or moist conditions (such as early in the rainy season). Search field populations carefully before collecting specimens for identification, and make microscope observations on several thalli.

Thirteen species in California.

Species Key

1. Photosynthetic tissue composed of large air-chambers separated by uniseriate walls, at least in young tissue near the apex; dorsal surface appearing spongy or lacunose with age in some species. . . . . **2.**

1. Photosynthetic tissue composed of uniseriate columns of cells, separated by narrow, finger-like air-channels; dorsal surface never appearing spongy or lacunose with age. . . . . **6.**
2. Plants terrestrial; sporophytes not protruding strongly on the ventral side of thallus. . . . . **3.**
2. Plants floating aquatics or terrestrial when stranded; sporophytes protruding prominently on the ventral side of the thallus. . . . . **5.**
3. Plants dioicous; female and, especially, male plants often tinged reddish; distal spore face with numerous wavy ridges that occasionally branch. . . . . **R. frostii**
3. Plants monoicous; plants seldom tinged reddish; distal spore face with complete or incomplete areolae. . . . . **4.**
4. Plants green, gray-green or yellowish-green; thallus with a spongy or lacunose appearance; spores 64–110 μm; distal spore face with 5–7 incomplete to complete areolae. . . **R. cavernosa**
4. Plants gray-green, becoming whitish when dried in the field; thallus not appearing spongy or lacunose; spores 56–84 μm; distal spore face with 7–10 complete areolae. . . **R. crystallina**
5. Thallus sparingly branched; branches usually less than 0.7 mm wide and 1.2–3 × as wide as thick. . . . . **R. canaliculata**
5. Thallus frequently branched; branches usually more than 0.8 mm wide and 3–6 × as wide as thick. . . . . **R. fluitans**
6. Thallus margin with few to many cilia. . . . . **7.**
6. Thallus margin without cilia. . . . . **10.**
7. Cilia 300–900 μm long, commonly on the dorsal thallus surface above each sporangium. . . . . **R. trichocarpa**
7. Cilia 50–400 μm long, but not present on dorsal thallus surface above each sporangium. . . . **8.**
8. Antheridial ostioles not or only little elevated above thallus surface; cilia slender and often forming an apical cluster. . . . . **R. californica**
8. Antheridial ostioles long, elevated 60–200 μm above thallus surface; cilia usually stout but not forming an apical cluster. . . . . **9.**
9. Dry mature thalli with thick apices and lateral margins usually with thick, rounded (tumid) ridges; dry thalli in cross-section 1.5–3.5 times as wide as thick. . . . . **R. beyrichiana**
9. Dry mature thalli with thin apices and lateral margins thin, not forming tumid ridges; dry thalli in cross-section 4–6 times as wide as thick. . . . . **R. glauca**
10. Ventral scales whitish to hyaline, conspicuously extending beyond the thallus lateral margin in both fresh and dry thalli. (some dry thalli of *R. sorocarpa* also can key here) **R. lamellosa**
10. Ventral scales variously colored, but not conspicuously extending beyond the thallus lateral margin in both fresh and dry thalli. . . . . **11.**
11. Ventral scales shiny black to purplish black. . . . . **R. nigrella**
11. Ventral scales hyaline to brown (but black in some populations of *R. sorocarpa*). . . . . **12.**
12. Thallus with scattered orange oil-cells; margins of older plants brownish-orange. . . . . **R. campbelliana**
12. Thallus without orange oil-cells; margins of older plants green, hyaline, or tinged with violet, but not tinged brownish-orange. . . . . **13.**
13. Thallus broad, up to 3 mm wide; thallus of dry plants in cross-section 4–6 times as wide as thick; dry plants with thin usually flat margins; antheridial ostioles conspicuous. . . **R. glauca**
13. Thallus narrow, up to 1.8 mm wide; thallus of dry plants in cross-section 2–3 times as wide as thick; dry plants with acute margins; antheridial ostioles not conspicuous. . . **R. sorocarpa**

Riccia californica, R. campbelliana, R. lamellosa, R. nigrella, R. sorocarpa, and *R. trichocarpa* usually occur in similar hot, summer-dry locations and often in the same general area; when one is found look for the others.

Exclude. Riccia violacea M. Howe. Steere (1954) reported this species from Santa Catalina Island, Los Angeles County based on his collection of a small number of plants on exposed soil from the rocky headlands of White's Landing. No collection number was cited. A search of CAS, UC, NY, UBC and other herbaria failed to locate a Steere (or any other California) collection of this species. *Riccia violacea* could not be confirmed for California.

Riccia beyrichiana Hampe ex Lehm. (subgenus *Riccia*)

This species occurs in a range of habitats from low to high elevation and has variable vegetative morphology. Examination of spore markings from several capsules is the best way to confirm species identification.

Distinctive features. In mature thalli in drying areas, look for a) thalli with raised rounded (tumid) lateral margins (the raised margins collapse when dry), b) usually thin-walled, finely granular cilia, 75–300 μm long, at the thallus apex and on the tumid lateral margins (some cilia can be slightly on the dorsal surface because of the rounded thallus margins), c) in thallus cross-section, dry main branches 1.5–3.5 times as wide as thick, and d) older thalli often with brownish to reddish-purple lateral margins and ventral surfaces.

In thalli of wet areas (such as shaded margins of vernal pools, seepages and drainages as well as early in the growing season during winter rains or following snow-melt), look for a) thalli with flat lateral margins (not or little tumid), b) few to no cilia at the apex and lateral margins, c) in thallus cross-section, main branches 4–6 times as wide as thick, and d) older thalli light green, whitish or light yellowish-brown. For these habitats, carefully search the drier periphery or raised drier areas for more "typical" plants.

Confirm identification by details of spore markings. Sporophytes of this monoicous species mature June through October above 1000 m; May through July below 1000 m. Look for a) conspicuous hyaline antheridial ostioles 60–200 μm high, b) plants from drier habitats often with a purple coloration on the dorsal thallus tissue over capsules, c) angular pale to dark brown spores mostly 80–125 μm in diameter, d) finely granular distal and proximal spore faces and spore wing, e) mostly 5–9 areolae across the distal spore face, each areola 10–20 μm wide (occasionally some spores in a capsule will have 5–9 areolae on the distal face while other spores in the same capsule will have up to 12 areolae, each areola of correspondingly smaller diameter), and f) proximal spore face with low and/or long branched or unbranched ridges, or faint to distinct incomplete or complete areolae (in some populations, spores from the same capsule can exhibit great morphological diversity—look at more than one spore).

Separation. Riccia beyrichiana can be confused with *R. glauca.* Both species a) have rather large thalli, b) have a variable presence of marginal cilia, c) grow in slow-to-dry habitats, and d) have conspicuous, long, hyaline antheridial ostioles. Details of spore morphology are the best way to separate these two species. In *R. beyrichiana* a) all spore surfaces are finely granular (vs. spore surfaces not or only sparsely granular in *R. glauca*), b) the spores are somewhat larger, mostly 80–125 μm (vs. spores 75–100 μm), c) mostly 5–9 areolae across the distal face (vs. 8–12 areolae across the distal face), and d) the proximal spore face typically has low ridges and weakly developed incomplete and complete areolae (vs. areolae well-developed and complete).

Fresh vegetative thalli of *R. beyrichiana* growing in drying or exposed habitats can be separated from *R. glauca* by a) the thallus dorsal groove soon widening and flattening behind the apex and becoming bordered by raised, rounded (tumid) lateral ridges (vs. the thallus dorsal groove soon vanishing behind the apex and the lateral margins not bordered by tumid ridges in *R. glauca*), b) the thallus lateral margin and ventral surface often with reddish or purplish coloration (vs. thallus lateral margin and ventral surface without reddish or purplish coloration), and c) dried thalli 1.5–3.5 times as wide as thick in cross-section (vs. dried thalli 4–6 times as wide as thick in cross-section). However, vegetative thalli of *R. beyrichiana* collected early in the growing season or from wet areas (such as margins of vernal pools) often lack raised tumid ridges and reddish or purplish coloration, and the dried thalli can be 4–6 times as wide as thick in cross-section. Use details of spore morphology to identify these plants.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992b.

Habitat. On sunny to lightly shaded mineral and peaty soil; margins of vernal pools, seepages, drainages, and mountain meadows; places that are slow to dry after winter rains and snow-melt. Elevation from 140 to 3440 m; more common above 330 m.

Distribution. Riccia beyrichiana occurs in Europe, North Africa, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 7461* (UC), **CR**: Shasta Co. *Doyle 8754* (UC), **KR**: Siskiyou Co. *Norris 99782* (UC), **MP**: Modoc Co. *Doyle 6681* (UC), **SC**: Riverside Co. *Doyle 7512* (UC), **SN**: Amador Co. *Norris 82681* (UC).

Riccia californica Austin (subgenus *Riccia*)

Caution. Very young plants and plants in wet areas (early in the season or a rainy year) may have few or no cilia. At the time of collection in the field, use the hand lens to carefully search for plants with cilia, and search again under the dissection microscope in the lab.

Distinctive features. Thalli of this species typically have slender hyaline cilia on the margins and usually a conspicuous cluster at the apex; cilia, however, can be absent from older parts of the thallus.

Also look for a) light- to whitish-green thalli, usually whitish when dry and with pale yellowish brown margins in older thallus areas, b) a dorsal groove that widens close behind the apex and soon disappears, and c) usually colorless and inconspicuous ventral scales (however, some populations have plants with conspicuous black scales).

Sporophytes of this monoicous species mature late March through May. Look for a) inconspicuous antheridial ostioles, little or not elevated above the thallus surface, b) light brown spores, turning dark brown at maturity, mosly 64–89 μm in diameter, c) distal spore face with 8–13 areolae, mostly 5–9 μm wide, and with blunt papillae at areolae corners, d) proximal spore face also areolate, but not as strongly.

Separation. This distinctive species is likely to be confused only with *R. beyrichiana* and *R. glauca*. *Riccia californica* has a) inconspicuous antheridial ostioles (vs. ostioles conspicuously elevated above the thallus surface in both *R. beyrichiana* and *R. glauca*), and b) smaller spores, not exceeding 90 μm (vs. larger spores, mostly 85–125 μm).

Illustrations. Howe 1899; Schuster 1992b.

Habitat. Soil of open and lightly shaded summer-dry hillsides, meadows, grasslands, chaparral and woodlands. Elevation usually below 700 m.

Distribution. Riccia californica primarily is a California species, although Schuster (1992b) reported it from Texas. Calif. Geographic Regions: **CC**: San Luis Obispo Co. *Doyle 7230* (UC), **CR**: Tehama Co. *Doyle 5769* (UC), **GV**: Sacramento Co. *Carter 478* (UC), **NC**: Marin Co. *Doyle 8396* (UC), **SC**: Riverside Co. *Doyle 7289* (UC), **SN**: Nevada Co. *Doyle 8499* (UC).

Riccia campbelliana M. Howe (subgenus *Riccia*)

Distinctive features. Thalli of this distinctive species are 1.0–2.5 mm wide and often form large populations. The thallus has a green to gray-green dorsal groove in young and shaded plants, whereas they are distinctively bordered by a brownish-orange margin later in the season and in exposed habitats. In older, drying thalli, the entire dorsal surface is a brownish-orange or brown. Also look for a) numerous oil-cells in the dorsal epidermis, b) usually inconspicuous, pale brown to nearly hyaline ventral scales; the scales occasionally extend slightly beyond the margin, especially in dry specimens, and c) thin thallus margins that generally do not greatly incurve over the dorsal surface of dry plants.

Sporophytes of this monoicous species mature March through June. Look for a) conspicuous antheridial ostioles extending above the dorsal surface, b) yellowish-brown to brown angular spores, 83–109 μm in diameter, c) a distal spore face with numerous low, usually short sinuous ridges that seldom intersect to form areolae, and d) a proximal spore face with numerous short low ridges and papillae.

Separation. Mature plants are readily recognized in the field—the thallus has a broad gray-green dorsal groove with brownish-orange lateral margins; the entire dorsal surface can be orange-brown in plants drying in the field. Although *R. nigrella* also can have an orange-brown dorsal surface, *R. campbelliana* can be separated by a) a wider thallus, 1.0–2.5 mm wide (vs. 0.5–1.1 mm wide in *Riccia nigrella*), b) conspicuous antheridial ostioles (vs. antheridial ostioles that are not or only little exserted, and c) pale brown to nearly hyaline ventral scales (vs. shiny purplish-black ventral scales).

Illustrations. Howe 1899; Schuster 1992b.

Habitat. Exposed summer-dry mineral soil in grasslands, openings in chaparral and woodlands, sandstone outcrops, margins of ephemeral seepages on thin soil over granite rock slabs. Elevation from near sea-level to 1950 m; mostly below 1500 m.

Distribution. Riccia campbelliana has been reported from Argentina, South Africa, and Russia, as well as from the Midwest and southern states of North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8072* (UC), **CR**: Tehama Co. *Doyle 5772* (UC), **GV**: Sacramento Co. *Carter 411* (UC), **NC**: Marin Co. *Carter 520* (ABSH), **SC**: Riverside Co. *Shevock 20531* (CAS), **SN**: Tulare Co. *Norris 87636* (UC).

Riccia canaliculata Hoffm. (subgenus *Ricciella*)

These aquatic or stranded plants earlier were interpreted to be the terrestrial form of *R. fluitans* because they frequently had sporophytes; contact with soil was considered to be important in inducing sexual reproduction.

Distinctive features. Look for a) sparingly branched thalli, 0.3–0.7 mm wide, with terminal branches often slightly tapered toward the apex, b) in cross-section, branches 1.2–3.0 times as wide as thick, c) small bilobed ventral scales at the branch apex, that often become divided and appear to be in two rows in older branches (the ventral scales can be nearly impossible to locate in dry specimens).

Sporophytes develop July through October. Look for a) capsules that protrude prominently from the ventral thallus surface, b) yellowish-brown spores, 79–95 μm in diameter, c) 4–6 areola across the distal face, the areolae with low walls that are slightly raised at the wall intersections, and d) markings on the proximal face less strongly developed than those on the distal face.

Separation. This species has been confused with *R. fluitans*. *Riccia canaliculata* can be separated by a) infrequently branched thalli (vs. frequently branched thalli in *R. fluitans*), b) branches mostly less than 0.7 mm wide (vs. branches mostly more than 0.8 mm wide), c) branch apices often tapered toward the apex (vs. usually round or truncate branch apices), d) in cross-section, a thallus 1.2–3.0 times as wide as high (vs. 3–8 times as wide as high), and e) plants occasionally with sporophytes (vs. sporophytes unknown in California plants and infrequently known elsewhere).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992b.

Habitat. Floating at or below the surface of ponds, lakes, reservoirs, and margins of slow-moving rivers; or terrestrial when stranded on banks. Elevation from near sea-level to 47 m.

Distribution. Riccia canaliculata occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **GV**: San Joaquin Co. *Carter 240* (soil) (UC) and *Carter s.n.* (July 29, 1931, aquatic) (UC); Merced Co. *Nobs & Smith 438* (UC).

Riccia cavernosa Hoffm. (subgenus *Ricciella*)

Taxonomic misunderstanding led to plants that are now identified as *R. cavernosa*, to be determined as *R. crystallina*. Jovet-Ast (1965) recognized and resolved this taxonomic problem. As a result, herbarium specimens identified as *R. crystallina* must be re-examined. The two species are quite distinctive and easy to separate as described below.

Distinctive features. This species has a highly variable thallus color: bright green (especially in very young plants), yellowish-green, light-green, grayish-green, and occasionally tinged reddish or reddish-purple. Look for the early disintegration of the dorsal epidermis; this results in a characteristic spongy or frothy appearance even of very young thalli.

Sporophytes of this monoicous species mature late May through October. Look for a) capsules that are deeply embedded in thallus tissue and easily over-looked, except in old and dry plants, b) somewhat triangular dark brown to nearly black spores, 65–95 μm diameter, c) the distal spore face with variable markings, usually little to irregularly areolate, with long anastomosing ridges, short spurs and tubercles; however, the number and extent of completion of areolae is highly variable, even on spores from the same capsule, d) distal spore face with low and relatively thick ridges and areolae walls that are devoid of spines or other elevations at wall intersections, and e) a proximal spore face with complete and/or incomplete areolae, and ridges of variable lengths.

Separation. The characteristic spongy or frothy appearance of even extremely young plants makes it unlikely that *R. cavernosa* would be confused with any other species of *Riccia*. In contrast, the thallus of *R. crystallina* never is conspicuously spongy or frothy until dry, if then. Spore markings of the two species also are distinctive. In *R. cavernosa*, the distal spore face has low, rounded ridges and complete and incomplete areolae, and there are no protuberances or spines at wall intersections (vs. the distal spore face of *R. crystallina* always areolate with thin high walls and spines or protuberances at wall intersections).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992b; Stotler and Doyle 2004.

Habitat. Exposed, seasonally moist, usually water-retentive soils. Diverse substrates: soils of granitic, volcanic and sedimentary origin; sand, silt or mud, often admixed with organic matter; drying lake-banks; pond and stream margins; and seepages on hillsides, below cliffs, in meadows, and drainages along roads. Elevation from 15 to 3200 m; mostly below 2500 m.

Distribution. Riccia cavernosa is widely distributed in the warmer temperate areas of the Northern and Southern Hemisphere. It is widespread in North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 7462* (UC), **CR**: Tehama Co. *Doyle 8591* (UC), **GV**: Yolo Co. *Doyle 7502* (UC), **KR**: Siskiyou Co. *Doyle 9222* (UC), **MP**: Modoc Co. *Doyle 7483* (UC), **NC**: Glenn Co. *Howell 632*

(UC), **SC**: Los Angeles Co. *Wheeler 6345* (UC), **SN**: Tulare Co. *Shevock 17509* (CAS), **SNE**: Mono Co. *Doyle 6762* (UC)

Riccia crystallina L. emend. Raddi (subgenus *Ricciella*)

Distinctive features. The thalli lack a dorsal groove even near the apices, and usually are bluish- to grayish-green, but whitish when field-dried. Look for a) air chambers in a single layer and the underlying non-photosynthetic tissue extending nearly to the thallus margin, b) the dorsal epidermis of younger thalli remaining intact, not giving a frothy or spongy appearance, and c) older and dry thalli usually appear scruffy due to the somewhat late disintegration of the dorsal epidermis.

Sporophytes of this monoicous species mature March through July. Look for a) capsules deeply embedded in thallus tissue (and easily over-looked), b) yellow-brown to brown spores, somewhat triangular in shape, and 63–89 μm in diameter, c) regularly areolate distal spore face, mostly with 6–8 areolae across the face, the areolae 6–11 μm wide, d) the distal spore face with notched or shallowly toothed projections at corners of the areolae, e) the proximal spore face with a prominent, thin triradiate ridge and intervening facets with thin-walled areolae similar to those on the distal face, and f) an irregularly dentate or crenate wing margin.

Separation. See notes under *R. cavernosa* for separation from that species. With its bluish- to grayish-green color, flat dorsal surface lacking a groove even near the thallus apex, and spore markings, *R. crystallina* should not be confused with other species of *Riccia*.

Illustrations. Paton 1999; Schuster 1992b; Stotler and Doyle 2004.

Habitat. Partial shade to full sun; seasonally moist, summer-dry, compacted silt along trails, dirt roads and similar disturbed sites (including soil around picnic tables in coastal State Parks). Elevation from near sea-level to 350 m.

Distribution. Riccia crystallina occurs in both the Northern and Southern Hemisphere. In North America, it has been documented only from California. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 9926* (UC), **NC**: Mendocino Co. *Doyle 6243* (UC).

Riccia fluitans L. (subgenus *Ricciella*)

Distinctive features. These aquatic plants float at or just below the water surface, or become stranded on soil by wind action or receding water level. With aquatic plants, look for a) thalli, mostly 0.8 mm or more wide, that frequently are branched, b) rounded to truncate branch apices, c) in cross-section, thalli 3–6 times as wide as thick, and d) semicircular ventral scales that are not bilobed or divided.

With stranded plants, look for a) thin thalli usually with a shiny dorsal surface that often appears fragile in dry plants, b) frequently branched thalli to 1.5 mm wide, and c) thallus apices rounded to truncate. In California, sporophytes have not been found in aquatic or terrestrial thalli.

Separation. This species and *R. canaliculata* both have narrow, strap-shaped thalli that occur on soil near water. See *Riccia canaliculata* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992b.

Habitat. Floating at or below the surface of ponds, lakes, reservoirs, and rivers, or terrestrial when stranded on banks. Elevation from near sea-level to 1200 m.

Distribution. Riccia fluitans occurs in Europe, Asia, Africa, Australia, and North America. Calif. Geographic Regions: **DMoj**: Inyo Co. *Wolf 9766* (CAS), **GV**: San Joaquin Co. *Carter 241* (UC), **NC**: Marin Co. *Carter 534* (UC), **SN**: Plumas Co. *Nobs & Smith 1422* (UC).

Riccia frostii Austin (subgenus *Ricciella*)

Distinctive features. Thalli of this species are compact when young and also near the apices, but moderately spongiose with age and when dry. In cross-section, the thallus is a mixture of small polyhedral air-chambers and columnar air-channels. Look for a) male plants usually in small reddish rosettes (gray-green when very young), b) often reddish antheridia with conspicuous elongate ostioles, and c) dull- to grayish-green female plants, often tinged reddish in sunny habitats and on older plants.

Sporophytes mature late July through November. Look for a) angular brown spores 42–65 μm in diameter, b) a distal spore face with numerous thin, wavy ridges that seldom anastomose, and c) a similar but less strongly marked proximal spore face.

Separation. This distinctive species is not likely to be confused with other California species of *Riccia*. Look for separate grayish-green female plants and reddish male plants. Occasionally, it grows with *R. cavernosa*, which has a much more conspicuously spongiose thallus than *R. frostii*.

Illustrations. Clark and Frye 1928; Schuster 1992b.

Habitat. Silt to fine sandy deposits along river and lake margins; sites that remain damp such as bends in rivers, shaded places and banks of streams near lakes. Elevation from 44 to 2122 m.

Distribution. Riccia frostii is widely distributed in the temperate climate of Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Contra Costa Co. *Norris 108167* (UC), **GV**: Sacramento Co. *Carter 379* (UC), **NC**: Marin Co. *Carter 988* (UC), **SC**: Los Angeles Co. *Wheeler 6344* (UC), **SN**: Alpine Co. *Doyle 6758* (UC), **SNE**: Mono Co. *Doyle 6761* (UC).

Riccia glauca L. (subgenus *Riccia*)

Distinctive features. Plants of this species usually lack marginal cilia, but a few short apical cilia occur in some populations. Look for a) a light green to whitish-or grayish-green thallus, 1–3 mm wide, and devoid of reddish or purplish pigmentation on the lateral margins and ventral surface, b) a narrow dorsal groove at the apex that soon vanishes in older thallus parts, c) in dry plants, very thin lateral margins, d) in cross-section, a thallus 4–6 times as wide as thick.

Sporophytes of this monoicous species mature from March through July. Look for a) prominent antheridial ostioles, elevated up to 160 μm above the dorsal surface, b) angular, brown to dark brown spores, mostly 75–100 μm in diameter, c) a distal spore face generally with 6–10 areolae, each 9–15 μm wide, the areolae tubercles at the angles, d) a proximal spore face similar to, but less strongly marked, than the distal face, and e) usually a smooth (occasionally granulose) wing surface and a crenulate wing margin that often appears (under the compound microscope) to have a somewhat thickened outer edge.

Separation. See *Riccia beyrichiana* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999.

Habitat. Moist soil and shady banks. Elevation mostly below 350 m.

Geographic regions. Riccia glauca occurs in Europe, Asia, North Africa, New Zealand, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 11437* (UC).

Riccia lamellosa Raddi (subgenus *Riccia*)

Distinctive features. Thalli of this monoicous species are light green to grayish-green, and lack reddish or purplish secondary pigmentation. Look for a) conspicuous large hyaline ventral scales that extend prominently beyond the thallus margins and form a conspicuous white border in both living and dry plants, b) relatively large thalli, 2.0–4.5 mm wide, with a sharp dorsal groove near the apex that disappears in older thallus areas.

Sporophytes of this monoicous species mature March through June. Look for a) antheridial ostioles not, or only weakly, elevated above the thallus surface, b) capsules deeply embedded in the ventral thallus tissue and easily overlooked even in dry plants, c) reddish-brown to dark brown to brownish-black spores, mostly 95–124 μm in diameter, d) an areolate distal spore face, the areolae 10–16 μm wide, e) a proximal spore face with smaller, less distinct areolae and low irregular, vermicular ridges, and f) an indistinct triradiate ridge.

Separation. Plants readily can be identified with a hand-lens because of the hyaline ventral scales that conspicuously extend beyond the thallus margins. Also definitive is the combination of grayish-green thallus, absence of secondary wall pigmentation, and small sporophytes embedded deep in the ventral thallus tissue. Occasionally, this species has been confused with *R. sorocarpa*. *Riccia lamellosa* has a) a much larger thallus, 2.0–4.5 mm wide (vs. 0.5–2.3 in *R. sorocarpa*) and b) hyaline ventral scales that conspicuously extend beyond the margins of both living, and dry thalli (vs. hyaline ventral scales that rarely extend beyond the thallus lateral margins, and which usually are visible only near the apices of dry thalli).

Illustrations. Frye and Clark 1937 (as *R. austini*); Howe 1899 (as *R. austini*); Schuster 1992b.

Habitat. Summer-dry sandy to gravelly soil; exposed to lightly shaded areas in meadows, openings in chaparral and *Quercus* woodlands. Elevation from 10 to 300 m.

Distribution. Riccia lamellosa occurs in Europe, Asia, Africa, and North and South America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 4214* (UC), **NC**: Marin Co. *Campbell s.n.* (CAS 119266), **SC**: San Diego Co. *Doyle 7198* (UC).

Riccia nigrella DC. (subgenus *Riccia*)

Distinctive features. Thalli of this species are narrow, 0.5–1.2 mm wide, with a sharp, narrow dorsal groove toward the apex, but obtuse and vanishing in older thallus areas, and glossy blackish-purple ventral scales. In young plants the dorsal surface often is a shiny gray-green. In mature and dry thalli the lateral margins are a brownish-orange. In exposed habitats, the entire dorsal surface is brownish-orange. The thallus margins usually are strongly incurved when dry, often only the glossy blackish-purple scales are exposed.

Sporophytes of this monoicous species mature March through June. Look for a) antheridial ostioles not, or only slightly, elevated above the thallus surface, b) numerous and often crowded capsules on the dorsal thallus surface, usually with a blackish spot over a mature capsule, c) dark brown to nearly black spores 67–82 μm in diameter), d) an areolate distal spore face with 7–12 areolae, each areola 5–10 μm wide, and with low, truncate tubercles at the corners of the areolae, e) an areolate proximal face with low, thick walls, and f) an often indistinct triradiate ridge.

Separation. This is a distinctive species. It can be confused with small thalli of *R. campbelliana*, which also has a brownish-orange dorsal surface and lateral margin. *Riccia nigrella* can be separated by a) thalli less than 1.2 mm wide (vs. 1.0–2.5 mm wide in *R. campbelliana*), b) glossy blackish-purple ventral scales (vs. brown to nearly colorless ventral scales), and c) areolate distal spore faces (vs. distal spore faces with low sinuous ridges that rarely form areolae).

Illustrations. Paton 1999; Schuster 1992b.

Habitat. Open summer-dry habitats; on soil of paths, hillsides, roadbanks, and cliff faces; openings in chaparral, meadows and woodlands; Elevation from 15 to 1550 m; mostly below 900 m.

Distribution. Riccia nigrella occurs in Europe, Asia, North Africa, Australia, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 6472* (UC), **CR**: Shasta Co. *Norris 72930A* (UC), **GV**: Kern Co. *Laeger 2228* (CAS), **KR**: Trinity Co. *Doyle 5823* (UC), **MP**: Modoc Co. *Doyle 4022* (UC), **NC**: Sonoma Co. *Carter 252* (UC), **SC**: San Bernardino Co. *Wagner 683* (UC), **SN**: Placer Co. *Whittemore 3523* (CAS).

Riccia sorocarpa Bisch. (subgenus *Riccia*)

Distinctive features. Thalli of this species are 0.6–1.8 mm wide. The dorsal surface is pale green, glaucous green or gray-green and usually becomes whitish with age and upon drying. Look for a) a dorsal surface with a distinct, sharp, deep, groove near the apex that becomes wider and usually disappears in older thalli, b) in thallus cross-section, branches 2–3 times as wide as high with acute lateral margins, c) terminal (epidermal) cells of chlorenchyma filaments soon collapse, leaving a thick-walled basal cup; the outer transverse wall of the sub-epidermal cells also are thick-walled, d) usually hyaline ventral scales that occasionally extend slightly beyond the thallus margin (scales can be blackish-purple on a few to many thalli in some California populations).

Sporophytes of this monoicous species mature March through September. Look for a) numerous, often crowded, sporangia, b) angular reddish to dark brown spores 60–98 μm in diameter, c) a distal spore face with both ridges and 8–12 areolae, each areola 6–11 μm wide, and with a finely granular surface texture, d) truncate papillae, 3–6 μm high at the intersection of areolae walls in the central region of the distal face, e) a proximal face with finely granular low ridges and tubercles, and f) an often indistinct triradiate ridge, with distinctly flattened facets between the ridge arms.

Separation. This species is separated from other *Riccia* species by a) its sharp, deep apical dorsal groove, which is clearly evident with a handlens, b) the acute lateral thallus margin with ascending sides, and c) reddish-brown spores, with an areolate distal face, a proximal face with short ridges, and a finely granular texture of both faces.

Illustrations. Damsholt 2002; Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. Soil; usually open habitats in meadows, grasslands, chaparral, oak woodlands, around rocks, base of cliffs, and along paths and roads; from 100 to 3500 m.

Distribution. Riccia sorocarpa occurs in Europe, Asia, Africa, New Zealand, Australia, and North and South America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 4347* (UC), **CR**: Shasta Co. *Doyle 764* (UC), **GV**: Sacramento Co. *Carter 314* (UC), **KR**: Trinity Co. *Doyle 6634* (UC), **MP**: Modoc Co. *Doyle 7493* (UC), **NC**: Napa Co. *Carter 448* (UC), **SC**: Riverside Co. *Doyle 7432* (UC), **SN**: Inyo Co. *Shevock 15784* (CAS).

Riccia trichocarpa M. Howe (subgenus *Riccia*)

The species name *R. trichocarpa* is used in this publication, although relationship (synonymy) with *R. ciliata, R. canescens, or R. crinata* has been proposed: see Schuster (1992b), Jovet-Ast (1994), Grolle and Long (2000), Damsholt (2002), and Schumaker and Váňa (2005) for discussion.

Riccia trichocarpa is widespread in California with both the thallus and spores showing morphological variation. A combination of fieldwork, culture studies, and molecular techniques would help determine whether a single species occurs in California and the degree of affinity of *R. trichocarpa* with the species listed in the above paragraph.

Distinctive features. The most distinctive feature of the vegetative plant is the numerous long, slender, rigid, hyaline cilia on the thallus margin and usually on the dorsal surface over the sporophyte capsules. The cilia are 300–900 μm long and the walls are unequally thickened. Also look for a) light- or yellow-green dorsal surface of young thalli, which, with age, darken and the lateral margins often blacken, and b) a blackish ventral surface of mature thalli; upon drying, the black margin and ventral surface usually obscure the dorsal surface, and the hyaline marginal cilia conspicuously stand out against the black ventral surface.

Sporophytes of this monoicous species mature March through August. Look for a) antheridial ostioles elevated 50–100 μm above the dorsal surface, b) a reddish-purple spot, with or without cilia, on the dorsal surface over a sporophyte, e) brown, soon opaque, angular spores, 109–125 μm in diameter, and c) distal and proximal spore faces with broad granular walls that surround depressions.

Separation. This species is separated from all other California species of *Riccia* by a) the numerous large rigid cilia on the thallus margins and b) the distinctive spore markings.

Illustrations. Frye and Clark 1937; Howe 1899.

Habitat. Usually on bare sandy to gravelly soil that dries quickly after cessation of spring rains. Exposed and lightly shaded locations, such as meadows, hillsides, base of cliffs, creek and trail banks, and clearings in chaparral and oak woodlands. Elevation from near sea-level to 1400 m, mostly below 950 m.

Distribution. Riccia trichocarpa occurs in western North America. Calif. Geographic Regions: **CC**: Contra Costa Co. *Norris 100532* (UC), **MP**: Modoc Co. *Doyle 6675* (UC), **SC**: Riverside Co. *Shevock 20530* (CAS), **SN**: Fresno Co. *Doyle 6330* (UC).

Ricciocarpos Corda 1829
(Ricciaceae)

A monotypic genus.

Ricciocarpos natans (L.) Corda

Distinctive features. This is the only aquatic liverwort that normally floats like a canoe on the water surface, rather than floating at or below the surface. This plant is easily overlooked because it frequently grows intermixed with *Lemna, Spirodela, Wolffia* (aquatic flowering plants) and *Azolla* (an aquatic fern). The thallus is green to dark-green, sometimes tinged with violet, and 4–10 mm long and 4–9 mm wide. Also look for a) a persistent sharp median groove in the dorsal surface, b) conspicuous long, purplish to brownish ventral scales that hang down in the water column.

Sporophytes mature April through June. Look for a) pale-brown spores, 42–57 μm in diameter, that turn dark-brown to fuscous with age, b) an areolate distal spore face, each areola 6–8 μm wide, with conspicuous rounded spines at the angles of the areolae, and c) a similar proximal face often with an indistinct triradiate ridge.

Young terrestrial (stranded) plants are grayish- or yellowish-green with a median dorsal groove; older plants often have a reddish tint, the median dorsal groove can be absent, and the dorsal surface of dry plants often has a shiny appearance. Also look for a) small, distinct air-pores in the dorsal

epidermis and b) hyaline to violet ventral scales (that usually are difficult to locate because of the numerous rhizoids).

Separation. This distinctive aquatic species has a) thalli that float on the water surface and b) large pendent purplish ventral scales. Plants of the aquatic phase should not be confused with any other liverwort. However, terrestral plants at the drying margins of bodies of water might be confused, especially with *Riccia cavernosa*. Mature terrestrial thalli of *R. natans* have a) an intact dorsal epidermis and do not appear frothy or lacunose (vs. frothy or lacunose thalli from an early age in *R. cavernosa*), and b) small, distinct air-pores in the dorsal epidermis of mature thalli (vs. a dorsal epidermis that disintegrates and no longer exists in mature thalli).

Illustrations. Damsholt 2002; Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. Floating on the surface of lakes, ponds, reservoirs, ditches, and slowly moving water; or terrestrial on damp margins of drying bodies of water. Elevation from 15 to 1600 m.

Distribution. Ricciocarpos natans is nearly worldwide in distribution. Calif. Geographic Regions: **CC**: Alameda Co. *Ertter 18643* (UC), **GV**: Madera Co. *Doyle 7590* (UC), **KR**: Trinity Co. *Tracy 7787* (UC), **MP**: Modoc Co. *True & Stokes 1003* (UC), **NC**: Humboldt Co. *Abrams 7205* (CAS), **SN**: Tulare Co. *Shevock 16904* (CAS).

Targionia L. 1753
(Targioniaceae)

A distinctive feature of this genus is the development of archegonia and sporophytes at the apex of what appears to be the ventral surface of a main thallus branch. Each sporophyte is enclosed by a large, 2-valved, laterally-compressed, shiny purplish-black involucre. When dry, the thallus apex bends upwards, exposing the black scales and sporophyte. Vegetative plants have a) simple pores in the dorsal epidermis, b) air-chambers in a single thin layer with photosynthetic filaments attached to the chamber floor, c) dorsal epidermal cells with nodose trigones, d) glossy blackish ventral scales, and e) antheridia embedded in the dorsal surface of short lateral branches of ventral origin.

Two species in California.

Species Key

The following key was modified from information provided in the spring of 2005 by Alan Whittemore.

1. Midrib 0.4–0.6 the width of the thallus; cell walls in the ventral tissue (at least some walls in some cells) thickened and with elliptical pits; ventral scales subtending the involucre linear to lanceolate. . . . . **T. hypophylla**
1. Midrib 0.7 the width, or more, of the thallus; cell walls in the ventral tissue thin and rarely pitted; ventral scales subtending the involucre lingulate to semi-circular. . . . . T., sp. nov.

Targionia hypophylla L.

Distinctive features. The thallus is green to gray-green, 1–2 cm long and 2–5 mm wide, and has both dichotomous and ventral branching. With reproductive plants, look for a) sporophytes enveloped by large, 2-valved, shiny purplish-black involucres, b) antheridia sessile, in receptacles on short lateral branches of ventral origin, c) yellow to brown to fuscous spores usually 45–85 μm in diameter, d) the distal spore face with large folds and (often incomplete) areolae that are 15–20 μm wide, and d) a finely areolate texture of both spore faces, which gives a frothy appearance to the spore. Sporophytes mature April to September.

With vegetative plants, look for a) cells of the dorsal epidermis with distinct, bulging trigones, b) purplish-black ventral surface and scales, c) a single appendage on each ventral scale, d) air-chambers containing branched and unbranched photosynthetic filaments in a single thin layer, and d) simple epidermal pores only slightly elevated above the thallus surface.

Separation. This species is easy to identify when sporophytes are present—look for large, shiny purplish-black involucres at the apices of the main branches. Vegetative plants, especially in the mountains of southern California and adjacent desert areas, however, have been mis-identified as *Asterella californica*, *Mannia californica* and *Reboulia hemisphaerica*. In these regions, thalli of *T.*

hypophylla usually have a thicker midrib, more rigid thallus and more robust growth than do thalli from coastal and more northern California habitats. Unlike *Asterella, Mannia* and *Reboulia*, however, *T. hypophylla* has air-chambers in a single thin layer.

Illustrations. Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992b.

Habitat. Summer-dry habitats; exposed locations and shade of chaparral, *Quercus*, and rock overhangs; shaded banks and hillsides; around and on rock outcrops; occasionally on shaded boulders with moss. Elevation from near sea-level to 1950 m.

Distribution. Targionia hypophylla occurs in Europe, Asia, Africa, Australia, and North and South America. In the United States it occurs mostly in the west coast and southwest. Calif. Geographic Regions: **CC**: Stanislaus Co. *Whittemore 6572* (CAS), **CR**: Tehama Co. *Doyle 5777* (UC), **KR**: Trinity Co. *Doyle 5860* (UC), **NC**: Colusa Co. *Kellman 2744* (CAS), **SC** San Bernardino Co. *Wagner 940* (UC), **SN**: Fresno Co. *Norris 101458* (UC).

Targionia, sp. nov.

To be described by Dr. Alan Whittemore.

Sphaerocarpoids

The Sphaerocarpoids form a small well-defined group of terrestrial and aquatic plants. Definitive features include a) the development of archegonia on the dorsal surface of the stem, each archegonium surrounded by a cylindrical, bottle-shaped involucre, b) the very short stalk or seta between the sporophyte capsule and foot never elongates, and c) elaters are absent from the capsule (instead, thin-walled, somewhat rounded cells are intermixed with the spores).

Two members of this group, *Geothallus tuberosus* and *Sphaerocarpos drewii*, are the only liverworts to be listed in the 6th edition of the Inventory of Rare and Endangered Plants of California (CNPS 2001).

In California, there are 3 genera and 7 species.

Genus Key

1. Plants aquatic, attached to the substrate; stems erect, elongate with a lateral wing-like expansion; scales in two rows on the the morphological ventral surface. . . . . **Riella**
1. Plants terrestrial; stems prostrate with lateral leaves and flask- or bottle-shaped involucres; scales absent from the ventral stem surface. . . . . **2.**
2. Plants annual, without tubers or other means of perennation; stems and leaves often nearly concealed by numerous bottle- or flask-shaped involucres; distal spore face with ridges or areolae. . . . . **Sphaerocarpos**
2. Plants perennial with tubers developing within stem tissue; stems and leaves clearly visible under involucres of reproductive plants; distal spore face smooth, devoid of ornamentation. . . . . **Geothallus**

Geothallus Campb. 1896
(Sphaerocarpaceae)

A monotypic genus.

Geothallus tuberosus Campb.

Geothallus is a rare and endangered monotypic genus endemic to the Peninsular Ranges, and coastal hills and mesas of San Diego and Riverside Counties. In San Diego Co., it has been found in small, isolated populations from the coast, east to the northwestern slope of Cowles Mountain, and south to the border with Mexico. Many of the early collection sites in San Diego Co. have been compromised by development. In Riverside Co., small populations occur in the Santa Rosa Plateau Ecological Reserve, Santa Ana Mountains. Plants should be searched for in Orange Co., as well as in northern Baja California because populations located on the slope of the Otay Mesa and ravine slope overlooking the Tijuana River are just north of the border with Mexico.

Distinctive features. Geothallus tuberosus is a dioicous plant that perennates by the development of tubers. The tubers develop within stem tissue and include the apical cell. Look for a) leaves variable in

size and shape, often with large and small lamellae, b) black tubers (in drying plants) that enable the plant to survive periods of unpredictable rainfall and drought, c) colorless rhizoids, d) absence of ventral scales, e) male and female plants of similar size, f) a dorsal stem surface not obscured by cylindrical (female plants) or flask-shaped (male plants) involucres, g) large spores, 117–145 μm in diameter separating at maturity, and h) a bald distal spore face, devoid of major markings, and proximal face with a small central areolate area. Sporophytes mature April through mid-May.

Separation. In the field, young, exposed vegetative plants of *Geothallus* can be confused with *Fossombronia* because of a similar green color and crisped appearance of leaves near the shoot apices. Look at the rhizoids with a hand-lens—*Fossombronia* has purplish rhizoids whereas those of *Geothallus* are colorless. Because of its larger size, involucres not obscuring the stem surface and large spores without distinctive markings, *Geothallus* should not be confused with any species of *Sphaerocarpos*.

Illustrations. Doyle 1962; Frye and Clark 1937; Schofield 2002.

Habitat. Gravelly soil; margins of vernal pools; flat and gently sloping areas in and near chaparral. Elevation from 25 to 550 m.

Distribution. Calif. Geographic Regions: **SC**: Riverside Co. *Doyle 9542* (capsules) (UC); San Diego Co. *Doyle 761* (capsules) (UC).

Riella Mont. 1852
(Riellaceae)

This is a genus of morphologically unusual annual, submerged aquatic plants that are attached to the substrate (or lie flat on the soil when the water level drops). Shoots consist of an erect, sparingly branched stem with an undulate, unistratose dorsal laminar wing, and rhizoids at the stem base. Two rows of lateral and two rows of small leaf-like scales occur on the stem axis. Antheridia develop serially in the wing tissue, each individually surrounded by an involucre. Archegonia develop serially on the stem, each surrounded by an involucre.

Two species in California.

Species Key

1. Archegonial involucres usually with 8 longitudinal lamellae; dioicous. . . . . **R. affinis**
1. Archegonial involucres devoid of longitudinal lamellae; monoicous. . . . . **R. americana**

The two species probably are more widespread in California than collections indicate. In addition to searching for living plants, collect dry or drying mud samples from lakes, ponds, reservoirs, and ephemeral pools. After a period of dryness, place a soil sample in a deep culture dish (or other glass container), cover with water and examine periodically with a dissection microscope.

Riella affinis M. Howe and Underw.

In California this species was first reported from Lagunita, an artificial lake on the Stanford University campus, Santa Clara Co. (Thompson 1940). In 1977 (Yeo 179 [UBC]), a second California population was discovered, having developed in a laboratory culture started from dry soil taken from the Cache Creek Settling Basin, northeast Yolo Co., Sacramento Valley.

Distinctive features. A key feature of this monoicous species is the presence of about 8 longitudinal lamellae on each archegonial involucre. Also look for a) in cross-section, a stem with a slightly flattened dorsal surface, b) lateral and ventral scales unistratose to the base, b) absence of gemmae, d) an antheridial body 120–160 μm long, e) brown spores 85–120 μm in diameter, and f) spores with the following 1) a distal face spinose, with the spines 6–15 μm long with the apices mostly truncate, slightly dilated and usually with a shallow apical depression; the spine bases mostly linked by a low network resembling areolae; and 2) a proximal spore face with truncate or obtuse spines, or tubercules, 2–5 μm long. Sporophytes mature late April through July.

Separation. This species is separated from *R. americana* by a) lamellated archegonial involucre (vs. a smooth involucre in *R. americana*), b) generally smaller spore size (85–120 μm vs. 100–130 μm), c) shorter spines on the distal spore face (6–15 μm vs. 10–24 μm), d) shorter antheridial body length (120–160 μm vs. 210–235 μm), and e) and apparent absence of gemmae (vs. gemma present in *R. americana*).

Illustrations. Howe and Underwood 1903; Schofield 2002.

Habitat. Soil; seasonally submerged margins of pools, ponds and lakes. Elevation from 14 to 65 m.

Distribution. Riella affinis occurs in Eurasia, Africa, and North America. In North America, it is known only from two California locations. Calif. Geographic Regions: **CC**: Santa Clara Co. *Thompson s.n.*, June 1940 (capsules) (YU), **GV**: Yolo Co. *Yeo 179* (capsules) (UBC).

Riella americana M. Howe & Underw.

In California, this species is known only from two collections, both from the southwest margin of Big Sage Reservoir, Modoc National Forest, Modoc Co., Modoc Plateau. The identification of the first collection (*Mason 13468a* [UC] was verified by V. Proctor [TTC]).

Distinctive features. A key feature of this dioicous species is the absence of longitudinal lamellae on the archegonial involucres. Also look for a) a somewhat elliptical stem in cross-section, b) lateral leaf scales that are mostly unistratose, but multistratose at the base, and ventral leaf scales unistratose to the base, c) multicellular gemmae on the ventral surface of young stems, d) antheridial body 210–235 μm long, e) brown to dark-brown spores 100–130 μm in diameter and f) spores with the following 1) spinose distal spore face with spines 10–24 μm long, occasionally curved, and with apices slightly dilated or acute; spine bases generally interconnected by a basal membrane, but seldom form well-defined areolae; and 2) proximal spore face with spinose or with short tubercules, the spines 3–6 μm long. Sporophytes mature August through September.

Separation. See discussion under *R. affinis*.

Illustrations. Frye and Clark 1937; Howe and Underwood 1903.

Habitat. Soil; seasonally submerged in margin of a reservoir. Elevation about 1615 m.

Distribution. Riella americana is a New World species; it has been reported from North America, Mexico, and South America. In North America it has been reported in greatly disjunct populations in California, Texas, New Mexico, and South Dakota. Calif. Geographic Region: **MP**: Modoc Co. *Mason 13468a* (young capsules) (UC); *Laeger 3100* (vegetative) (CAS).

Sphaerocarpos Boehm. 1760
(Sphaerocarpaceae)

Sphaerocarpos is a genus of dioicous, short-lived annual plants. The gametophyte consists of a relatively broad, thin stem with succubous, mostly unistratose lateral leaves. There are no underleaves or scales, and the rhizoids are colorless. Antheridia and archegonia are individually enveloped by cylindrical (female) or flask-shaped (male) involucres. In most species, male plants are noticeably smaller than female plants. The antheridial and archegonial involucres usually obscure the dorsal stem surface. The antheridial involucres usually develop a reddish-purple coloration, especially in sunny habitats. Female plants and involucres usually are a light green, but develop reddish areas on involucres in sunny exposures. Involucres on female plant are cylindrical when fertilization does not occur, and nearly globose at the base when containing sporophytes. Sporophytes consist of a capsule, a very short seta and a foot. Elaters are lacking, but thin-walled cells (that are filled with starch grains during early spore development) are intermixed with spores. **Note: spore markings are distinctively species-specific.**

Four species in California.

Gametophytes of all four species collected in the field exhibit such great environmentally induced morphological variation that species identification of plants without spores can be difficult at times. Observations on spore markings, which can be discerned even on very young developing spores, are the most accurate way to identify field-collected plants. Another reason to examine immature capsules is that spores of some species are nearly opaque when mature and spore markings then can be difficult to discern. February to June is the best time to collect plants that have developing to mature spores.

Species Key

1. Spores separating long before capsule maturity. . . . . **S. cristatus**
1. Spores remaining united in tetrads after capsule dehiscence. . . . . **2.**

2. Spores lamellate with low, thick, nearly parallel ridges (a few areolae occasionally occur in the middle of the outer face of each spore). . . . . **S. drewiae**
2. Spores areolate, never with parallel ridges. . . . . **3.**
3. Areolae with prominent protuberances at the corners of the areolae (view in silhouette). . . . . **S. michelii**
3. Areolae of spores lacking prominent protuberances at the corners of the areolae (view in silhouette). . . . . **S. texanus**

Caution. It is often difficult to distinguish between field-collected plants of *S. drewiae, S. michelii,* and *S. texanus.* The female plants are larger than the male plants and usually are more easily located. Male plants are very small, reddish, and often nested within clusters of female plants. The sizes and shapes of the female plants, including sizes and shapes of the involucres, vary with the microhabitat (e.g., moisture availability, exposure).

Sphaerocarpos cristatus M. Howe

Distinctive features. This species often occurs in large patches. Search populations for female plants with capsules and the slightly smaller male plants (often with reddish coloration). In plants with capsules, look for a) yellow- to light-brown spores, 62–78 μm in diameter, that separate long before capsule maturity, b) spores with somewhat sinuous spore markings, often of nearly parallel ridges (cristae) that occasionally branch and anastomose to form a few areolae, and c) ridges on spores that often extend from one pole to the other. Rarely, are spores completely areolate (an exception: *Doyle 8457* [UC], El Dorado Co., Sierra Nevada western foothills, where both completely areolate and typical cristate spores occur in the same capsule; both cristate and areolate spores separate long before capsule maturity as is typical for *S. cristatus*).

Sporophytes mature late March through June.

Separation. Sphaerocarpos cristatus readily can be identified because the spores separate long before maturity (vs. spores remaining united in tetrads in the other three species of *Sphaerocarpos*).

Illustrations. No accurate illustrations are yet published of mature female and male plants, unfortunately, the illustrations in Howe 1899 and Frye and Clark 1937 are inaccurate renderings of very young plants.

Habitat. Plants occur in small patches or as extensive mats in slow-to-dry habitats; silty to gravelly soil of flat areas and hillsides, near and under chaparral and oaks, gardens, dirt roads, paths, banks of rivers, and margins of drainages; occasionally on rocks in splash of ephemeral creeks. Elevation from 7 to 900 m, but more common between 30 and 725 m.

Distribution. Sphaerocarpos cristatus is endemic to Californa. Although not rare, its distribution is imperfectly documented. Calif. Geographic Regions: **CC**: Contra Costa Co *Shevock 15033* (CAS), **GV**: Kern Co. *Laeger 1215* (CAS), **NC**: Mendocino *Doyle 6206* (UC), **SC**: Ventura Co. *Sagar 002* (SFV), **SN**; Fresno *Mueller 1215* (UC).

Sphaerocarpos drewiae Wigglesworth

This is a rare and endangered species endemic to the Peninsular Ranges and coastal hills and mesas of southern California. In Riverside Co., small populations occur in the San Jacinto, Santa Margarita and Santa Rosa Mts. In San Diego Co, small populations occur on the Kearney and Otay Mesas, Soledad Mt., and the hills and mesas between the coast and the Laguna Mts.

Distinctive features. Spores of this species remain united in tetrads at maturity; tetrads are 125–163 μm in diameter. When possible, make observations on spores from immature capsules because mature spore tetrads are dark-brown to black and opaque at maturity. If only mature spores are available, use reflected light and the highest magnification of the dissection microscope. Look for dark, thick, more-or-less parallel ridges that occasionally branch and anastomose, and form one or more areolae at the center of the distal spore face. Sporophytes mature late January through May (depending upon the time of onset of the rainy season).

Separation. The dark, thick, somewhat parallel ridges on spore tetrads easily separate *S. drewiae* from both *S. michelii* and *S. texanus*, which have areolate spore tetrads. These features can be observed on developing spore tetrads soon after meiosis.

Illustrations. Wigglesworth 1929; Frye and Clark 1937.

Habitat. Exposed and easily disturbed gravelly soil under and near chaparral, near vernal pools, margins of drainages, along dirt paths, and on road-cuts. Elevation between 25 and 1450 m, but usually from 100 and 650 m.

Distribution. Sphaerocarpos drewiae is endemic to southern California. Calif. Geographic Regions: **SC**: Riverside Co. *Doyle 2426* (UC); San Diego Co. *Doyle 6171* (UC).

Sphaerocarpos michelii Bellardi

Distinctive features. Spore tetrads are 85–120 μm in diameter, brown to dark-brown, and often opaque at maturity. Look for a) areolate spores, which appear somewhat spinose in profile because of prominent protuberances at the intersections of areolae walls, and b) 6–10 areolae across the distal spore face, with the the areolae 8–17 μm wide. **Note:** Occasionally, there is a single papilla in the center of an areola. Stieperaere, Arts and De Bock (1988) suggested that the presence of such a papilla in each areola of a spore is a species-determining characteristic. On the other hand, Thompson (1948) previously had reported that a papilla may or may not be present even on spores from the same capsule. Observations on California populations by the senior author agree with those of Thompson's and it is concluded that the prominent protuberances at wall intersections, not the presence of papillae, is important in identification of North American populations of this species. Sporophytes mature late May through early August.

Separation. Spores of this species superficially can be confused with those of *S. texanus*. In *S. michelii* a) areolae have an elevated protuberance at the angles between adjacent areolae (vs. the absence of such protuberances in *S. texanus*, b) spore tetrads are smaller (85–120 μm vs. 125–171 μm), and c) generally, there are more areolae across the spore face (6–10 vs. 4–6 in *S. texanus*). **Caution:** Be careful with measurements because some populations of both *S. michelii* and *S. texanus* have tetrads with two larger spores and two smaller ones; the number and width of areolae can be variable even on spores of the same tetrad.

Illustrations. Paton 1999; Schuster 1992a; Thompson 1948.

Habitat. Summer-dry soil of hillsides, and banks and floodplains of creeks; usually in the partial shade of *Pinus* and other conifers. Elevation usually from 1400 to 1900 m.

Distribution. Sphaerocarpos michelii occurs in Europe, and North and South America. Calif. Geographic Regions: **MP**: Lassen Co. *Doyle 828* (UC); Modoc Co. *Doyle 7489* (UC).

Sphaerocarpos texanus Austin

This is the most common species of the genus in California and the one most likely to be collected.

Distinctive features. Spore tetrads are mostly 125–171 μm in diameter, light- to dark-brown, and often opaque when fully mature. Look for a) areolate spore tetrads that are not spinose in profile (lacking prominent protuberances at areolae wall intersections) and b) 4–6 areolae across the distal spore face, the areolae 13–26 μm wide. Sporophytes mature mid-March through June.

Separation. Because this species often grows intermixed with, or in close proximity to, the other three species, collection of plants with developing spores is very important. See *S. michelii* for separation from that species, and *S. drewiae* for separation from that species.

Illustrations. Howe 1899; Paton 1999; Schofield 2002; Schuster 1992a; Thompson 1948.

Habitat. Often a weedy pioneer on easily disturbed summer-dry sites; on soil of hillsides, dirt roads, trails, creek banks, meadows, and margins of ephemeral seepages; open areas in chaparral and woodlands. Elevation from 10 to 1940 m.

Distribution. Sphaerocarpos texanus is widely distributed worldwide: Europe, North Africa, Australia, and North and South America. Calif. Geographic Regions: **CC**: Alameda Co. *Norris 87182* (UC), **CR**: Butte Co. *Griggs 1037* (CHSC), **GV**: Sacramento Co. *Howell 360* (CAS), **KR**: Trinity Co. *Doyle 5846* (UC), **NC**: Sonoma Co. *Eastwood s.n.* (CAS 119198), **SC**: San Diego *Doyle 7151* (UC), **SN**: Kern Co. *Shevock 14850* (CAS).

Simple Thalloid Liverworts

The simple thalloid liverworts form a morphologically diverse group of mostly thalloid plants, but it includes a few leafy liverworts as well (e.g., *Fossombronia*). Features that characterize this group are: a) development of archegonia and antheridia on the dorsal surface of a main stem or lateral branch, b) lack of underleaves, and c) presence of only smooth-walled rhizoids.

Simple thalloid liverworts differ from complex thalloid liverworts by a) the lack of pores in the dorsal epidermis and air-spaces in the underlying photosynthetic tissue (vs. generally with epidermal pores and with internal air-spaces present in complex thalloid liverworts) and b) only smooth-walled rhizoids (vs. both smooth-walled and pegged rhizoids). Simple thalloid liverworts are separated from hornworts by the presence of many chloroplasts in all thallus cells (vs. hornworts have only a single chloroplast in each cell of the thallus apex [some California hornworts have 2 chloroplasts in some mature cells]). *Fossombronia*, the only California leafy member of this group, is separated from the leafy liverworts by the continued apical growth of the stem during formation of archegonia, resulting in archegonia and sporophytes sequentially developed on the dorsal stem surface (vs. archegonia development terminating the apical growth of the branch, resulting in archegonia and sporophytes terminal at the apices of a main stem or short lateral branch in leafy liverworts).

In California, there are 7 genera, 13 species, and 2 previously reported species excluded from the flora.

Genus Key

1. Plants clearly differentiated into stem and leaves; rhizoids purple. . . . . **Fossombronia**
1. Plants thalloid with entire or somewhat lobed margins; rhizoids colorless or brownish. . . **2.**
2. Thallus margin lobed; cyanobacteria colonies on the ventral side of the thallus; gemmae multicellular, stellate and usually present at the thallus apex; long-necked flask-shaped gemma-receptacles occasionally on the dorsal surface. . . . . **Blasia**
2. Thallus margin plane or crisped, but not lobed; cyanobacteria colonies absent; gemma-receptacles absent. . . . . **3.**
3. Thallus with a conspicuous, narrow stem-like midrib and clearly unistratose wings. . . . . **4.**
3. Thallus with an indistinct midrib, gradually thinning to the wing margins. . . . . **5.**
4. Thallus with few to many unicellular cilia on the wing margin and ventral midrib surface; midrib without a central strand of elongate, thick-walled cells; antheridia and archegonia developing on dwarf branches of ventral origin. . . . . **Metzgeria**
4. Thallus lacking unicellular cilia on wing margin and ventral midrib surface; midrib with a central strand of elongate, thick-walled cells; antheridia and archegonia developing on the dorsal surface of a main thallus or branch. . . . . **Pallavicinia**
5. Thallus usually less than 2 mm wide; cells with 0–5 large, usually brownish, oil-bodies. . . . . **Riccardia**
5. Thallus 2–9 mm wide; cells with 6 to more than 30 small, colorless oil-bodies. . . . . **6.**
6. Antheridia and archegonia developing on short lateral branches; 1-celled slime-hairs on the ventral surface at the thallus apex. . . . . **Aneura**
6. Antheridia and archegonia developing on the dorsal surface of a main axis; 2–6 celled slime-hairs on the ventral surface at the thallus apex. . . . . **Pellia**

Aneura Dumort. 1822
(Aneuraceae)

These dioicous plants are sparingly and irregularly branched. The thallus is rather fleshy and has an indistinct midrib. There are 6 to many small oil-bodies per thallus cell. Archegonia and antheridia develop on short lateral branches.

One species in California.

Aneura pinguis (L.) Dumort.

Distinctive features. Plants of this species are sparingly and irregularly branched. The branches of living plants usually are opaque and brittle, and generally have a greasy luster. Thallus color usually is light- to dark-green, but somewhat bluish plants have been found in the high Sierra Nevada (e.g., *Laeger 1977* [CAS]); the bluish color fades to green upon drying. Also look for a) the center of the thallus 7–18 cells thick in thallus cross-section, and gradually thins toward the margin, b) 6 or more small oil-bodies in each cell, c) male plants usually smaller than female plants, d) antheridia embedded

in short lateral branches, and e) archegonia developing on lateral branches that are mostly hidden by the reflexed margin of the branch.

Separation. Vegetative plants of *Aneura pinguis* can be confused with the liverworts *Pellia* and *Riccardia* and the hornwort *Phaeoceros*. In contrast to *Riccardia*, *Aneura* has a) an indistinct midrib region (vs. a more distinct midrib in *Pellia*, and b) an opaque, brittle and greasy appearing thallus (vs. a somewhat translucent, non-brittle and non-greasy appearing thallus). Small thalli of *Aneura* can be confused with *Riccardia*. However, *Aneura* has a) 6 or more small oil-bodies per cell (vs. 0–3 large oil-bodies per cell in *Riccardia*) and b) a thallus that is greasy in appearance (vs. a non-greasy appearing thallus). *Aneura* is separated from *Phaeoceros* by a) cells near the thallus apex each with several chloroplasts (vs. cells near the thallus apex each with one chloroplast in *Phaeoceros*) and b) absence of colonies of cyanobacteria in the ventral thallus tissue (vs. presence of colonies of cyanobacteria in the ventral thallus tissue).

Illustrations. Damshot 2002; Frye and Clark 1937; Paton 1999; Schofield 2002; Schuster 1992a.

Habitat. Wet shaded soil, rocks, and organic matter of stream banks, ditches, marshes, and seepages. Elevation from about 12 to 3620 m.

Distribution. Aneura pinguis is widely distributed in the Northern and Southern Hemispheres. Calif. Geographic Regions: **CC**: Contra Costa Co. *Mason 2486* (UC), **CR**: Shasta Co. *Doyle 9863* (UC), **DMoj**: Inyo Co. *Laeger 1229* (CAS), **KR**: Siskiyou Co. *Shevock 20078* (CAS), **MP**: Modoc Co. *Doyle 8645* (UC), **NC**: Humboldt Co. *Bourell 3677* (CAS), **SC**: San Bernardino Co. *C. Wagner 815* (UC), **SN**: Tuolumne Co. *Laeger 1977* (CAS).

Blasia L. 1753
(Blasiaceae)

Blasia is a distinctive thalloid genus separated from other California liverworts by a) a thallus with clearly lobed lateral margins, b) multicellular, stellate gemmae at the thallus apex, c) long-necked, flask-shaped gemma-receptacles on the dorsal thallus surface, and d) the usual presence of colonies of cyanobacteria in small scale-like auricles at lobe bases on the ventral thallus surface.

Note. This genus traditionally has been classified with the simple thalloid liverworts. However, He-Nygrén, et al. (2006) recently have shown that *Blasia* should be classified with the complex thalloid liverworts. Two morphological characters that it shares are the development of two rows of ventral scales and the presence of gemma-receptacles. In this publication, *Blasia* is included in the simple thalloid liverworts for the convenience of keying plants.

A monotypic genus.

Blasia pusilla L.

Distinctive features. The thallus of this dioicous species is light- to dark-green. Look for a) a thallus with an ill-defined midrib that grades gradually into unistratose wings with scalloped, often leaf-like lobes, b) two kinds of multicellular gemmae: 1) flat, stellate, multicellular gemmae usually present at the thallus apex and 2) slightly flattened, circular gemmae that develop in long-necked, flask-shaped gemma-receptacles on the dorsal thallus surface, c) two rows of scales on the ventral surface of the midrib, and d) two rows of cyanobacteria colonies that occur in scale-like auricles at the base of the lobes on the ventral thallus surface.

Separation. This is a very distinctive thalloid liverwort. Diagnostic in the field, and visible with the hand-lens, are a) the lobing of the thallus margin, b) stellate gemmae usually present at the thallus apex, and c) cyanobacteria colonies present on the ventral thallus surface. On casual observation, plants of *B. pusilla* without gemmae can be confused with gametophytes of hornworts and the liverworts *Aneura pinguis* and *Pellia* species. Hornworts, however, a) lack scales on the ventral thallus surface, b) have cyanobacteria colonies within (endogenous) thallus tissue, c) have a single, large chloroplast in cells at the thallus apex, and d) lack gemmae. Unlike *Blasia*, *Aneura pinguis* and *Pellia* spp. lack a) scales on the ventral thallus surface, b) association with cyanobacteria colonies, and c) stellate gemmae or gemmae in specialized structures.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1992a; Smith 1990.

Habitat. Wet, shaded gravelly and clayey soil of stream floodplains, banks of creeks and ditches, and margins of marshy areas. Elevation from 25 to 830 m.

Distribution. Blasia pusilla occurs in cooler areas of Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 2007* (UC), **NC**: Humboldt Co. *Doyle 10962* (UC). (The report of *B. pusilla* in Santa Barbara Co. was based on a mis-identification. The 1921 C. C. Haynes collection (CAS, NY) from the Hope Ranch, Santa Barbara Co. identified as *B. pusilla* contains vegetative plants of *Phaeoceros* cf. *pearsonii*).

Fossombronia Raddi 1818
(Fossombroniaceae)

This is the only California genus of simple thalloid liverworts in which the shoot is differentiated into stem and leaves. *Fossombronia* is readily recognized with a 10× handlens. Look for a) stems with succubous leaves and long purplish rhizoids, b) archegonia and whitish or yellowish-orange antheridia naked on the dorsal stem surface of main branches, c) a conspicuous cup-like pseudoperianth around each sporophyte, and d) stem growth and sex organ development continuing after fertilization so that more than one sporophyte often occurs on the same branch. All California plants can develop tuberous stem apices at the end of the growing season. These modified stem tips permit survival of conditions when water is unavailable for growth (drought in lower elevation, summer-dry habitats and freezing in higher elevation, winter-snow habitats). When favorable growing conditions re-occur, plants can resume growth from these apices.

In general, the vegetative morphology of plants of lower elevations (below 1400 m), and especially plants of the North, Central, and South Coast Regions, often exhibit variability in color, leaf shape, and manner of leaf insertion on the dorsal stem surface. At least some of this variation appears to be related to seasonal changes during the growing season (e.g., rainfall, cloud cover, onset of dormancy), substrate (e.g., rapidity or slowness of substrate drying between rain events), and exposure. This morphological variability makes it difficult to use vegetative characters alone to identify plants.

On the other hand, details of spore morphology have proven useful to separate California species. The spore characters used in the following key are consistent within a capsule and in several capsules occurring on the same branch of a single plant. Because antheridia and archegonia continuously develop throughout the growing season on reproductively mature plants, a new crop of capsules with mature spores usually develops about 2 weeks following a rain event.

Two species in California.

Species Key

1. Spores typically with 11 to 28 lamellae around the circumference as seen in equatorial optical section with the compound microscope; lamellae of spores spaced 4.5–10 μm apart, in side view; leaf attachment usually does not exceed the midline on the dorsal stem surface of vegetative plants. . . . . **F. pusilla**
1. Spores typically with 30 to 44 lamellae or spines around the circumference as seen in equatorial optical section with the compound microscope; lamellae or spines of spores spaced 1.5–3.5 μm apart, in side view; leaf attachment usually exceeds the midline on the dorsal stem surface of vegetative plants. . . . . **F. longiseta**

Fossombronia longiseta (Austin) Austin

The treatment of this species by Howe (1899) is a composite of the two species recognized here.

Distinctive features. Vegetative plants can exhibit great morphological variation on the same shoot during a single growing season, depending upon temporal variation in moisture, sunlight and maturity level. Search for capsules at the apices of nearly fully elongated setae. Spores in capsules before seta elongation (related to water stress or premature death by collection) often have shorter lamellae and spine heights than do spores in capsules in which the seta has elongated. Look for a) spores with 30 or more lamellae or spines as seen in equatorial optical section with the compound microscope, b) in side view, spores with closely spaced lamellae or spines, 1.5–3.5 μm apart, c) mature spores 40–53 μm in diameter, and d) elaters from 125–290 μm long and with 2 (occasionally 3 in the elater middle) thickened helical bands. There is variation in spore markings, often within the same capsule. At one extreme are spores that are entirely echinate; at the other extreme are spores only with lamellae. The lamellae can a) extend unbranched from one side across the distal face to the other side, b) divide and anastomose to form one to several areolae on the distal face, c) be a mixture of short and long

lamellae; d) be a mixture of mostly short lamellae on the side and entirely echinate on the distal face, and e) be a mixture of short lamellae and spines on both the side and distal face, etc. When we rely soley on spore markings to delimit the two California species, none of the variations consistently correlate with the variations in vegetative morphology.

Vegetative plant color and morphology, including leaf size and shape, are variable within and among populations and it often is not possible to be sure of species identification without examination of spore markings. In general, the attachment of the leaf base extends across the midline on the dorsal stem surface, but this not always true. In addition, pseudoperianths usually lack lamellar outgrowths on their outer surface, but lamellar outgrowths do occur on some pseudoperianths of populations with *longiseta*-type spores.

Separation. In general, *F. longiseta* frequently occurs in more exposed, quicker to dry sites than does *F. pusilla*. As indicated in the key, however, the number of lamellae as seen in equatorial optical section with the compound microscope is the simplest and quickest way to separate these two species. In field-collected material, both *F. longiseta* and *F. pusilla* exhibit similar diversity in vegetative plant morphology, including leaf size and shape, place of leaf attachment on the dorsal stem surface (up to or beyond the stem middle), and development of tuberous stem apices. Use non-spore features with caution in separation of these two species. Recognizing that there are exceptions, *F. longiseta* generally has a) leaf base attachment that extends across the midline on the dorsal stem surface (vs. leaf base attachment that does not extend across the midline in *F. pusilla*) and b) pseudoperianth often without lamellar outgrowths (vs. pseudoperianth usually [not always] with lamellar outgrowths).

Illustrations. Howe 1899 (Figs. 17, 19 and 20 only); The treatment of *Fossombronia longiseta* in Schuster (1992a) is based on specimens that do not belong to that species.

Habitat. Generally exposed clay, silty and gravelly soil of hillsides, road banks, paths, and base of sandstone and other rock outcrops. Elevation from 140 to 1415 m.

Distribution. Fossombronia longiseta occurs in western North and South America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 11352* (UC), **NC**: Glenn Co. *Doyle 6303* (UC), **SC**: Santa Barbara Co. *Doyle 10349* (UC), **SN**: Fresno Co. *Shevock 17128* (CAS).

Fossombronia pusilla (L.) Nees

This is the first published report to confirm the occurrence of *Fossombronia pusilla* in North America. As Schuster (1992b) pointed out, earlier reports of *F. pusilla* from eastern North America are suspect at best. Morphologically, the California populations of this species are indistinguishable from those of Europe (see Stotler and Crandall-Stotler 2005b).

Distinctive features. As in *F. longiseta*, vegetative plants can exhibit color and morphological variation. Spore markings are the most straight-forward way to identify this species. Look for a) with the compound microscope, spores with 16–28 lamellae in equatorial optical section, b) in side view, spores with lamellae 4.5–10 μm apart, c) mature spores 38–55 μm in diameter, and d) elaters 130–250 μm long and with 2 (occasionally 3 in the elater middle) thickened helical bands. In vegetative plants, the leaf base on the dorsal stem surface generally does not cross the stem midline. In addition, pseudoperianths often (not always) have short or long lamellar outgrowths on their outer surface.

Separation. See *F. longiseta* for separation from that species.

Illustrations. Damsholt 2002; Howe 1899 (Figs. 16 and 18); Paton 1999; Smith 1990.

Habitat. Damp shaded places somewhat slow-to-dry after spring rains or snow-melt; soil and organic matter of meadows, lake and stream banks, rock outcrops. Elevation from 9 to 2670 m.

Distribution. Fossombronia pusilla occurs in Europe, Asia, Africa, Australia, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10386* (UC), **CR**: Shasta Co. *Doyle 9344* (UC), **KR**: Siskiyou Co. *Doyle 9158* (UC), **MP**: Modoc Co. *Doyle 7495* (UC), **NC**: Lake Co. *Doyle 8362* (UC), **SC**: San Diego Co. *Doyle 9535* (UC), **SN**: Mariposa Co. *Shevock 21451* (CAS).

Metzgeria Raddi 1818
(Metzgeriaceae)

Thalli of this genus are long and strap-shaped, usually less than 2 mm wide, and have a) a narrow, sharply defined midrib (costa) that lacks elongate, thick-walled cells, b) unistratose wings, and

c) dwarf sexual reproductive branches developing from the ventral surface of the midrib. California species have a variable development of unicellular cilia (hairs) on both the wing margin and midrib ventral surface.

Two species confirmed in California. See Grolle and So (2003) for use of the species name *Metzgeria violacea* rather than *M. fruticulosa.*

Species Key

1. Midrib usually with 2–3 rows of cells on the dorsal surface and mostly 3–5 rows of cells on the ventral surface; marginal cilia of the wing mostly in pairs (some are single); gemmae absent. . . . . **M. conjugata**
1. Midrib usually with 2 rows of cells on the dorsal surface and mostly 2–3 rows of cells on the ventral surface; marginal cilia of the wing usually single; gemmae developing on specialized attenuated branches. . . . . **M. violacea**

Excluded. Metzgeria temperata Kuwah. Kuwahara (1976) segregated this species from *M. fructiculosa* (Dicks.) A. Evans. Based on *Yurky 166*, Yurky (1995) reported *M. temperata* from Marin County. Damsholt (2002) and Paton (1999) provided detailed descriptions and excellent illustrations of both *M. temperata* and *M. fruticulosa* (=*M. violacea*). Examination during this study found that *Yurky 166* had the definitive characteristics of *M. violacea. M. temperata* could not be confirmed for California.

Metzgeria conjugata Lindb.

Distinctive features. This monoicous species usually occurs in loose green or pale-green mats. Look for a) marginal thallus wings recurved, b) a midrib 2–3 cells wide as seen from the dorsal surface and 3–5 cells wide on the ventral surface as seen from the ventral surface, c) cilia commonly present on wing margins and ventral midrib surface, d) marginal cilia straight or slightly curved, in pairs or single, and e) attenuated branches with gemmae absent.

Separation. This species is separated from *M. violacea* by a) marginal cilia usually in pairs (vs. marginal cilia mostly single in *M. violacea*), b) the dorsal midrib surface mostly 2–3 cells wide and the ventral surface 3–5 cells wide (vs. the dorsal midrib surface 2 cells wide and the ventral surface mostly 2–3 cells wide), and c) the absence of gemmae development (vs. the frequent development of gemmae in *M. violacea*).

Illustrations. Damshot 2002; Paton 1999; Schofield 2002; Schuster 1992a; Smith 1990.

Habitat. In diffusely lit, humid areas; on bark of shrubs and angiosperm trees, and rock outcrops. Elevation from 30 to 250 m.

Distribution. Metzgeria conjugata occurs in Europe, Asia, Africa, and North and South America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 1995* (UC), **NC**: Humboldt Co. *Doyle 2114* (UC).

Metzgeria violacea (Ach.) Dumort.

Although many collections of this species develop a persistent postmortem bluish coloration of the whole shoot, California specimens mostly develop a bluish coloration only in the shoot apices and erect, attenuated gemmiferous branches. The bluish coloration often takes months for maximum development and it persists for years. However, do not use the presence or distribution of color as the only guide to species identification.

Distinctive features. Look for a) relatively short branches, generally less than 1.5 cm long, b) widest region of the wing mostly 9–12 cells wide, c) cells in the middle of mature wing tissue that are mostly 17–30 μm wide × 22–45 μm long, d) dorsal midrib surface with 2 rows of cells, and ventral surface with 2–4 rows of cells, e) attenuated gemmiferous branches usually erect, with gemmae on both wing margins and midrib tissue, and usually with an apical cluster of gemmae, f) central cells of the dorsal gemma surface without protruding conical walls, and g) adventitious shoots common (with the midrib cells of the adventitious shoot occasionally not connected to the midrib of the main branch).

Separation. See *Metzgeria conjugata* for separation from that species. *M. violacea* can be confused with *M. temperata.* It can be separated by a) shorter shoots, 0.4–1.5 cm long (vs. shoots mostly 1.5–

2.5 cm long in *M. temperata*), b) smaller wing cell size, 17–30 μm wide × 22–45 μm long (vs. wing cell size 25–43 μm wide × 33–58 μm long), c) ventral midrib surface with 2–4 rows of cells (vs. ventral midrib surface with 2 (occasionally 3) rows of cells), d) adventitious shoots common (vs. adventitious shoots uncommon), e) gemmae from midrib and wing margins (vs. gemmae only from wing margins), and f) central cells of the the dorsal gemma surface without conical protuberances (vs. central cells of the dorsal gemma surface with conical protuberances).

Illustrations. Damsholt 2002 (as *M. fruticulosa*); Paton 1999 (as *M. fruticulosa*).

Habitat. Trunks of shrubs in shaded, humid understory of redwoods, and mixed hardwood/conifer forest. Elevation under 430 m.

Distribution. Metzgeria violacea occurs in Europe, Asia, and North America. Calif. Geographic Regions: **NC**: Humboldt Co. *Kofranek 1589* (UC) and Marin Co. *Yurky 166* (a robust, gemmiferous population) (SFSU).

Pallavicinia Gray 1821
(Pallaviciniaceae)

Distinctive features of this genus include a) a narrow and distinct midrib with a well-defined central strand of elongate, thick-walled cells, b) a unistratose wing, c) absence of cilia on the wing margin and midrib, d) antheridia in two rows, one row on each side of the midrib dorsal surface, and e) archegonia in groups on the dorsal surface of the midrib. This genus should not be confused with any other.

One species in California.

Pallavicinia lyellii (Hook.) Carruth.

Distinctive features. Thalli of this dioicous species are pale to deep-green and usually translucent. Look for a) sparingly branched thalli with a distinct midrib and unistratose wings, b) a well-defined central strand of elongate, narrow diameter, thick-walled cells in the midrib (usually visible with transmitted light of the dissection miscoscope), c) absence of cilia on both the midrib and wing, d) over 30 oil-bodies per thallus cell, e) male plants with antheridia, each subtended by a scale, in two rows, one row on each side of the midrib dorsal surface, and f) female plants with archegonia in groups on the dorsal surface of the midrib and surrounded by basally fused scales or lamellae.

Separation. The presence in the midrib of a clearly defined central strand of elongate, thick-walled cells separates *P. lyellii* from all other California liverworts.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992a; Smith 1990.

Habitat. In California, in a moist recess in a rotten log, and on soil (D. Wagner, personal communication). Elevation about 91 m.

Distribution. Pallavicinia lyellii occurs in Europe, Asia, Africa, and North, Central, and South America. It mostly occurs in the eastern and central states of North America. In the west, it is known only from a single collection in California—from a second growth redwood forest on the campus of Humboldt State University, Arcata. Calif. Geographic Regions: **NC**: Humboldt Co. *Wilson 1534* (NY, CAS).

Pellia Raddi 1818
(Pelliaceae)

Species of this genus have a) a definite, but rather poorly delimited midrib that gradually thins toward the margin, b) often undulating wings, c) no central strand of elongate, thick-walled cells in the midrib, d) 2–8-celled slime-filaments near the apex of the thallus ventral surface, e) rhizoids that are brownish rather than hyaline, f) antheridia individually embedded in chambers in the midrib of the dorsal thallus surface, and g) small groups of archegonia that develop in a depression on the thallus dorsal surface.

Two species in California.

Species Key

1. Slime-filaments on the ventral thallus apex usually 2-celled, the terminal cell subtended by a nearly isodiametric 1-celled stalk cell; midrib cells usually with transverse and vertical

bands of colorless to brownish wall thickening in thallus cross-section; pseudoperianth tubular, but the side toward the apex lower than the back side, generally lying on the thallus surface with the opening toward the thallus apex; pseudoperianth mouth entire to slightly crenulate. . . . . **P. neesiana**

1. Slime-filaments on the ventral thallus apex 3–6-celled (seldom 2-celled), the terminal cell subtended by 2–5 elongate stalk cells; midrib cells without transverse and vertical bands of colorless to brown wall thickening in thallus cross-section; pseudoperianth tubular and erect; pseudoperianth mouth dentate to ciliate. . . . . **P. endiviifolia**

Excluded. Pellia epiphylla (L.) Corda. Frye and Clark (1937) reported *P. epiphylla* for California. However, all herbarium specimens labeled *P. epiphylla* examined in this study were found to be either *P. endiviifolia* or *P. neesiana*. *Pellia epiphylla* could not be confirmed for California. For this monoicous species, look for plants with antheridia and archegonia on the same branch or on separate branches of the same thallus.

Pellia endiviifolia (Dicks.) Dumort.

Distinctive features. This dioicous species often has purplish coloration in the fall. Look for a) slime-filaments 3–6-celled near the apex of the thallus ventral surface, b) mature midrib tissue in thallus cross-section without colorless to brown transverse and vertical bands of secondary wall thickening; and c) erect tubular pseudoperianths with dentate to ciliate mouths.

Separation. This species and *P. neesiana* can grow in close proximity, and occasionally thallus sizes and forms are similar. *Pellia endiviifolia* can be separated by a) slime filaments of 3–6 cells (vs. usually only 2 cells in *P. neesiana*), b) the absence of colorless to brown transverse and vertical bands of wall thickening on cells of mature midrib tissue (vs. transverse and vertical bands of wall thickening usually present: **Caution:** wall thickenings are not always well-developed or present in all thalli of *P. neesiana*), and c) erect tubular pseudoperianths with a dentate to ciliate mouth (vs. pseudoperianths with the side toward the thallus apex lower than the back side, and with an entire to crenulate mouth).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1992a; Smith 1990.

Habitat. Shaded creek banks, drainages and seepages in meadows and forests. Elevation from 1400 to 2900 m.

Distribution. Pellia endiviifolia occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **CR**: Siskiyou Co. *Shevock 26195* (CAS), **KR**: Siskiyou Co. *Doyle 1993* (male) (UC), **MP**: Modoc Co. *Doyle 807* (UC), **SN**: Fresno Co. *Doyle 2463* (female & male) (UC).

P. neesiana (Gottsche) Limpr.

Distinctive features. Look for a) 2-celled slime-filaments on the ventral surface of the apical region, the basal cell of the filament is short and has conspicuous brownish-gray contents, b) mature midrib tissue in thallus cross-section usually with colorless to brown transverse and vertical bands of secondary wall thickening, c) tubular young pseudoperianths with the side away from the thallus apex lower, resulting in what appears to be a pseudoperianth that is prostrate on the thallus with the opening toward the thallus apex, and c) an entire to crenulate pseudoperianth mouth (but older ones can be lacerated).

Separation. Vegetative and male plants of *P. neesiana* can be confused with *P. endiviifolia*. For separation see *P. endiviifolia*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992a.

Habitat. Full sun to partial shade; creek banks, drainages, seepages and marshes in meadows and forests. Elevation from near sea-level to 3100 m.

Distribution. Pellia neesiana occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Doyle 9394* (UC), **KR**: Del Norte Co. *Doyle 7730* (female) (UC), **MP**: Modoc Co. *Doyle 11089* (female) (UC), **NC** Mendocino Co. *Bourell 3628* (CAS), **SN**: Plumas Co. *Dillingham 2173* (UC). The *Schallert 210* (NY 263663) collection of *P. neesiana* from **CC**, Big Sur State Park, Monterey Co., was mis-identified; the packet contains a mixture of non-reproductive *Phaeoceros sp.* and *Riccardia chamedryfolia*.

Riccardia Gray 1821
(Aneuraceae)

These thalloid plants are pinnately, palmately or irregularly branched. The thallus has a poorly defined midrib that lacks a central strand of elongate, thick-walled cells. Determination of the number and distribution of oil-bodies in living plants is a great aid in species identification, because of the morphological variability of the vegetative thallus. Oil-bodies are lost on drying; try to keep alive a small sample of your collection for later microscopic examination and keep your notes with the collection.

Four species in California.

Species Key

1. Thallus 1–3 times pinnately branched. . . . . **2.**
1. Thallus palmately or irregularly branched. . . . . **3.**
2. Lateral margins of terminal and secondary branches usually unistratose for 2–4 cells; branches often narrowed toward the apex; oil-bodies usually absent from epidermal and ultimate cells of the lateral margins, but present in internal tissue. . . . . **R. multifida**
2. Lateral margins of terminal and secondary branches unistratose for 1 (seldom more than 2) cells; branches usually narrowed toward the base; oil-bodies usually present in all thallus cells. . . . . **R. chamedryfolia**
3. Thallus irregularly to sub-palmately branched; branches up to 2 mm wide, somewhat broadened at apex; median epidermal cells of dorsal surface 30–60 μm wide × 60–120 μm long; oil-bodies usually lacking in all cells (rarely present in some older internal cells). . . . . **R. latifrons**
3. Thallus palmately branched; branches usually less than 0.5 mm wide, more-or-less parallel sided or slightly narrowed toward apex; median epidermal cells of dorsal surface 16–42 μm wide × 28–56 μm long; oil-bodies usually absent in epidermal cells, but present in internal cells. . . . . **R. palmata**

Riccardia chamedryfolia (With.) Grolle

Distinctive features. These pinnately branched, autoicous plants generally are light-green in shade and occasionally blackish in sun-forms. Look for a) branches usually slightly narrowed toward the branch base, b) branch lateral margins usually of 1 unistratose row of cells (margins of some branches occasionally have 2, rarely more, unistratose rows of cells), c) dorsal epidermis generally with hexagonal cells with thin colorless walls, d) mature median cells of the dorsal epidermis 22–50 μm wide × 55–90 μm long, e) brownish oil-bodies present in nearly all epidermal, marginal and internal cells.

Separation. This species is highly polymorphic and can be confused with *R. latifrons* and *R. multifida*. It is separated from *R. latifrons* by a) irregular 1–3 pinnate branching (vs. usually subpalmate branching in *R. latifrons*), and b) nearly all epidermal cells with oil-bodies (vs. oil-bodies absent in all epidermal cells). *Riccardia chamedryfolia* is separated from *R. multifida* by a) lateral margins of branches usually unistratose for only 1 cell row (vs. branch lateral margins unistratose for 2–4 cell rows in *R. multifida*), b) branches usually narrowed toward the apices (vs. branches narrowed toward the base), and c) oil-bodies present in most epidermal and marginal cells (vs. oil-bodies lacking in most epidermal and marginal cells).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992a; Smith 1990.

Habitat. Wet rocks, damp soil of banks, decayed wood, and tree roots; generally near, or submersed in dripping, running or slowly moving water. Elevation from near sea-level to 2300 m.

Distribution. Riccardia chamedryfolia occurs in Europe, Asia, and North and South America. Calif. Geographic Regions: **CC**: San Francisco Co. *Shevock 19017* (UC), **CR**: Shasta Co. *Doyle 10991* (UC), **DMoj**: Inyo Co. *Laeger 2623b* (CAS), **KR**: Siskiyou Co. *Doyle 9218* (UC), **NC**: Humboldt Co. *Doyle 11380* (UC), **SN**: Nevada Co. *Doyle 10004* (UC).

Riccardia latifrons (Lindb.) Lindb.

Distinctive features. These autoicous, pale to bright green plants are subpalmately or irregularly branched. Look for a) lateral branches 0.5–1 mm (or more) wide and usually narrowed toward the

base, b) lateral branch margins of 1 cell wide, c) epidermal cells large, 5–6-angled and thin-walled, d) mature median cells of the dorsal epidermis usually 30–54 μm wide × 60–150 μm (or more) long, and e) oil-bodies generally absent in all thallus cells (vs. occasionally present in some older internal thallus cells).

Separation. This species and *R. palmata* grow on decaying logs and stumps, and can be confused. *R. latifrons* is separated from *R. palmata* by a) large dorsal epidermal cells, usually 60–150 μm long × 30–54 μm wide (vs. dorsal epidermal cells 28–56 μm × 16–42 μm in *R. palmata*), b) all dorsal epidermal cells with colorless, thin walls (vs. older dorsal epidermal cells with brownish, equally thickened walls), c) branches 0.5–1 mm (or more) wide and narrowed toward the base (vs. branches less than 0.5 mm wide and not narrowed toward the base), and d) oil-bodies normally absent from epidermal and internal cells (vs. oil-bodies absent in epidermal cells, but present in internal cells). See *R. chamedryfolia* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1992a; Smith 1990.

Habitat. Damp, shaded areas: moist decaying logs; cut ends of tree trunks; soil with moss in seepages; soil at base of wet, shaded cliffs. Elevation from near sea-level to 1825 m; but mostly below 1000 m.

Distribution. Riccardia latifrons occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 6445* (UC), **CR**: Tehama Co. *Doyle 8766A* (UC), **KR**: Trinity Co. *Doyle 8654* (UC), **MP**: Modoc Co. *Doyle 6673* (UC), **NC**: *Norris 85083* (UC), **SN**: Tuolumne Co. *Norris 104020* (UC).

Riccardia multifida (L.) Gray

Distinctive features. These autoicous, green to brownish-green thalloid plants are 2–3-times pinnately branched. Look for a) branches often crowded and mostly narrowed toward the tip, b) margins of ultimate and subterminal branches unistratose for a width of 2–4 cells, giving the branches a translucent appearance, c) dorsal epidermal cells polygonal and with thin colorless walls, d) mature median dorsal epidermal cells 25–40 μm wide and 50–75 μm (or more) long, e) large brownish-gray oil-bodies present in the internal thallus cells, but absent from most epidermal and marginal cells.

Separation. This species usually is easy to identify because of the 2–4 cells wide unistratose lateral margins of ultimate and sub-terminal branches. *Riccardia multifida* occasionally can be confused with the polymorphic *R. chamedryfolia*. See *R. chamedryfolia* for separation from that species.

Illustrations. Damsholt 2002, Paton 1999; Schuster 1992a.

Habitat. Shaded, wet areas; usually on decaying logs and organic matter; also on wet rocks and soil of stream banks. Elevation from near sea-level to 1700 m.

Distribution. Riccardia multifida occurs in Europe, Asia, North Africa, New Zealand, and North America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 8872* (UC), **KR**: Trinity Co. *Doyle 6711* (UC), **NC**: Mendocino Co. *Doyle 6278* (sporophytes) (UC), **SN**: Yuba Co. *Doyle 9579* (UC).

Riccardia palmata (Hedw.) Carruth.

Distinctive features. These dioicous plants are pale- to deep-green, becoming brownish or grayish when older. The main axis is prostrate (adhering to substrate), from which arise erect, narrow and rather rigid, simple or palmately-lobed branches. Look for a) branches usually with rounded margins in cross-section, b) equally thick-walled epidermal cells, c) small mature median dorsal epidermal cells usually 16–42 μm wide × 28–56 μm long, and d) 1 or 2 oil-bodies in the internal thallus cells, but mostly absent from the epidermal and marginal cells. Endogenous gemmae often developing near branch apices in such large numbers that the thallus has a light-green, powdery appearance.

Separation. Young plants of this species and *R. latifrons* occasionally grow together on decaying logs and stumps, can be confused in the field; see *R. latifrons* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1992a; Smith 1990.

Habitat. On shaded, moist decaying logs. Elevation from 100 to 1300 m.

Distribution. Riccardia palmata occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Doyle 11101* (UC), **NC**: Humboldt Co. *Doyle 9007* (UC).

Leafy Liverworts

Leafy liverworts comprise the largest group of liverworts in California. Distinctive characteristics include a) archegonia developing at the apex of a main stem or lateral branch, resulting in the termination of continued apical growth of that shoot, b) stems with two rows of lateral leaves (a third row of leaves, underleaves, may or may not be present), and c) rhizoids always smooth-walled.

In California, there are 29 genera, 87 species, 6 infraspecific taxa (subspecies/varieties), and 1 species to be described in a subsequent paper. Two genera (*Jamesoniella* and *Pleurocladula*) previously reported for California could not be confirmed, 1 genus (*Herbertus*) is questionable, and 12 species previously reported for California, could not been confirmed.

Genus Key (See Glossary [Appendix I] for Definition of Terms)

Because many collections will consist only of non-reproductive plants, this key primarily uses vegetative characteristics. Some genera will show in the key more than once because of morphological diversity of species in those genera.

1. Leaves complicate-bilobed (lobes folded 180°; the ventral lobe cylindrical in most species of *Frullania*). . . . **2.**
1. Leaves unlobed, or bilobed to 4-lobed, but never complicate-bilobed. . . . **7.**
2. Dorsal lobe larger than the ventral lobe. . . . **3.**
2. Dorsal lobe slightly to greatly smaller than the ventral lobe. . . . **5.**
3. Underleaves absent. . . . **Radula**
3. Underleaves present. . . . **4.**
4. Underleaves bilobed. . . . **Frullania**
4. Underleaves entire (not bilobed). . . . **Porella**
5. Leaf lobes lanceolate, tapering from near the base to an acute or acuminate apex. . . **Douinia**
5. Leaf lobes narrowly lingulate or narrowly ovate to reniform, not tapering from near the base to an acute or acuminate apex. . . . **6.**
6. Shoot tips mostly curving upwards; leaf lobes narrowly lingulate; perianths cylindrical, narrowing to the mouth. . . . **Diplophyllum**
6. Shoot tips mostly curving downwards; leaf lobes narrowly to broadly ovate to suborbicular or reniform; perianths flattened, wide at the mouth. . . . **Scapania**
7. Leaves mostly 3–4 lobed. . . . **8.**
7. Leaves unlobed or mostly 2-lobed (occasionally 2 and 3 lobed on the same shoot). . . . **13.**
8. Leaves deeply divided to (or nearly to) the base; leaf lobes linear. . . . **9.**
8. Leaves clearly not divided to the base (i.e., with a laminar base); leaf lobes not linear. . . . **10.**
9. Leaves divided into 3 or 4 uniseriate filaments (lobes), to within one cell of the leaf base. . . . **Blepharostoma**
9. Leaves divided into 3 or 4 lobes that are mostly 2 cells wide at the lobe base. . . . **Kurzia**
10. Plants yellowish- to reddish-brown; leaf lobe apices and margins with filaments. . . **Ptilidium**
10. Plants green, bluish-green or yellowish-green; leaf lobe apices and margins without filaments. . . . **11.**
11. Leaves incubous (the front margin of a leaf lies over the rear margin of the leaf closer to the stem apex in dorsal view); leaf lobes equal. . . . **Lepidozia**
11. Leaves succubous (the front margin of a leaf lies under the rear margin of the leaf closer to the stem apex in dorsal view); leaf lobes unequal. . . . **12.**
12. Underleaves present (observe at shoot apex because of dense rhizoid growth in older stem areas); leaves 3–4-lobed on vegetative stems. . . . **Barbilophozia**
12. Underleaves absent; leaves all or mostly 2-lobed on vegetative stems. . . . **Lophozia**
13. Leaves and underleaves of similar size and shape (three rows of more-or-less similar leaves = isophyllous). . . . **14.**
13. Leaves and underleaves, if present, of dissimilar size and shape (two rows of lateral leaves and one row of smaller underleaves = anisophyllous). . . . **15.**
14. Plants grayish- to whitish-green; leaf cells uniformly thickened without conspicuous trigones; leaf tips appressed to the stem. . . . **Anthelia**
14. Plants brownish-green to yellowish-brown; leaf cells with bulging trigones; leaf tips spreading. . . . **Herbertus**
15. Leaves incubous (the front margin of a leaf lies over the rear margin of the leaf closer to the stem apex). . . . **16.**

15. Leaves succubous (the front margin of a leaf lies under the rear margin of the leaf closer to the stem apex), or transversely or subtransversely inserted. . . . . **17.**
16. Leaf apices entire or with an apical notch; underleaves bilobed or notched. . . . . **Calypogeia**
16. Leaf apices with 2–4 shallow apical teeth; underleaves with 0–4 shallow teeth. . . . **Bazzania**
17. Leaf apices rounded, truncate, notched, or broadly indented. . . . . **18.**
17. Leaf apices clearly lobed. . . . . **25.**
18. Underleaves present and conspicuous unless obscured by dense rhizoid growth (to minimize problem with rhizoid observation, look at the ventral surface of the stem very near the apex). . . . . **19.**
18. Underleaves absent or small and inconspicuous. . . . . **21.**
19. Rhizoids in tufts mostly surrounding reddish cushions on the ventral stem surface. **Gyrothyra**
19. Rhizoids in tufts from leaf or underleaf bases and/or scattered on the ventral stem surface. **20.**
20. Leaf apices rounded, truncate, slightly notched, or broadly indented; leaves decurrent on the dorsal stem surface; perianths on dwarf branches with modified leaves. . . . **Chiloscyphus**
20. Leaf apices usually shallowly bilobed, at least on some leaves; leaves not or short decurrent on the dorsal stem surface; perianths on main branches with normal leaves. . . . . (some species of) **Lophocolea**
21. Underleaves present at least near the shoot apex, small. . . . . **22.**
21. Underleaves absent, or very small and ephemeral. . . . . **23.**
22. Median leaf cells 38–50 μm wide × 50–75 μm long; gemmae often on the margins of modified leaves. . . . . **Mylia**
22. Median leaf cells 20–38 μm wide × 25–50 μm long; gemmae absent. . . . . **Nardia**
23. Leaf margin usually toothed or serrate, with the margin away from the shoot apex often reflexed, especially when dry. . . . . **Plagiochila**
23. Leaf margin smooth, not toothed or serrate, with the margin not reflexed. . . . . **24.**
24. Underleaves absent; perianth mouth smooth or toothed. . . . . **Jungermannia**
24. Underleaves very small, often present near the shoot apex; perianth mouth ciliate. **Jamesoniella**
25. Epidermal cells of the stem larger than and forming a differentiated layer (hyalodermis) around the internal cells (the hyalodermis is obvious in dry specimens). . . . . **26.**
25. Epidermal cells of the stem not forming a distinct hyalodermis. . . . . **27.**
26. Underleaves present, distinct. . . . . **Pleurocladula**
26. Underleaves absent. . . . . **Cephalozia**
27. Underleaves present on both vegetative and reproductive stem regions. . . . . **28.**
27. Underleaves absent, scarce, or restricted to reproductive stem regions. . . . . **32.**
28. Underleaves large. . . . . **29.**
28. Underleaves small. . . . . **30.**
29. Underleaves usually with 1 or 2 lateral teeth; rhizoids in tufts from underleaf base; leaf lobes ending in 2–5 superposed cells; plants green to whitish-green, not opaque. . . . . **Lophocolea**
29. Underleaves without lateral teeth; rhizoids from both underleaf base and stem tissue; leaf lobes not ending in 2–5 superposed cells; plants green to yellowish-green, opaque. . **Geocalyx**
30. Plants thin and thread-like, 0.1–0.5 mm wide. . . . . (some species of) **Cephaloziella**
30. Plants not thin and thread-like, 0.6–3.5 mm wide. . . . . **31.**
31. Leaves usually broadly spreading from the stem, seldom concave; underleaves usually with 1 or 2 lateral teeth or thread-like appendages. . . . . (some species of) **Lophozia**
31. Leaves usually erect and concave; underleaves usually without 1 or 2 lateral teeth or thread-like appendages. . . . . (some species of) **Nardia**
32. Leaves closely overlapping and appressed, the stem not visible. . . . . **Gymnomitrion**
32. Leaves often overlapping, but the stem visible in mature shoot areas. . . . . **33.**
33. Leaves bilobed 0.5 or more their length; shoots usually thin and threadlike. . . . . (some species of) **Cephaloziella**
33. Leaves bilobed mostly less than 0.5 their length; shoots usually not thin and threadlike. **34.**
34. Leaves mostly clearly obliquely inserted. . . . . **35.**
34. Leaves transversely or sub-transversely inserted. . . . . **36.**
35. Leaf lobe apices (of California species) rounded; underleaves absent or small and infrequent; perianth smooth from base to mouth. . . . . **Gymnocolea**
35. Leaf lobe apices acute, underleaves absent; perianth smooth below, but plicate above middle to mouth. . . . . (some species of) **Lophozia**
36. Leaves bilobed with the base of the dorsal and ventral leaf lobes transversely to sub-transversely inserted; dorsal and ventral lobes generally of similar size; perianths short, not exserted above female bracts. . . . . **Marsupella**

36. Leaves bilobed with the base of the dorsal lobe transversely inserted, but base of the ventral lobe obliquely inserted; dorsal lobe slightly smaller than ventral lobe; perianths long exserted above female bracts. . . . . **Anastrophyllum**

Uncertain status. Lophocolea gemmiparous A. Evans. *Thiers 5403a* was identified as *Lophocolea gemmiparous*. However, rhizoids scattered on the stem surface and the nature of the antheridial branch removes the Type specimen (and *Thiers 5403a*) from *Lophocolea* and the Geocalycaceae (P. Davison, personal communication). Additional material would help determine whether "*Lophocolea gemmiparous*" should be included in an existing or a new genus. The California collection site data are: Sierra County; Tahoe National Forest; seasonal stream in meadow along Webber Lake Road; Red fir forest; 6 June 1987; bryophyte cohorts included *Fontinalis antipyretica, Scapania irrigua, Chiloscyphus polyanthos* var. *rivularis*, and *Calypogeia* sp. (B. Thiers, personal communication). It is a high priority to relocate this taxon.

Anastrophyllum (Spruce) Steph. 1893
(Scapaniaceae)

Plants of this genus usually have a) strongly concave and unequally bilobed leaves with the dorsal lobe smaller than the ventral lobe, b) leaf cells with equally thickened walls or strongly bulging and occasionally confluent trigones, and c) stems with no underleaves. Gemma clusters are common at shoot tips.

One species in California.

Anastrophyllum minutum (Schreb.) R. M. Schust.

Distinctive features. These dioicous, dark green to yellowish-brown plants are 0.4–1.5 mm wide and 1–3 cm long. Look for a) unequally bilobed leaves that are strongly concave and in two rows (distichous), b) dorsal leaf lobes smaller than the ventral lobes, c) cells in the leaf lobes in concentric rows, d) median leaf cells 14–24 μm wide and 18–26 μm long, e) leaves that are obliquely inserted ventrally and transversely inserted dorsally, approaching complicate-bilobed in appearance, f) cells in the upper part of the leaf equally thick-walled and without trigones; those in the lower part often with distinct trigones, g) 2–5 oil-bodies per cell, h) underleaves lacking, i) red to reddish-brown clusters of 2–4-celled, angular to knobby gemmae at the apices of erect shoots, and j) perianth mouths lobed and with teeth 1–3 cells long.

Separation. This species is likely to be confused only with small species of *Marsupella*. *Anastrophyllum minutum* has a) lobe cells often in concentric rows (vs. not organized into rows in *Marsupella*), b) asymmetrical leaf lobes (vs. symmetrical leaf lobes) c) gemmae common (vs. gemmae absent), d) hyaline rhizoids (vs. rhizoids usually with some pigmentation), and e) 2–5 oil-bodies per cell (vs. usually only 2 large oil-bodies per cell).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969.

Habitat. Damp, dimly-lit soil and rock habitats, e.g., base of dripping cliffs and seeps; in deep crevices below massive overhanging ledges. Elevation over 1200 m.

Distribution. Anastrophyllum minutum occurs in Europe and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Jessup 7408* (SOC).

Anthelia (Dumort.) Dumort. 1835
(Antheliaceae)

This is a distinctive, easily recognized genus of higher elevations. Leaves and underleaves a) are similar in size and form (isophyllous) and transversely inserted, b) overlap each other, appearing 3-ranked and tightly appressed to the stem, and c) are deeply bilobed, the lobes narrow and with acute apices. Oil-bodies are absent from all cells. When dry, plants in mats and large cushions often are conspicuously covered with what appears to be fungal hyphae, but is whitish material formed by the plants.

One species in California.

Anthelia juratzkana (Limpr.) Trevis.

Distinctive features. These paroicous plants often occur in compact grayish-green or bluish-gray or whitish-gray mats. Shoots usually are 2–7 (rarely over 12) mm long. Look for a) in the field, mats covered

with a whitish substance, b) rhizoids usually present on both main and side branches, c) wide ovate perianths common, each emergent less than 0.5 its length above the bracts, d) elaters with 2–4 thickened helical bands, each band less than 3 μm wide, and e) spores 15–21 μm in maximum diameter.

Separation. This distinctive liverwort is likely to be confused only with young and non-reproductive plants of *Anthelia julacea* (a species not confirmed, but possible, for California). Young plants of the two species can be nearly impossible to separate. *Anthelia juratzkana* usually can be separated by a) shoots generally less than 7 mm long (vs. up to 35 mm long in *A. julacea*), b) thallus color of grayish-green or bluish-gray (vs. yellowish-green or green, often with a brownish coloration), c) paroicous (vs. dioicous), d) wide ovate perianths emergent less than 0.5 their length beyond the bracts (vs. narrowly ovoid perianths emergent by 0.5 or more their length beyond the bracts), e) elaters with 2–4 thickened helical bands, each band less than 3 μm wide (vs. elaters with 2 helical bands, each band 3.5–4.0 μm wide) and f) spores 15–21 μm in diameter (vs. spores 12–16 μm in *A. julacea*).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Banks of drainages and on hummocks in meadows, and banks and margins of lakes, seepages and creeks. Elevation from 2700 to 3725 m.

Distribution. Anthelia juratzkana is widespread in the arctic-alpine zones of Europe, Asia, North and South America, and New Zealand. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 9829* (perianths) (UC), **SN**: Fresno Co. *Shevock 13864* (CAS).

Excluded. Anthelia julacea (L.) Dumort. Based on *Howell 584 & 585* (CAS), Sutliffe (1942, 1947) reported the presence of *A. julacea* from the high Sierra Nevada of Madera County. Both Howell collections, however, are *A. juratzkana*, as were other California collections of *Anthelia* examined in this study. *A. julacea* could not be confirmed for California but is expected.

Barbilophozia Loeske 1907
(Scapaniaceae)

Distinctive features of the genus include a) leaves that usually are 3–4-lobed (occasionally 2–3-lobed in some species), and b) usually conspicuous, deeply bifid underleaves often with filaments on the margins.

One species confirmed for California.

Barbilophozia hatcheri (A. Evans) Loeske

Distinctive features. These green to yellowish-brown plants usually are 1.5–2.8 mm wide and 2–4 cm long. Look for a) leaves 3–4-lobed, b) leaf lobes mostly straight-sided and often with apiculate apices of 1–2 (or 3) rather short, thick-walled cells, c) leaves slightly decurrent on the dorsal stem surface, d) leaf base on the ventral stem surface with 1–3 (occasionally up to 5) multicellular filaments, e) large bilobed underleaves with numerous, contorted multicellular filaments on the margins, and f) brownish-red gemmae, angular and 1–2-celled, usually present on lobe apices and leaf margins (older leaf margins often are erose because of gemmae development).

Separation. The combination of leaves 3–4 lobed, large bilobed underleaves with numerous multicellular marginal filaments, and angular brownish-red gemmae separates *B. hatcheri* from the other species of *Barbilophozia*, and from species of *Lophozia*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On shaded soil of rocky banks, slopes and cliffs, and on organic matter. Elevation from 1400 to 3665 m.

Distribution. Barbilophozia hatcheri occurs in Europe, Asia, Antarctica, and North and South America. Calif. Geographic Regions: **CR**: Siskiyou Co. *Harling WCH221* (UC), **KR**: Siskiyou Co. *Doyle 5991* (UC), **SN**: Inyo Co. *Doyle 6021* (UC).

Bazzania Gray 1821
(Lepidoziaceae)

Species of this genus have a) asymmetric leaves with incubous insertion, b) leaf apices that are shallowly, sometimes obscurely, lobed or toothed, c) underleaves entire or with 1–4 shallow apical

lobes or teeth, and d) flagelliform branches arising from the axils of the underleaves and downwardly directed.

One species in California.

Bazzania denudata (Torr. ex Gottsche, Lindenb. and Nees) Trevis.

Note. This species distinctively has stem areas devoid of leaves. However, the extent of leaf loss is highly variable, even within a single population. For example a) many leaves on some stems are deciduous (caducous), or b) all leaves persist on some stems, or c) some stems have short denuded regions, separated by long regions with persistent leaves. Look at more than one shoot during identification.

Distinctive features. Living plants are light green to green. Look for a) short or long stem areas devoid of leaves, b) highly variable leaf apices, even on the same stem, the leaf apex can gradually taper to an obtuse point, or be broad and rounded, or be truncate, c) leaf apices usually with 1–3 blunt teeth, but varies from 0 to 4 teeth, d) median leaf cells 10–30 μm wide and 23–36 μm long, e) underleaves about twice as wide as the stem, f) broad and truncate apices of underleaves with with 0–4 shallow lobes or teeth, and g) five or more oil-bodies per cell.

Separation. Bazzania denudata should not be confused with any other California leafy liverwort.

Illustrations. Schofield 2002; Schuster 1969.

Habitat. On moist, shaded decaying logs in redwood forests; near sea-level to 30 m.

Distribution. Bazzania denudata is widely distributed in North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 11041* (UC), **NC**: Humboldt Co. *Doyle 10955* (UC).

Excluded. Bazzania tricrenata (Wahlenb.) Lindb. The report by Clark and Frye (1936) of *B. tricrenata* from near Crescent City, Del Norte County was based on the mis-identification of *Frye 139* (WTU); this specimen is *Calypogeia fissa* subsp. *neogaea*. Also *Branscomb 22373* (WTU) was mis-identified as *B. tricrenata*; this specimen is *Calypogeia muelleriana*. No herbarium specimen examined in this study confirmed this species in California; however *Norris 52921* (DUKE) cited by Hong (1988) was not studied.

Blepharostoma (Dumort.) Dumort. 1835
(Pseudolepicolaceae)

Species of *Blepharostoma* can hardly be confused with any other California liverwort. Distinctive are leaves and underleaves divided to the base into 2–4 uniseriate filaments.

Two species in California.

Species Key

1. Lateral leaves and underleaves divided to base into 3–4 uniseriate filaments; leaf filaments unbranched; transverse walls of leaf filaments usually slightly bulging outwards in profile. . . . . **B. trichophyllum**
2. Lateral leaves and underleaves divided to base into 2–3 uniseriate filaments; leaf filaments occasionally once-branched 2–4 cells above leaf base; transverse walls of leaf filaments slightly depressed or smooth in profile. . . . . **B. arachnoideum**

Blepharostoma arachnoideum M. Howe

Additional field-work is needed to better understand the distribution and reproduction of this seldom collected species. Culture-studies in the laboratory are needed to a) try to induce sexual reproductive structures and b) compare growth and morphology of this species with that of *B. trichophyllum* when both are grown under identical environmental conditions. Molecular studies are needed to assess the degree of relatedness of *B. arachnoideum* and *B. trichophyllum*.

Distinctive features. The grayish-green shoots of this species are easily overlooked; they occur in small patches and often grow intermixed with other bryophytes. Look for a) leaves and underleaves divided nearly to the base into 2–3 uniseriate filaments, some leaf filaments are once-branched 2–4 cells above the leaf base, b) transverse walls of the leaf and underleaf filaments not thickened at the

juncture of lateral walls, the walls appear slightly depressed, seldom smooth in profile, c) stem epidermal cells 23–60 μm wide × 50–150 μm long, and d) unicellular gemmae common, the terminal cell of a filament dividing conidia-like forming a chain of small unicellular gemmae. Sexual reproduction is not known.

Separation. See *B. trichophyllum* for separation of these two species.

Illustrations. Clark and Frye 1928.

Habitat. Shaded, damp decaying logs, and soil and rocks of creek-banks. Elevation from 15 to 1600 m.

Distribution. Blepharostoma arachnoideum is endemic to the Pacific Coast of North America. Calif. Geographic Regions: **KR**: Siskiyou Co. *Doyle 11072* (UC), **NC**: Humboldt Co. *Doyle 10579* (UC).

Blepharostoma trichophyllum (L.) Dumort.

Distinctive features. Shoots of this species usually occur in pale- to yellowish-green patches. Look for a) leaves divided nearly to the base into 3–4 unbranched, uniseriate filaments and underleaves divided nearly to the base into 2–4 unbranched, uniseriate filaments, b) cells of leaves and underleaves with evenly thickened walls without trigones, c) transverse cell walls of leaf and underleaf filaments usually thickened outwardly, appearing as a bulge, but occasionally smooth in profile, d) stem epidermal cells 15–38 μm wide and 28–95 μm long, e) perianths common, mouth ciliate, and f) unicellular gemmae not common.

Separation. Blepharostoma trichophyllum is separated from *B. arachnoideum* by a) leaves that are divided into 3–4 uniseriate lobes (vs. 2–3 lobes in *B. arachnoideum*), b) unbranched uniseriate leaf lobes (vs. uniseriate leaf lobes occasionally branched 2–4 cells from the base), c) transverse walls of filament usually thickened outwardly, appearing as bulges in profile (vs. transverse walls unthickened, appearing slightly indented or smooth in profile, d) smaller stem epidermal cells, generally 15–38 μm wide and 28–95 μm long (vs. stem epidermal cells 23–60 μm wide and 50–150 μm long, and e) perianths frequently present (vs. perianths not known).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1966; Smith 1990.

Habitat. Shaded wet rocks, soil and decaying wood; banks of creeks, lakes, and depressions; margins of seepages. Elevation from 25 to 3850 m.

Distribution. Blepharostoma trichophyllum occurs in Europe, Asia, and North, Central, and South America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Kellman 345* (CAS), **CR**: Tehama Co. *Doyle 11103* (UC), **KR**: Siskiyou Co. *Norris 105072* (UC), **NC**: Humboldt Co. *Doyle 10634* (perianths) (UC), **SN**: Fresno Co. *Shevock 17448* (CAS).

Calypogeia Raddi 1818
Calypogeiaceae

Species in this genus have incubous and obliquely inserted leaves. An important aid in the field identification of the genus is the presence of conspicuous clusters of gemmae at the apices of erect specialized shoots. Some plants in a population almost always have gemma-bearing shoots. Also look for a) well-developed underleaves, b) the presence of rhizoids from a specific region, the rhizoid-initial area, at the abaxial base of the underleaves, and c) the development of sporophytes in a colorless and usually subterranean pouch, called a marsupium.

Note. At times, species of this genus can be difficult to identify. Whenever possible, use living plants to note oil-body color (bluish, grayish or colorless) and distribution (e.g., presence or absence in cells of the leaf middle). Keep these data with the herbarium specimen. Also examine mature regions of several healthy shoots (i.e., not immature or etiolated regions of shoots). Some species of the genus (e.g., *C. muelleriana*) exhibit great morphological variation and species identification sometimes can be determined only with use of a combination of characters from mature, healthy plants.

Five species and 1 subspecies in California.

Species Key

1. Oil-bodies distinctly blue in living plants (begin key at 2 for dry plants). . . . . **C. azurea**

1. Oil-bodies colorless to grayish in living plants; oil-bodies absent in dry plants. . . . . **2.**
2. Underleaf apices rounded, truncate, shallowly notched, or divided to within 7–14 cells of the rhizoid-initial area. . . . . **3.**
2. Underleaf apices clearly and deeply divided to within 1–6 cells of the rhizoid-initial area. **4.**
3. Healthy mature plants 0.8–2.5 mm wide; many to most marginal cells of leaf tangentially elongate, usually forming a distinct border; marginal cells at leaf apex usually tangentially elongate; narrow transverse rhizoid-initial area, 3–4 × as wide as high; oil-bodies absent from cells in leaf middle. . . . . **C. neesiana**
3. Healthy mature plants usually 2.4–3.2 mm wide; leaf margin with both isodiametric and tangentially elongate cells, forming a discontinous, indistinct border; marginal cells at leaf apex usually isodiametric; rhizoid-initial area transversely oval to nearly round, less than 2× as wide as high; oil-bodies normally present in all cells of the leaf. . . . . **C. integristipula**
4. Mature healthy shoots usually less than 2 mm wide; median leaf cells 24–32 × 28–42 μm, with small, often slightly bulging trigones. . . . . **C. suecica**
4. Mature healthy shoots usually more than 2 mm wide; median leaf cells 32–45 × 24–70 μm, trigones lacking. . . . . **5.**
5. Leaf apices apiculate, acute or bidentate; underleaf divided 1–2 cells from sinus to rhizoid-initial area. . . . . **6.**
5. Leaf apices usually rounded or obtuse, seldom apiculate, acute or bidentate; underleaf divided 2–6 cells to rhizoid-initial area. . . . . **7.**
6. All or most leaves on well-developed stems strongly bidentate; spores more than 14 μm in maximum diameter. . . . . **C. fissa** subsp. **fissa**
6. Most leaves on well-developed stems mostly acute or apiculate, occasionally some, but not most on a stem bidentate; spores less than 14 μm in diameter. . . . . **C. fissa** subsp. **neogaea**
7. Underleaf lobe apices usually obtuse or rounded, with rounded lateral margins (rarely with teeth or angulations); underleaf divided to within 3–6 cells of the rhizoid-initial area; rhizoid-initial area narrow, strongly transverse. . . . . **C. muelleriana**
7. Underleaf lobe apices acute to subacute, lateral margins occasionally with a blunt tooth, otherwise rounded; underleaf divided to within 2–4 cells of the rhizoid-initial area; rhizoid-initial area transversely oval to nearly round. . . . . **C. azurea**

Excluded. Calypogeia fissa (L.) Raddi subsp. *fissa*. Hong (1990) reported subsp. *fissa* for the Klamath Ranges and Central Coast Region, but cited no specimen. Most or all leaves of this subspecies of *C. fissa* have strongly bidentate apices. During this study, no herbarium specimen was located that had shoots with most or all leaves with strongly bidentate apices. In most California populations, many shoots have a few to several leaves with bidentate leaf apices, which is typical of the subspecies *neogaea*, but never most shoots with strongly bidentate apices, which is typical for subsp. *fissa*. Although left in the key for comparison, *Calypogeia fissa* subsp. *fissa* could not be confirmed for California (see Damsholt 2002, Paton 1999 or Schuster 1969 for illustrations).

2) *Calypogeia suecica* (Arnell and J. Perss.) Müll. Frib. Based on *Frye s.n.*, July 30, 1933 (WTU), Clark and Frye (1936) reported this species for California. Examination during this study indicated that the WTU collection consists of small plants of *C. fissa* subsp. *neogaea* (growing on burned wood, or charcoal). Although Hong (1990) did not list California in the distribution of this species in western North America, he showed two northwestern California and one Sierra Nevada sites in his Figure 3. No herbarium specimens of *C. suecica* were located during this study; it could not be confirmed for California. This species is retained in the key because it likely occurs in the state. Look for *C. suecica* on decaying logs (see Damsholt 2002; Paton 1999; Schuster 1969 for illustrations).

Calypogeia azurea Stotler & Crotz

Distinctive features. Living plants of this species are slightly aromatic and readily identified by the presence of pale to deep blue oil bodies that generally occur in all leaf, underleaf and stem epidermal cells. Although the cell walls of dry shoot apices can have a bluish tint for a variable time, the color quickly disappears in California plants. Examine your specimens while they are still fresh.

With dry plants look for a) subacute, rounded or obtuse leaf apices (occasionally one or more leaf apices on some stems can be acute or bidentate), b) leaf cells with thin to moderately thick walls, c) bilobed underleaves with subacute, triangular or lanceolate lobes; *Doyle 9822* (UC) from Shasta Co. occasionally has trifid underleaves, d) underleaf lobe margins usually round, but occasionally with a blunt tooth on one or both margins, and e) underleaves divided to within 2–4 cells of the rhizoid-initial area.

Separation. Calypogeia azurea is morphologically variable and some long-dried specimens can be virtually impossible to separate from *C. muelleriana* and *C. fissa*. Details of leaf and underleaf morphology usually can be used to separate dry plants of *C. azurea* from these two species. Generally, *C. azurea* can be separated from *C. fissa* by a) leaf apices subacute, rounded or obtuse (vs. leaf apices acute or bidentate in *C. fissa*), and b) underleaves divided within 2–4 cells from the rhizoid-initial area (vs. underleaves divided within 1–2 cells from the rhizoid-initial area). *Calypogeia azurea* usually can be separated from *C. muelleriana* by a) underleaves divided within 2–4 cells from the rhizoid-initial area (vs. underleaves usually divided within 4–6 cells from the rhizoid-initial area in *C. muelleriana*), and b) underleaves usually with acute to subacute sinuses and acute to obtuse lobe apices (vs. underleaves usually with obtuse to rounded sinuses and obtuse to rounded lobe apices).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Damp, shaded decaying logs and organic rich soil near the coast; shaded peaty soil on stream banks and edges of seepages and drainages in the mountains. Elevation from near sea-level to 2965 m.

Distribution. Calypogeia azurea occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Doyle 9411* (UC) **KR**: Trinity Co. *Doyle 9358* (UC), **MP**: Modoc Co. *Doyle 8638* (UC), **NC**: Humboldt Co. *Doyle 9004* (UC), **SN**: Alpine Co. *Doyle 10797* (UC).

Calypogeia fissa (L.) Raddi subsp. **neogaea** R. M. Schust.

Distinctive features. Look for the following in these grayish- to whitish- to pale-green plants: a) leaves usually with acute, apiculate or bidentate apices (occasionally some shoots in a population will have a few to several [but never most] bidentate leaves, while other shoots in the same population will have few to no bidentate leaves. Carefully examine the population, not selectively only one or two shoots), b) underleaves deeply bilobed to within 1–2 cells of the rhizoid-initial area, and c) underleaves frequently with a blunt tooth on one or both margins.

Separation. Calypogeia fissa subsp. *neogaea* can be confused with some forms of *C. muelleriana* (e.g., forms of *C. muelleriana* from the western slope of the Sierra Nevada that approach what Schuster [1969] called subsp. *blomquistii*). *Calypogeia fissa* subsp. *neogaea* usually can be separated from *C. muelleriana* by a) leaf apices acute, apiculate or bidentate (vs. leaf apices usually narrowly rounded in *C. muelleriana*), b) underleaves divided within 1–2 cells of the rhizoid-initial area (vs. underleaves usually divided within 4–6 cells of the rhizoid-initial area), and c) a blunt tooth on one or both underleaf margins (vs. underleaf margins usually smooth and rounded).

Illustrations. Schuster 1969.

Habitat. Shaded silty and sandy mineral soil of hillsides, paths and roads; less often on decaying logs and other organic matter. Elevation from near sea-level to 1625 m, but more common below 1000 m.

Distribution. Calypogeia fissa subsp. *neogaea* is North American in distribution. Calif. Geographic Regions: **CC**: Monterey Co. *Kellman 3035* (CAS), **KR**: Trinity Co. *Doyle 8550* (UC), **NC**: Humboldt Co. *Doyle 10632* (UC), **SN**: Yuba Co. *Doyle 9580*.

Calypogeia integristipula Steph.

Distinctive features. In California, these are high elevation plants. Look for a) underleaves large, nearly circular, with round, truncate or notched apices, and divided to within 7–14 cells of the rhizoid-initial area, b) marginal leaf cells mostly isodiametric, but with isolated or occasional series of 2–4 tangentially elongate cells, but not forming a distinct border, c) oil bodies in all leaf cells, and d) a rhizoid-initial area transversely oval to nearly round.

Separation. Calypogeia integristipula can be confused with *C. neesiana*. Both species have underleaf apices that are round, truncate or notched, and have highly variable leaf and underleaf size and shape. Oil-body distribution in living plants is the simplest way to separate these two species. *Calypogeia integristipula* has oil-bodies in all leaf cells (vs. oil-bodies absent from cells of the leaf middle in *C. neesiana*). For dry plants without oil-bodies, *C. integristipula* often has 1–4 tangentially elongate marginal leaf cells separated by a varable number of isodiametric cells, and usually has isodiametric cells at the leaf apices (vs. leaves with tangentially elongate marginal and apical cells forming a distinct [but occasionally incomplete] border in *C. neesiana*). Some populations of *C. integristipula*, especially

those with notched underleaves, superficially can be confused with *C. muelleriana*. *Calypogeia integristipula* can be separated by the a) underleaves truncate or notched to within 7–14 cells of the rhizoid-initial area (vs. underleaves distinctly bilobed to within 2–6 cells of the rhizoid-initial area in *C. muelleriana*), and b) presence in leaves of some tangentially elongate marginal cells (vs. usual absence of tangentially elongate leaf marginal cells).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On peaty soil; shaded creek banks and margins of seepages. Elevation from 2540 to 3212 m.

Distribution. Calypogeia integristipula occurs in Europe and North America. Calif. Geographic Regions: **SN**: Fresno Co. *Doyle 10198* (UC).

Calypogeia muelleriana (Schiffn.) Müll. Frib.

Distinctive features. Plants are green to yellowish- to whitish-green and usually shiny when dry. Look for a) leaves generally heart-shaped with rounded apices, b) large median leaf cells 32–45 μm wide and 45–70 μm long, c) underleaves distinctly bilobed with obtuse to rounded lobe tips, d) underleaves usually divided within 4–6 cells of the rhizoid-initial area, and e) a narrow, transverse rhizoid-initial field.

Separation. This species is morphologically variable and often exists in forms that appear intermediate with other species (see Schuster, 1969, for a discussion of variation within this species). It can be confused with *C. azurea*, *C. fissa* and *C. integristipula*. A suite of characters often must be used to decide species identification. *Calypogeia muelleriana* can be separated from *C. azurea* by a) colorless oil-bodies (vs. blue oil-bodies in *C. azurea*), b) usually heart-shaped leaves (vs. leaves usually wide-ovate), and c) underleaf lobes usually with obtuse or rounded sinuses (vs. sinuses usually acute to subacute). *Calypogeia muelleriana* can be separated from *C. fissa* by a) usually heart-shaped leaves, about as wide as long (vs. oblong-ovate leaves, longer than wide in *C. fissa*), b) leaves with broadly- to narrowly-rounded apices (vs. leaf apices acute, apiculate or bidentate), and c) underleaf lateral margin rarely with a blunt tooth (vs. underleaf margin usually with one or two blunt teeth). *Calypogeia muelleriana* can be separated from *C. integristipula* by a) shiny texture of dry plants (vs. generally dull texture in *C. integristipula*), b) leaves usually heart-shaped, about as wide as long (vs. leaves narrowly ovate, as wide as or longer than wide), and c) underleaves distinctly bilobed, divided to within 4–6 cells of the rhizoid-initial area (vs. underleaves entire or notched, divided to within 7–14 cells of the rhizoid-initial area).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969.

Habitat. On shaded, damp decaying logs; also on soil rich in organic matter; near sea-level to 2900 m, but mostly below 1800 m.

Distribution. Calypogeia mulleriana occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10403* (UC), **CR**: Shasta Co. *Doyle 8752* (UC), **KR**: Trinity Co. *Doyle 9362* (UC), **MP**: Modoc Co. *Doyle 9650* (UC), **NC**: Humboldt Co. *Doyle 10562* (UC), **SN**: Fresno Co. *Laeger 1683* (CAS).

Calypogeia neesiana (C. Massal. and Carestia) Müll Frib.

Distinctive features. Shoots of this species usually are opaque and grayish-green when living, and a glaucous gray-green when dry. Look for a) large nearly circular underleaves with round to notched apices, b) marginal cells of leaves mostly tangentially elongate, forming a distinct border, and c) oil-bodies typically absent from the median leaf cells, but present in the surrounding cells, including the leaf base.

Separation. Calypogeia neesiana has been confused with *C. integristipula*. See *C. integristipula* for separation.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On shaded soil of creek banks. Elevation from 100 to 210 m.

Distribution. Calypogeia neesiana occurs in Europe, Asia, and North America. Calif. Geographic Regions: **NC**: Humboldt Co. *Doyle 10583* (UC).

Cephalozia (Dumort.) Dumort. 1835
(Cephaloziaceae)

For this genus, look for a) stems generally with large, usually translucent epidermal cells (=hyalodermis) b) succubous bifid leaves, c) underleaves usually absent (occasionally present or restricted to certain areas in a few species), d) unicellular gemmae, and e) oil-bodies absent. Mature, well-developed plants generally are readily identified to species; however, young or etiolated shoots can make identification challenging.

Cephalozia is separated from *Cephaloziella* by a) large, usually translucent stem hyalodermis (vs. hyalodermis lacking in *Cephaloziella*), b) 1-celled gemmae (vs. 2-celled gemmae), c) absence of underleaves (vs. underleaves present in many species), and d) oil-bodies absent in leaf cells (vs. oil-bodies present in leaf cells).

Four species plus two subspecies in California; one species excluded.

Species Key

1. Leaves transversely or sub-transversely inserted on stem; leaves not decurrent on the dorsal stem surface; leaves divided 0.5–0.7 their length; leaf insertion on the dorsal surface of mature stem to, or slightly beyond the midline. . . . . **2.**
1. Leaves obliquely to nearly horizontally inserted on stem; leaves short or long decurrent on the dorsal stem surface; leaves divided 0.25–0.5 their length; leaf insertion on the dorsal surface of mature stem clearly not to the midline. . . . . **4.**
2. Dorsal epidermal cells of mature stem 12–25 μm wide × 20–36 μm long; leaves about as long as wide; cells at base of leaf lobes small, 14–26 μm wide × 16–40 μm long. . . . . **C. bicuspidata** subsp. **ambigua**
2. Dorsal epidermal cells of mature stem 25–60 μm wide × 35–82 μm long or longer; leaves longer than wide; cells at base of leaf lobes 23–54 μm wide × 35–82 μm long or longer. . **3.**
3. Stem dorsal epidermal cells 25–46 μm wide × 40–80 μm long (or longer); cells at base of leaf lobes usually 23–45 μm wide × 35–54 μm long; stolons frequently present. . . . . **C. bicuspidata** subsp. **bicuspidata**
3. Stem dorsal epidermal cells 30–60 μm wide × 60–160 μm long; cells at base of leaf lobes 30–54 μm wide × 40–82 μm long or longer; stolons rare or lacking.. . . . . **C. bicuspidata** subsp. **lammersiana**
4. Leaves strongly decurrent; leaf lobe apices usually clearly connivent. . . . . **5.**
4. Leaves not, or only shortly decurrent; leaf lobe apices not, or only weakly connivent. . . . **6.**
5. Leaves nearly horizontally inserted; cells at base of leaf lobes 30–56 μm wide × 41–75 μm long (or longer); perianth mouth lobed and laciniate, with lacinae ending with 2–6 uniseriate cells. . . . . **C. connivens**
5. Leaves obliquely inserted; cells at base of leaf lobes 20–35 μm wide × 26–42 μm long; perianth mouth crenate-dentate, usually with 1 elongate cell. . . . . **C. lunulifolia**
6. Plants rather large; dorsal cortical cells of stem over 35 μm wide; leaves conspicuously concave; leaf cells usually thin-walled, at base of lobes 28–36 μm wide (or wider) × 33–50 μm long (or longer); perianth mouth crenate-dentate. . . . . **C. pleniceps**
6. Plants smaller; dorsal cortical cells about 15–25 μm wide; leaves only slightly concave; leaf cells usually thick-walled, at base of lobes 15–21 μm wide and 16–25 μm long; perianth mouth ciliate. . . . . **C. catenulata**

Excluded. Cephalozia catenulata (Huebener) Lindb. Hong (1988b) reported this species for California; Fig 6 showed a collection north of San Francisco Bay (**NC**). However, no herbarium specimen was located with the combination of features definitive for *C. catenulata*. Although retained in the key, *C. catenulata* could not be confirmed for California. See Damsholt (2002) and Paton (1999) for description and illustration of this species.

Cephalozia bicuspidata (L.) Dumort.

Three subspecies occur in California. Because of morphological variability, Schuster (1974) reported that chromosome number is the surest method to identify the three subspecies: subsp. *ambigua* has 9 chromosomes, subsp. *bicuspidata* has 18 chromosomes, and subsp. *lammersiana* has 27 chromosomes. Determination of chromosome number is not an option in most cases. Some authors (e.g., Damsholt, 2002; Paton 1999) treat *lammersiana* as a variety of *C. bicuspidata* subsp. *bicuspidata*; some authors (e.g., Paton 1999) treat *ambigua* as a separate species of *Cephalozia*. Robust mature plants of the three

readily can be separated by morphological features and here are treated as three subspecies of *C. bicuspidata.* Measurement of the width and length of dorsal epidermal cells **from several different stems** usually is a good way to separate the three subspecies.

Cephalozia bicuspidata (L.) Dumort. subsp. **bicuspidata**

Distinctive features. This autoicous pale-green to dark-green to yellowish-brown subspecies morphologically is highly variable. When growing on shaded decaying logs, shoots of this species can be large and pale-green, with large leaves and leaf lobes, and thin to moderately thickened cell walls: these plants approach those of subsp. *lammersiana.* In sunny exposed meadow areas of the high Sierra Nevada, the shoots can be small and reddish- to golden-brown, with small leaves and leaf lobes, and thickened cell walls: these plants approach those of subsp. *ambigua.* Look for a) stem dorsal epidermal cells mostly 25–46 μm wide × 40–80 μm long (or longer), b) slight to distinctly concave leaves, c) cells at leaf lobe base mostly 23–45 μm wide × 35–54 μm long (or occasionally longer), d) no underleaves, and e) a perianth mouth with 1–3-celled teeth.

Separation. For separation of this subspecies with subsp. *ambigua*, see under that subspecies. Large growth forms of subsp. *bicuspidata* can be difficult to separate from subsp. *lammersiana.* Typical forms of subsp. *bicuspidata* are separated by a) stem dorsal epidermal cells mostly 25–46 μm wide × 40–80 μm long (vs. stem dorsal epidermal cells 30–60 μm wide × 60–160 μm long in subsp. *lammersiana*), b) cells at the leaf lobe base generally 25–40 μm wide × 35–54 μm long (vs. cells at the leaf lobe base 30–54 μm wide × 40–82 μm long or longer), and c) absence of underleaves (vs. infrequent presence of underleaves near the shoot apex).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974.

Habitat. Shaded soil of damp, slow to dry habitats, such as decaying logs, peaty soil and mineral soil. Elevation from near sea-level to 3173 m.

Distribution. Cephalozia bicuspidata subsp. *bicuspidata* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Kellman 406* (CAS), **CR**: Lassen Co. *Doyle 9799* (UC), **KR**: Del Norte Co. *Doyle 10597* (UC), **MP**: Modoc Co. *Doyle 8642* (UC), **NC**: Humboldt Co. *Doyle 10996* (UC), **SN**: Fresno Co. *Shevock 17448* (CAS).

Cephalozia bicuspidata (L.) Dumort. subsp. **ambigua** (C. Massal.) R. M. Schust.

Distinctive features. For this autoicous yellowish-, greenish-, to grayish-green subspecies, look for a) small shoots less than 0.6 mm wide × up to 1.5 cm long, b) stem dorsal epidermal cells mostly 12–25 μm wide × 20–36 μm long, c) leaves nearly transversely inserted, d) leaf cells mostly with thick brownish walls, e) cells at the leaf lobe base 14–26 μm wide × 16–40 μm long, f) occasional presence of subulate underleaves near the shoot apex, and g) a perianth mouth with 1-celled teeth.

Separation. Some growth forms of *C. bicuspidata* subsp. *ambigua* are difficult to impossible to distinguish from some high elevation forms of *C. bicuspidata* subsp. *bicuspidata.* Typical forms of *C. bicuspidata* subsp. *ambigua* are separated by a) narrower stem dorsal epidermal cells, 12–25 μm wide (vs. stem dorsal epidermal cells 25–46 μm wide in *C. bicuspidata* subsp. *bicuspidata*) and b) smaller cells at the leaf lobe base 14–26 μm wide × 16–35 μm long (vs. cells at the leaf lobe base usually 23–45 μm × 35–54 μm).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974.

Habitat. On damp to wet usually peaty soil in high elevations; especially banks of drainages in meadows, marshes and seepages. Elevation from 2700 to 3000 m.

Distribution. Cephalozia bicuspidata subsp. *ambigua* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Tuolumne Co. *Doyle 11191* (UC).

Cephalozia bicuspidata (L.) Dumort. subsp. **lammersiana** (Huebener) R. M. Schust.

Distinctive features. This autoicous whitish- to pale-green subspecies is the largest of the three subspecies of *C bicuspidata.* Look for a) stem dorsal epidermal cells 30–60 μm wide × 60–160 μm long, b) cells at the leaf lobe base 30–54 μm wide × 40–82 μm long, c) lingulate to subulate underleaves infrequently present near the shoot apex, and d) a perianth mouth with teeth 2–5 cells long.

Separation. Subspecies *lammersiana* and larger growth forms of subsp. *bicuspidata* often can be difficult to separate. See *C. bicuspidata* subsp. *bicuspidata* for separation from that subspecies.

Illustrations. Damsholt 2002; Paton 2002; Schuster 1974.

Habitat. On shaded, damp, decaying logs. Elevation from 25 to 170 m.

Distribution. Cephalozia bicuspidata subsp. *lammersiana* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Showers 3846* (SFSU), **KR**: Del Norte Co. *Doyle 9771* (UC), **NC**: Humboldt Co. *Doyle 10588* (perianths) (UC).

Cephalozia connivens (Dicks.) Lindb.

Distinctive features. For this autoicous species look for a) leaves nearly horizontally inserted, long-decurrent on the dorsal stem surface, and with distinctly connivent lobe apices, b) stem dorsal epidermal cells 42–75 μm wide × 60–102 μm long, c) cells at the base of the leaf lobes 30–56 μm wide × 41–75 μm long or longer, d) apices of terminal cells of leaf lobes usually with additional wall thickening, e) absence of underleaves and stolons, and f) a perianth mouth that is deeply laciniately lobed with lobes ending in uniseriate filaments 2–6 cells long.

Separation. Both *C. connivens* and *C. lunulifolia* have nearly circular, conspicuously decurrent leaves with connivent lobes, and apices of terminal cells of leaf lobes with additional wall thickening. *Cephalozia connivens* can be separated by a) the larger size of the stem dorsal epidermal cells 42–75 μm wide (vs. stem dorsal epidermal cells 24–50 μm wide in *C. lunulifolia*), b) cells larger at the base of leaf lobes 30–56 μm wide and 41–75 μm long (vs. cells at the leaf lobe base 20–35 μm and 25–42 μm), and c) perianth mouth laciniately lobed, with lobes ending in 2–6 uniseriate cells (vs. perianth mouth crenulate/dentate, with 1-celled teeth).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974.

Habitat. On shaded, damp decaying logs and wet humus. Elevation from 136 to 1500 m.

Distribution. Cephalozia connivens occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Trinity Co. *Doyle 8658* (UC).

Cephalozia lunulifolia (Dumort.) Dumort.

Distinctive features. This autoicous/dioicous species is highly variable, depending on whether growing in wet or dry habitats, or on mineral soil or decaying wood. Look for a) semi-circular leaves nearly horizontally to obliquely inserted, clearly long-decurrent and with connivent lobe apices, b) stem dorsal epidermal cells 24–50 μm wide × 45–60 μm long, c) cells at the base of the leaf lobes 20–35 μm wide × 26–42 μm long, d) apices of terminal cells of leaf lobes usually with thickened walls, e) absence of underleaves and stolons, and f) a perianth mouth that is crenate/dentate, usually with 1-celled elongate teeth.

Separation. Cephalozia lunulifolia can be confused with *C. connivens* and some growth forms of *C. pleniceps*. See *C. connivens* for separation from that species. *Cephalozia lunulifolia* is separated from *C. pleniceps* by a) leaves distinctly long-decurrent (vs. leaves little or not decurrent in *C. pleniceps*), b) leaf lobe apices clearly connivent (vs. leaf lobe apices little or not connivent), c) apices of terminal cells of leaf lobes usually with additional wall thickening (vs. apices of terminal cells usually without additional wall thickening), and d) smaller cells at the leaf lobe base 20–35 μm wide × 26–42 μm long (vs. cells at the leaf lobe base 20–60 μm wide × 24–65 μm long).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974.

Habitat. Shaded, moist surfaces; commonly on decaying logs and stumps, but also on humus, mineral soil and rocks; Elevation from 50 to 435 m.

Distribution. Cephalozia lunulifolia occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8172* (UC), **KR**: Trinity Co. *Doyle 8655* (UC), **NC**: Mendocino Co. *Doyle 10526* (UC), **SN**: Placer Co. *Doyle 9974* (UC).

Cephalozia pleniceps (Austin) Lindb.

Distinctive features. For this autoicous species look for a) leaves nearly semi-circular and usually strongly concave, obliquely inserted, and only slightly decurrent on the dorsal stem surface, b) leaf

lobes not or only little connivent, c) dorsal epidermal cells 40–60 μm wide, d) cells at the base of the leaf lobe 28–36 μm wide × 33–55 μm long, e) apices of terminal cells of leaf lobe apices usually without walls thickened more than the cell middle or base, f) stolons frequently present, g) underleaves usually absent, but occasionally small subulate underleaves or 2–3-celled slime-hairs present near the shoot apex, and h) perianth mouth crenulate to dentate.

Separation. See *C. lunulifolia* for separation from that species. *Cephalozia pleniceps* is separated from *C. connivens* by a) dorsal leaf margin not or only little decurrent (vs. dorsal leaf margin long-decurrent in *C. connivens*), b) smaller cells at the lobe base, mostly 20–60 μm wide × 24–54 μm long (vs. cells at the leaf lobe base 30–56 μm wide × 45–75 μm long), c) apices of terminal cells of leaf lobes usually without additional wall thickening (vs. apices of terminal cells usually with additional wall thickening), and d) perianth mouth crenulate to dentate (vs. perianth mouth laciniately lobed ending in 2–5 uniseriate cells).

Illustrations. Damsholt 2002; Howe 1899; Paton 1999; Schuster 1974.

Habitat. Usually on damp, peaty soil near margins of marshy and boggy areas; less often on shaded rocks and decaying logs. Elevation from 1424 to 3270 m.

Distribution. Cephalozia pleniceps occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 9861* (perianths) (UC), **KR**: Siskiyou Co. *Doyle 9255* (UC), **MP**: Modoc Co. *Doyle 8643* (UC), **NC**: Sonoma Co. *Howell 670* (CAS), **SN**: Fresno Co. *Doyle 10215* (perianths) (UC).

Cephaloziella (Spruce) Schiffn. 1893
(Cephaloziellaceae)

Plants of this genus are small, less than 0.5 mm wide × up to 1.2 cm long, and often threadlike. The study of these plants requires a steady hand, a compound microscope, and a high frustration threshold.

Mature, typical plants, upon which species descriptions are based, usually are readily identified. Unfortunately, non-typical plants are common and some vegetative plants cannot be identified with certainty. For example, plants collected during the early flush of growth following the onset of rain or snowmelt can look unlike plants collected later in the season from the same population. Under some environmental conditions, such as during prolonged rain and cloudy periods, species that normally are pigmented can lack pigmentation, and leaf shape, cell size and wall thickness can be "non-typical".

Things to look for include a) in the field, search thoroughly for reproductive plants, because details of reproduction can be helpful in identification, b) the presence or absence of underleaves, including whether underleaves occur only on reproductive, but not vegetative shoots, c) the number of oil-bodies in mid-leaf cells, d) the number of cells across the base of the leaf lobe, e) the width and length of cells at the base of leaf lobes, and f) whether the leaf margins are smooth or have short or long teeth.

Cephaloziella superficially can resemble small or etiolated plants of *Cephalozia*. *Cephaloziella*, however, a) lacks a large, nearly translucent stem epidermal cells (called a hyalodermis), b) has oil-bodies in leaf cells, and c) usually has 2-celled gemmae, whereas *Cephalozia* has a hyalodermis, lacks oil-bodies in leaf cells, and has only 1-celled gemmae.

Six species plus one variety in California.

Species Key

1. Underleaves absent on vegetative regions of stems. . . . . **2.**
1. Underleaves common or infrequent on some or all vegetative regions of stems. . . . . **3.**
2. Leaf margins spinose-dentate; gemmae angular; no underleaves on reproductive stems. . . . . **C. turneri**
2. Leaf margins not spinose-dentate; gemmae ovoid; underleaves present on reproductive stems. (some shoots of *C. rubella var. sullivantii* and *C. spinigera* also might key here) . . . . . **C. hampeana**
3. Underleaves infrequently developed on vegetative stems. . . . . **4.**
3. Underleaves always present on vegetative stems. . . . . **5.**
4. Leaves deeply bilobed, more than 0.8 their length; cells at base of lobes mostly 14–22 μm long; leaf base occasionally with 1 or 2 marginal teeth. . . . . **C. spinigera**
4. Leaves bilobed less than 0.6 their length; cells at base of lobes 12–25 μm long; leaf base without marginal teeth. . . . . **C. rubella var. sullivantii**

5. Leaf margins smooth; leaf cells with thin or moderately thickened walls; cells at lobe base large, 12–20 μm wide; paroicous. . . . . **C. stellulifera**
5. Leaves margins smooth to dentate; leaf cells with thickened walls; cells at lobe base small, 9–15 μm wide; dioicous. . . . . **6.**
6. Plants green to reddish to blackish; leaf lobe margins smooth; abaxial leaf surface smooth; gemmae reddish, 2-celled. . . . . **C. divaricata var. divaricata**
6. Plants green to gray-green to greenish-brown; leaf lobe margins dentate; abaxial leaf surface with coarse, conical protuberances; gemmae greenish, usually 1-celled. **C. divaricata var. scabra**

Cephaloziella divaricata (Sm.) Schiffn

Plants of this dioicous species grow in loose to compact mats or as individual shoots among bryophytes. Female and male plants often grow in close proximity; in the field, look for female plants with perianths and then search for nearby male plants. Male plants have spike-like clusters of overlapping bracts, each with a concave base subtending one antheridium. For species identification, look for a) underleaves consistently present on vegetative shoots, b) leaf lobes 6–9 cells wide at the base, c) cells at the leaf lobe base 9–15 μm wide, and d) distinctive white perianth apices that contrast strongly with the perianth base and leafy shoots. **Note:** Gemmae develop on leaf margins, and gemmae-bearing leaves often are strongly erose and can appear "abnormal" in size and shape.

This species grows in a wide variety of habitats and exhibits great morphological diversity. Two varieties are recognized in California, var. *divaricata* and var. *scabra*. Gradations between the two varieties do exist. However, populations of var. *scabra* can be so strikingly different from those of var. *divaricata* that this publication follows the traditional approach in recognition of both as varieties.

The following combination of characteristics separates both varieties of *Cephaloziella divaricata* from other California species of *Cephaloziella*: a) underleaves consistently present on vegetative stems, b) leaf cells usually with thickened walls, c) leaf lobes 6–9 cells wide at the base, d) cells at base of leaf lobes 9–15 μm wide, and e) being dioicous.

Cephaloziella divaricata (Sm.) Schiffn. var. **divaricata**

Distinctive features. This is the most widespread and morphologically variable of the two varieties. The color varies from green to dark green (usually in more shaded and humid or wet habitats) to purplish or black (in exposed and summer-dry habitats). The shoot apex of new growth often has a reddish coloration, especially early in the growing season. Also look for a) leaf margins with no or few marginal teeth and b) the lack of cellular protuberances on the abaxial surface of the leaf.

Separation. Cephaloziella divaricata var. *divaricata* can be separated from var. *scabra* by a) usually entire leaf margins (vs. usually dentate leaf margins in var. *scabra*) and b) prominent cellular protuberances absent on the abaxial leaf surface (vs. prominent cellular protuberances present on the abaxial leaf surface).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. On soil, organic matter, rocks, surface of rocks and boulders. Elevation from 106 to 1067 m.

Distribution. Cephaloziella divaricata var. *divaricata* occurs in Europe, North Africa, North and South America, and New Zealand. Calif. Geographic Regions: **CC**: San Francisco Co. *Bourell 4392* (CAS), **KR**: Trinity Co. *Norris 72829* (UC), **NC**: Lake Co. *Shevock 17106* (CAS), **SC**: Los Angeles Co. *Sagar 259* (SFV), **SN**: Plumas Co. *Janeway 5391* (CHSC).

Cephaloziella divaricata (Sm.) Schiffn. var. **scabra** M. Howe

Distinctive features. This variety usually has a distinctive grayish-green or yellowish-green coloration. Examine mature, well-developed regions of the shoot. The apical regions of shoots developed early in the growing season, or of etiolated or weak shoots, can lack or have poorly developed leaf marginal teeth and abaxial protuberances. Use shoots from different parts of your collection for examination and look for a) leaves with dentate margins and b) prominent cellular protuberances on the abaxial leaf surfaces.

Separation. See *C. divaricata* var. *divaricata* for separation of these two varieties.

Illustrations. Frye and Clark 1945 (as *Cephaloziella papillosa* (Douin) Schiffn.)

Habitat. Mostly on shaded mineral soil, rock outcrops and cliff faces; less commonly on decaying wood. Elevation from 330 to 1100 m.

Distribution. Cephaloziella divaricata var. *scabra* occurs in North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 6526* (UC), **KR**: Del Norte Co. *Doyle 11027* (UC), **NC**: Mendocino Co. *Doyle 9079* (UC), **SN**: Calaveras Co. *Shevock 21740* (CAS).

Cephaloziella hampeana (Nees) Schiffn.

Distinctive features. This autoicous species of green to brownish-green plants a) lacks underleaves on vegetative stems regions, b) has thin-walled leaf cells, c) has leaf lobes usually with 6–12 cells at the base, these cells mostly 11–16 μm wide, and d) has 2–7 oil-bodies in median leaf cells.

Separation. Cephaloziella hampeana lacks underleaves on vegetative stem regions; in this, it resembles some stems of *C. rubella* var. *sullivantii. C. hampeana* can be separated by a) green to brownish-green shoots (vs. green to reddish or reddish brown shoots in *C. rubella* var. *sullivantii*), b) leaves with thin-walled cells (vs. leaves usually with thick-walled cells), c) leaf lobes bases mostly 6–12 cells wide (vs. leaf lobe bases mostly 3–5 cells wide), and d) 2–7 oil-bodies in median leaf cells (vs. 6–11 oil-bodies in median leaf cells).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. Soil.

Distribution. Cephaloziella hampeana occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SC**: Los Angeles Co. *Kingman 704* (YU) (Reported by Hong 1986; the specimen was not available for examination).

Cephaloziella rubella (Nees) Warnst. var. **sullivantii** (Austin) Müll. Frib.

Distinctive features. Like the other species of *Cephaloziella, C. rubella* is a highly variable plant with several named varieties; the variety *sullivantii* occurs in California. It has small and often inconspicuous underleaves on some, but seldom on all non-reproductive stem regions. Look for a) shoots usually with reddish-brown pigmentation, b) leaves bifid 0.5–0.75 their length and 3–5 cells wide at the lobe base, c) thick-walled cells at the lobe base mostly 9–14 μm wide, d) small underleaves sometimes present on vegetative stem regions, and e) 6–11 oil-bodies in median leaf cells.

Separation. Cephaloziella rubella can have infrequent to no underleaves on vegetative regions of the stem and can be confused with *C. hampeana.* See *C. hampeana* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. On soil and decaying logs. Elevation mostly below 500 m.

Distribution. Cephaloziella rubella var. *sullivantii* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Ventura Co. *Haynes 2041* (YU) (Reported by Evans 1923 and Hong 1986; the specimen was not available for examination).

Cephaloziella spinigera (Lindb.) Jörg.

Distinctive features. This autoicous plant can be overlooked because it often grows as scattered shoots among other bryophytes. Shoots are light green in wet, shaded habitats and often copper-red in sunny locations. Look for a) leaves deeply divided to 0.9 their length into 2 narrow lobes, 2–5 cells wide at the lobe base, b) slightly elongate, evenly thick-walled cells at leaf lobe bases mostly 9–12 μm wide and 14–23 μm long, c) leaves occasionally with a small spinose tooth near the base of one or both lateral margins, d) cuticle of leaf weakly to coarsely papillose, and e) small subulate or bilobed underleaves often sparsely developed or lacking on some vegetative stem regions.

Separation. With the combination of a) slightly elongate cells at leaf bases, b) leaves often with marginal teeth, and c) sparse development of small underleaves, this species is not easily confused with other California species of *Cephaloziella.*

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. On soil, often as scattered shoots in other bryophytes.

Distribution. Cephaloziella spinigera occurs in Europe, Asia, and North America. Calif. Geographic Regions: **MP**: Modoc Co. *Doyle 9652* (UC), **NC**: Mendocino Co. *Doyle 10513* (UC).

Cephaloziella stellulifera (Taylor) Schiffn.

Distinctive features. Shoots of this paroicous species usually are green to yellowish-green, and often have brownish wall pigmentation when growing in exposed habitats. Look for a) underleaves present on all vegetative stems, the underleaves mostly subulate, but occasionally lanceolate or bifid, b) leaves with narrow lobes mostly 4–7 cells wide at the lobe base, c) cells at the leaf lobe base thin- to slightly thick-walled, mostly 12–20 μm wide and 16–21 μm long, d) dorsal cortical cells mostly 12–14 × 18–35 μm, e) usually 2–8 oil-bodies per cell, and f) perianth mouth with elongate thick-walled cells.

Separation. Both *C. stellulifera* and *C. divaricata* consistently have distinct underleaves on vegetative stems. *C. stellulifera* is separated by a) paroicous sexual reproduction (vs. dioicous sexual reproduction in *C. divaricata*), b) brownish secondary wall pigmentation (vs. a reddish or purplish or blackish wall pigmentation), c) leaf cells thin to slightly thick-walled (vs. leaf cells moderately to strongly thick-walled), and d) cells at the leaf lobe base mostly 12–20 μm wide (vs. cells at the leaf lobe base 9–15 μm wide).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. On shaded soil. Elevation from 30 to 1700 m.

Distribution. Cephaloziella stellulifera occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 8855* (UC), **KR**: Shasta Co. *Doyle 9123* (UC), **SC**: Santa Barbara Co. *Shevock 20894* (CAS), **SN**: Tulare Co. *Shevock 17037* (CAS).

Cephaloziella turneri (Hook.) Müll. Frib.

Distinctive features. This distinctive, autoicous species usually grows in green, brown or reddish-brown patches. Look for a) leaves divided 0.65 or more their length, with margins conspicuously dentate to serrate, b) underleaves lacking on both vegetative and reproductive stems, c) polyangular gemmae, and d) plicate perianths.

Separation. With its deeply divided leaves with dentate to serrate margins and complete absence of underleaves, mature shoots of this species are not likely to be confused with other California species of *Cephaloziella*. Poorly developed plants (etiolated, young or from wet, dimly-light habitats) of *C. turneri* can be separated from *C. divaricata* var. *scabra* by the absence of underleaves (vs. underleaves present in *C. divaricata* var. *scabra*).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1980; Smith 1990.

Habitat. Summer-dry habitats; exposed to partially shaded soil; occasionally on organic material and charred surface of stumps. Elevation from 120 to 1560 m.

Distribution. Cephaloziella turneri occurs in Europe, North Africa, and western North America. Calif. Geographic Regions: **CC**: San Benito Co. *Doyle 11257* (UC), **KR**: Del Norte Co. *Doyle 10630* (UC), **NC**: Humboldt Co. *Doyle 10065* (UC), **SC**: Los Angeles Co. *Sagar 361* (SFV), **SN**: Placer Co. *Doyle 8475* (UC).

Chiloscyphus Corda 1829
(Geocalycaceae)

These leafy liverworts generally occur in humid, damp and wet habitats. Leaves are succubous with smooth lateral margins. Leaf apices are rounded, truncate or emarginate.The leaf is decurrent on the dorsal stem surface. The conspicuous underleaves are bilobed and usually have a tooth on one or both sides. Rhizoids develop in tufts from the bases of underleaves.

The genus *Lophocolea* can be confused with *Chiloscyphus* and some bryologists (e.g., Damsholt, 2002) treat species of *Lophocolea* as species of *Chiloscyphus*. The two are treated as separate genera in this publication. *Chiloscyphus* can be separated by a) leaf apices truncate, rounded or emarginate, (vs. apices of some to all leaves shallowly to deeply bilobed in *Lophocolea*), and b) perianths at the apices of short lateral branches that have reduced leaves (vs. perianths at the apices of main branches that have normal leaves). See also Grolle (1995) for reasons to maintain *Lophocolea* and *Chiloscyphus* as separate genera.

Two species in California.

Species Key

1. Median leaf cells generally 17–33 (seldom to 35) μm wide × 23–45 μm long (seldom longer); oil-bodies usually 2–4 per median leaf cell; perianth mouth lobes entire or with short teeth. . . . . **C. polyanthos**
1. Median leaf cells generally 25–45 *u*m wide × 33–64 *u*m long (or longer); oil-bodies usually 4–8 (or more) per median leaf cell; perianth mouth lobes clearly toothed to spinose. . . . . **C. pallescens**

The two California species are polymorphic and occasionally difficult to separate. The two species can confidently be separated on the basis of differing chromosome numbers, *C. polyanthos* has 9 chromosomes and *C. pallescens* has 18, but this information is not helpful for the identification of dried specimens. Although shoot coloration, and median and marginal leaf cell size varies considerably within each species, cells of *C. pallescens* mostly are larger than those of *C. polyanthos*. We have not found that the width of marginal cells at the leaf apices was any more reliable in separating these two species than the use of mid-leaf cell width and length. Make all measurements on leaves from fully mature regions of the shoot, and make measurements on leaves from several shoots. Details of the perianth mouth also can be used to separate the two species; unfortunately, most collections consist only of vegetative plants. Whenever possible, therefore, examine fresh plants to determine the number of oil-bodies in median cells of mature leaves and keep these data with the specimen.

Chiloscyphus pallescens (Ehrh. ex Hoffm.) Dumort.

Distinctive features. Shoots generally are pale-, yellowish- to whitish-green, to a dark green. Look for a) oil-bodies usually 4–8 (or more) in each mature median leaf cell, b) median leaf cells mostly 25–45 μm wide × 33–64 μm long (or longer), c) leaves usually only slightly decurrent on the dorsal stem surface and often with truncate apices, and d) perianth mouth distinctly toothed to ciliate.

Separation. The two species of this genus exhibit great and overlapping variation in color, habitat occurrence and median leaf cell size. The number of oil-bodies in mature median leaf cells of fresh plants is the easiest character to use: *C. pallescens* generally has 4–8 oil-bodies per cell; *C. polyanthos* generally has 2–4 oil-bodies per cell. In addition, *C. pallescens* has a) leaves slightly decurrent on the stem dorsal surface (vs. leaves clearly decurrent on the stem dorsal surface in *C. polyanthos*), and b) median leaf cells mostly 25–45 μm wide × 33–64 μm long (vs. median leaf cells mostly 17–33 μm wide × 23–45 μm long).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On shaded soil, rocks and decaying logs; submerged, seasonally inundated or high humidity habitats. Elevation from 970 to 2356 m.

Distribution. Chiloscyphus pallescens occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 1968* (UC), **SN**: El Dorado Co. *Doyle 11167* (UC).

Chiloscyphus polyanthos (L.) Corda

Distinctive features. Shoots generally are a dull-, deep- to brownish-green; however, some populations are lighter green in color. Look for a) 2–4 oil-bodies in each mature median leaf cell, b) median leaf cells mostly 17–33 μm wide (seldom wider) × 23–45 μm long (seldom longer), c) leaves usually clearly decurrent on the dorsal stem surface and often with rounded, truncate or slightly emarginate apices, and d) perianth smooth or with short teeth.

Separation. See *C. pallescens* for separation.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. On shaded rocks, soil, organic debris, and decaying logs; usually seasonally inundated or permanently submerged; also above the water line. Elevation from 34 to 3030 m.

Distribution. Chiloscyphus polyanthos occurs in Europe, Asia, Africa, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 8958* (UC), **CR**: Shasta Co. *Doyle 10165* (UC), **KR**:

Trinity Co. *Doyle 9793* (UC), **MP**: Modoc Co. *Doyle 9673* (UC), **NC**: Mendocino Co. *Doyle 10530* (UC), **SN**: Butte Co. *Doyle 11412* (UC).

Diplophyllum (Dumort.) Dumort. 1835
(Scapaniaceae)

Plants of this genus have complicate-bilobed leaves with the dorsal lobe smaller than the ventral lobe. Features of the genus include a) lingulate ventral lobes with rounded, obtuse or truncate apices, b) marginal cells of leaf lobes 15 μm wide or less, c) angular to stellate gemmae, and d) perianths that are slightly flattened and narrowed from above the middle to the mouth. *Douinia* and *Scapania* also have complicate-bilobed leaves with the dorsal lobe smaller than the ventral. Unlike *Diplophyllum*, *Douinia* has lanceolate leaf lobes that taper from near the base to an acute apex, and *Scapania* has a) ovoid to ellipsoidal gemmae, b) ventral leaf lobes that rarely are lingulate, and c) perianths that are not or only little narrowed to the mouth.

Three species in California.

Species Key

1. Ventral leaf lobe strongly decurrent; cells in middle of ventral lobe more than 20 μm wide, with prominent, rounded, knob-like (nodose) trigones; gemmae 2–4-celled, cubic often with rounded edges; perianths plicate from near the mouth to the base. . . . . **D. plicatum**
1. Ventral leaf lobe not decurrent; cells in middle of ventral lobe less than 20 μm wide and equally thick-walled (no trigones); gemmae usually 1-celled, stellate to bluntly stellate; perianths plicate above, but smooth toward the base. . . . . **2.**
2. Shoots small, less than 1.2 cm long; oil-bodies smooth in profile; gemmae not common; paroicous; perianth basal areas often with reddish coloration; mostly on soil; lower elevations toward the coast. . . . . **D. obtusifolium**
2. Shoots large, 1–3 cm long; oil-bodies coarsely papillose in profile; gemmae common; dioicous; perianths without reddish coloration; mostly on rocks; higher elevations. . . . . **D. taxifolium**

Diplophyllum obtusifolium (Hook.) Dumort.

Distinctive features. These paroicous plants usually grow in small pale- to yellowish-green patches, with shoots up to 1.2 cm long. Shoots are pale- to yellowish-green; in sunny exposures, the stem, leaf base and perianth base often develop vinaceous coloration. Look for a) rhizoids developing nearly to the stem apex, b) dorsal and ventral lobes with rounded apices, c) perianths frequently present, and d) antheridial bracts conspicuous, saccate, immediately below the perianth.

Separation. With shoots less than 1.2 cm long, rhizoids nearly to the stem apex, and perianths with a reddish basal coloration, this species should not be confused with *D. plicatum* or *D. taxifolium*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974.

Habitat. On soil of banks, paths, crevices in rocks and cliff faces; rarely on decayed logs. Elevation from 50 to 500 m

Distribution. Diplophyllum obtusifolium occurs in Europe, Asia, and western North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 10587* (UC), **NC**: Humboldt Co. *Doyle 1383* (UC).

Diplophyllum plicatum Lindb.

This is a rare species in Oregon; in California it is known from a single collection—intermixed with *Plagiochila porelloides* on a *Sequoia* trunk, Howland Summit area of Jedediah Smith Redwoods State Park, Del Norte County. On casual observation, it is about the same color and size as *P. porelloides* and was not noticed in the field. Examine field populations of *P. porelloides* carefully.

Distinctive features. These are large green to dark-green plants. Distinctive characteristics include: a) leaf lobes 2–4 times as long as wide, b) median cells of mature ventral lobes greater than 20 μm wide, with prominent nodose trigones, c) ventral lobes with decurrent bases and strongly toothed basal margins, and d) the cell walls of the ventral lobe teeth and adjacent leaf cells usually orange to orange-red. Reproductive plants have not been located in California.

Separation. This species is separated from other species in the genus by a) the median cells of the ventral lobe greater than 20 μm wide and with nodose trigones, and b) ventral lobes strongly decurrent and with orange-red toothed basal margins.

Illustrations. Frye and Clark 1946.

Habitat. Areas of high humidity and cool summer temperatures; on trunk of trees, intermixed with other liverworts. Elevation about 85 m.

Distribution. Diplophyllum plicatum occurs in the North Pacific, from NE Asia to coastal Alaska, then south to northern Oregon and disjunct to California. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 7729* (UC).

Diplophyllum taxifolium (Wahlenb.) Dumort.

Distinctive features. These dioicous plants usually occur in large populations with shoots often more than 2.5 cm in length. Look for a) shoots that are green to grayish-green, occasionally yellowish-brown, b) median cells of the ventral lobe equally thick-walled, less than 20 μm wide, without trigones, c) dorsal lobe apices usually obtuse, and d) ventral leaf lobes non-decurrent, without teeth on the dorsal lobe margin. Populations with perianths are infrequent in California.

Separation. This species generally grows at higher elevations and more inland than does *D. obtusifolium*. It is separated from *D. obtusifolium* by a) shoots up to 2.5 cm long (vs. shoots less than 1.2 cm long in *D. obtusifolium*), b) shoots and perianths without reddish coloration, even in sun-forms (vs. shoots and perianths reddish in sun-forms, c) dorsal leaf lobes with obtuse apices (vs. dorsal leaf lobes with rounded apices), and d) being dioicous with infrequent sporophytes (vs. being paroicous and commonly with sporophytes). The absence of an orange-red, toothed and long decurrent basal margin of the ventral lobe separates *D. taxifolium* from *D. plicatum*.

Illustrations. Damsholt 2002; Paton 1999; and Schuster 1974.

Habitat. On sunny to shaded soil in crevices of rock outcrops, rock faces, deep canyons, and underhang of boulders in open talus slopes. Elevation from 1300 to 2150 m.

Distribution. Diplophyllum taxifolium occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Trinity Co. *Norris 85408* (perianths) (UC), **NC**: Humboldt Co. *Norris 13344* (UC).

Douinia (C. E. O. Jensen) H. Buch 1928
(Scapaniaceae)

This genus has complicate-bilobed leaves with the dorsal lobe smaller than the ventral lobe. Look for a) dorsal and ventral leaf lobes lanceolate, tapering from near the base to the apex and b) irregular "waxy" markings on the surface of leaves. *Diplophyllum* and *Scapania* also have complicate-bilobed leaves with the dorsal lobe smaller than the ventral lobe. Unlike *Douinia*, *Diplophyllum* has a) ventral lobes lingulate with rounded or obtuse apices and b) lacks irregular "waxy" layers, and *Scapania* lacks a) perianth mouths with curved, branched cilia and b) irregular, "waxy" layers.

A monotypic genus.

Douinia ovata (Dicks.) H. Buch

Distinctive features. These dioicous plants are relatively small, less than 1.5 cm. long, and usually grow in glaucous green to yellowish-brown patches. Look for a) dorsal leaf lobes somewhat erect with apices pointed toward the stem apex, b) ventral leaf lobes flat with apices pointed outwards, b) dorsal and ventral lobes both tapering to an acute apex, c) trigones absent or small on the somewhat thickened walls of the median cells of the ventral lobe d) cell walls covered by irregular "waxy" material, and e) perianth mouths that have curved branched cilia and usually become whitish with age. Gemmae are absent.

Separation. This species can be confused with *Anastrophyllum minutum*. *Douinia* can be separated by a) the leaf surface with irregular "waxy" material (vs. the leaf surface without "waxy" material in *A. minutum*), b) gemmae absent (vs. gemmae frequently present), and c) perianth mouth with curved, branched teeth (vs. perianth mouth with unbranched cilia in *A. minutum*).

Illustrations. Damsholt 2002; Frye and Clark 1946; Paton 1999; Schofield 2002; Smith 1990.

Habitat. In canyons; on and around rocks; near sea-level to 1500 m.

Distribution. Douinia ovata occurs in Europe and western North America. Calif. Geographic Regions: **KR**: Siskiyou Co. *Wheeler 8292* (UC), **NC**: Humboldt Co. *Norris 23487* (perianths) (ABSH).

Frullania Raddi 1818
(Frullaniaceae)

Select for study only leaves and underleaves from healthy, mature shoots and main branches. Observations on immature, diseased or etiolated plant parts can result in incorrect identification.

This genus has complicate-bilobed leaves with incubous dorsal lobes that are larger than the ventral lobes. Distinctive features are a) leaves bilobed nearly to the base, b) ventral lobes (often called lobules: technically, a lobule is the smaller of the two lobes in complicate-bilobed leaves of *Frullania, Porella, Radula, Diplophyllum, Douinia,* and *Scapania*; its use often is incorrectly restricted to the ventral lobes only of *Frullania*) somewhat flattened (explanate) or form distinctive helmet-shaped (galeate) or cylindrical structures, c) dorsal lobes of several species with scattered, groups or rows of specialized colored cells (= ocelli), d) bilobed underleaves, e) rhizoids develop in tufts from the base of the underleaves, and f) perianths constricted to a beak-like mouth. The genus has both paroicous and dioicous species. For diocous species search populations carefully for perianths, which indicate nearby male plants.

Frullania, Porella and *Radula* have complicate-bilobed leaves with incubous dorsal lobes that are larger than the ventral lobes. However, a) the underleaves of *Porella* are entire (vs. underleaves bilobed in *Frullania*), and b) *Radula* lacks underleaves (vs. underleaves present).

Five species in California. The Evans (1897) monograph of North American species of *Frullania* contains excellent keys, descriptions and illustrations of all five California species.

Species Key

1. Ventral lobes helmut-shaped (galeate) about as long as wide, or frequently flattened (explanate); perianth terminal on the main stem or a long branch. . . . . **2.**
1. Ventral lobes cylindrical, clearly longer than wide; perianth terminal on a short lateral branch. . . . . **3.**
2. Erect branches with caducous leaves present in mature parts of healthy populations; leafy stems 0.5–0.7 mm wide; ventral lobes usually galeate; dioicous. . . . . **F. bolanderi**
2. Erect branches with caducous leaves absent; leafy stems 0.8–1.2 mm wide; ventral lobes mostly explanate; autoicous. . . . . **F. catalinae**
3. Dorsal lobes on main branches usually with a single or double median line of discolored cells (ocelli); underleaves gradually narrowed to the base; lobes each usually with a broad shoulder near the middle. . . . . **F. franciscana**
3. Dorsal lobes on main branches usually without discolored cells, but when present, seldom in a single line; underleaves auriculate or narrowed to the base; lobes mostly without a broad shoulder near the middle. . . . . **4.**
4. Underleaves usually clearly auriculate at the base; ventral lobe separated from the stem by more than half the ventral lobe width; perianths gradually narrowed from about the middle to near the beak. . . . . **F. nisquallensis**
4. Underleaves either gradually narrowed to the base or auriculate; ventral lobe separated from the stem by less than half the ventral lobe width; perianths truncate, abruptly contracted from near the apex to the beak. . . . . **F. californica**

Excluded. Frullania inflata Gottsche. Clark and Svihla (1944) placed *F. catalinae* A. Evans in synonymy with *F. inflata.* Subsequently, some California specimens of *F. catalinae* were annotated, and other collections identified, as *F. inflata.* This synonymy was not accepted by Stotler and Crandall-Stotler (1977) and Hong (1989). Specimens examined during the present study support the conclusion that *F. catalinae* and *F. inflata* are separate species. All California specimens labelled *F. inflata* examined in this study, including those cited by Frye and Clark (1946) and Hong (1989), are confirmed as *F. catalinae. Frullania inflata* could not be confirmed for California.

Frullania bolanderi Austin

Distinctive features. These green to reddish-brown plants are 0.5–0.7 mm wide and usually tightly adherent to the substrate. The most distinctive feature, visible with a 10x handlens, is the presence in most populations of short, abruptly erect branches with leaves that detach (caducous) as propagules in asexual reproduction; modified underleaves remain on the erect branches. Also look for a) ventral lobes mostly galeate with a wide mouth, but occasionally flat (explanate), b) underleaves bifid to about 0.5 their length and margins usually with one or two blunt teeth, and c) perianths abruptly contracted near the apex to a short, broad beak.

Separation. The presence of short, stiffly erect branches with caducous leaves separates *F. bolanderi* from other California species. When erect branches with caducous leaves are absent (e.g., from small populations), the small shoot width of 0.5–0.7 mm wide coupled with mostly galeate ventral lobes separates this species from others in the genus.

Illustrations. Damsholt 2002; Evans 1897; Schuster 1992a.

Habitat. On bark of angiosperms; less commonly on trunks of young conifers; occasionally on rocks, soil and decaying wood. Elevation from near sea-level to 2000 m, but mostly from 20 to 1500 m.

Distribution. Frullania bolanderi has the interesting distribution of eastern Asia, northeastern North America (Canada and New England), and western North America. Calif. Geographic Regions: **CC**: Alameda Co. *Shevock 26218* (CAS), **CR**: Tehama Co. *Doyle 8614* (UC), **KR**: Trinity Co. *Doyle 5914* (UC), **NC**: Lake Co. *Doyle 10005* (UC), **SC**: San Diego Co. *Stark 412* (MO), **SN**: Yuba Co. *Doyle 9594* (UC).

Frullania californica (Austin) A. Evans

Distinctive features. Plants of this dioicous species usually are green in shaded, humid habitats, and brownish-red in sunnier, drier habitats. Look for a) dorsal lobes without discolored cells, or, when present, few and scattered, and only rarely in a short median line, b) the dorsal lobe apex rounded, obtuse or acute, c) median cells of the dorsal lobes 10–20 μm wide, d) ventral lobes cylindrical and separated from the stem by less than 0.5 their width, e) underleaves bilobed about 0.5 their length or less, with lobe margins flat or sometimes slightly reflexed, f) underleaves gradually narrowed to the base or occasionally auriculate, and g) perianths truncate, abruptly contracted near the apex to a short beak.

Separation. This species can be separated from *F. franciscana* by a) the usual absence of a single or double median line of discolored cells in the dorsal lobe (vs. the usual presence of 1–2 rows of discolored cells in *F. franciscana*), and b) underleaves bilobed less than 0.5 their length (vs. underleaves bilobed 0.5 or more their length). Populations of *F. californica* that have dorsal lobes with a high proportion of acute to nearly acuminate apices, or underleaves with auriculate bases can be confused with *F. nisquallensis*. *Frullania californica* is separated by a) underleaf lobe margin and apex mostly not (or only slightly) reflexed (vs. underleaf lobe margin and apex strongly reflexed in *F. nisquallensis*), and b) perianths truncate, abruptly contracted to a short beak (vs. perianths more gradually narrowed to a beak).

Illustrations. Evans 1897; Clark and Frye 1928.

Habitat. Shaded, humid areas, usually near canyon bottoms; on bark, especially of angiosperms and young conifers; also on logs, rock outcrops and limestone boulders. Elevation between 15 and 1000 m, but mostly below 650 m.

Distribution. Frullania californica is endemic to western North America. Calif. Geographic Regions: **CC**: Contra Costa Co. *Shevock 24535* (UC), **KR**: Siskiyou Co. *Doyle 9281* (UC), **NC**: Sonoma Co. *Parks 2966* (CAS), **SC**: Santa Barbara Co. *Bratt s.n.* (9 November 1993) (UC).

Frullania catalinae A. Evans

Distinctive features. This is our only paroicous species of the genus. The plants often grow in large reddish-brown mats. Look for a) dorsal leaf lobes generally squarrose, with median cells 16–20 μm wide and 20–36 μm long, b) ventral lobes mostly explanate (but both explanate and galeate lobes can occur on the same stem), c) underleaves bifid to about 0.5 their length, the lobes often with a blunt

tooth or angulation on each lateral margin, d) perianths gradually narrowed from near the middle to a short apical beak (**caution:** a few perianths in some populations can be abruptly constricted near the apex.), and e) bracteoles connate on one margin with bracts.

Separation. Frullania catalinae is separated from *F. inflata* by a) perianths gradually narrowed from near the middle to a short apical beak (vs. perianths truncate, abruptly narrowed near the apex to a short beak in *F. inflata*), b) dorsal leaf lobes generally squarrose (vs. dorsal leaf lobes mostly flat), c) underleaves bifid to about 0.5 their length, the lobes on robust stems usually with blunt marginal teeth (vs. underleaves bifid to about 0.3 their length, the lobes without blunt marginal teeth); and d) bracteoles connate on one side with bracts (vs. bracteoles free on both sides from bracts). *Frullania catalinae is separated* from *F. bolanderi* by a) short, erect branches with caducous leaves absent (vs. branches with caducous leaves present in *F. bolanderi*), b) ventral lobes mostly explanate (vs. ventral lobes mostly galeate), and c) perianths gradually narrowed toward the apex (vs. perianths truncate, abruptly contracted at the apex.

Illustrations. Evans 1897.

Habitat. Shaded trunks of angiosperms and rock outcrops. Elevation from 15 to 405 m; mostly below 250 m.

Distribution. Frullania catalinae is endemic to coastal California. Calif. Geographic Regions: **CC**: San Luis Obispo Co. *Doyle 5752* (UC), **SC**: Los Angeles Co. *McClatchie 550* (Type!) (YU).

Frullania franciscana M. Howe

Distinctive features. Plants of this dioicous species can be green, yellow-green or reddish-brown. Distinctive features include a) dorsal leaf lobes mostly with 1–2 (occasionally 3) median lines (sometimes incomplete) of discolored cells (ocelli), b) dorsal lobes with rounded, obtuse or apiculate apices and usually with narrow and acute sinuses, c) ventral lobes cylindrical, separated from the stem by 0.5 or more of the lobe width, d) underleaves bilobed 0.5 their length or more, e) underleaf margin usually with a broad angulation about the middle of one or both lobes, f) underleaf gradually narrowed to the base (not auriculate), and g) perianth truncate, abruptly contracted from near the apex to the beak.

Separation. This species can be confused with *F. californica* and *F. nisquallensis*. It is separated from both *F. californica* and *F. nisquallensis* by a) the dorsal lobes usually with 1–2 (or three) median lines of discolored cells, and b) the underleaves gradually narrowed to the base (not auriculate).

Illustrations. Clark and Frye 1928; Evans 1897; Howe 1894.

Habitat. Shaded, humid habitats; usually on trunks and branches of angiosperms; occasionally on boulders. Elevation between 3 and 200 m; mostly below 110 m.

Distribution. Frullania franciscana is endemic to the Pacific Coast of North America. Calif. Geographic Regions: **CC**. San Mateo Co. *Whittemore 4067* (CAS), **KR**. Del Norte Co. *Doyle 10680* (UC), **NC**. Mendocino Co. *Doyle 10447* (UC).

Frullania nisquallensis Sull.

Distinctive features. Plants of this dioicous species vary from greenish to yellow-brown to reddish-brown. Look for a) dorsal lobe apices usually acute or acuminate, b) dorsal lobes with no (occasionally a few) scattered discolored cells, only rarely in a line, c) ventral lobes cylindrical, separated from the stem by about the lobe width, d) underleaf shallowly lobed, divided 0.25 to 0.3 their length, clearly auriculate at the base, and with or without short marginal basal spurs, e) underleaf lobe strongly reflexed on mature stems, and f) perianths mostly somewhat fusiform, gradually narrowing from about the middle to a beaked apex.

Separation. For separation from *F. californica* and *F. franciscana*, see comments under those species.

Illustrations. Evans 1897; Clark and Frye 1928; Schofield 2002.

Habitat. On angiosperms, gymnosperms, logs, and rocks. Elevation between 10 and 625 m.

Distribution. Frullania nisquallensis is endemic to western North America. Calif. Geographic Regions: **CC**: San Francisco Co. *Howe 198* (ABSH), **KR**: Del Norte Co. *Doyle 7723* (UC), **NC**: Humboldt Co. *Doyle 10580* (UC).

Geocalyx Nees 1836
(Geocalycaceae)

Plants of this yellowish- to grayish-green genus have a) rhizoids from the stem surface and underleaf base, b) leaf cells with distinct trigones, c) underleaves large and deeply divided, and d) a sporophyte that develops in a fleshy, rhizoid-covered, subterranean structure, called a marsupium.

One species in California.

Geocalyx graveolens (Schrad.) Nees

Distinctive features. These are opaque yellow- to olive-green plants with succubous leaves. They often grow in loose patches and are aromatic when living. Look for a) leaves shallowly bilobed with slightly unequal lobes, b) underleaves divided nearly to the base and appressed closely to the stem, c) underleaf lobes entire and often nearly parallel, d) rhizoids densely developed and often obscuring the underleaves except near the shoot apex, and e) lack of gemmae development.

Separation. With its a) opaque shoots, b) aroma of living plants, c) large and deeply bifid underleaves closely appressed to the stem and nearly obscured by dense rhizoid growth, and d) lack of gemmae, *G. graveolens* is not easily confused with other California liverworts.

Illustrations. Damsholt 2002; Frye and Clark 1945; Paton 1999; Schofield 2002; Schuster 1980; Smith 1990.

Habitat. Shaded, damp logs and organic matter; also on damp mineral soil; Elevation from 120 to 1135 m.

Distribution. Geocalyx graveolens occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 8915* (UC), **KR**: Siskiyou Co. *Doyle 9169* (UC), **NC**: Humboldt Co. *Norris 72078* (CAS), **CR** Tehama Co. *Doyle 4030* (UC).

Gymnocolea (Dumort.) Dumort. 1835
(Jungermanniaceae)

Species of this dioicous genus often occur in green to brownish to blackish mats. Look for a) leaves bilobed, obliquely inserted, succubous and widest about the middle, b) leaf cells with equally thickened-walls, c) rhizoids with scattered development on the stem, and d) perianths smooth (not plicate), contracted near the apex to a non-beaked mouth.

One species in California.

Gymnocolea inflata (Huds.) Dumort.

Distinctive features. This is a variable species. The shoots are green and lax in shaded and submerged habitats; shoots usually are in erect brownish-black patches, often with a somewhat burnt appearance in exposed habitats. A distinctive feature is the development of apically inflated perianths which, in the absence of fertilization, detach (caducous) and become a means of asexual reproduction. Thoroughly search field populations for these perianths. For vegetative plants, look for a) leaves generally widest about the middle, b) leaf lobes with obtuse to rounded apices and entire lateral margins, c) median leaf cells 17–29 μm wide × 20–42 μm long and marginal cells 15–33 μm wide, d) leaf cells with evenly thickened walls without trigones, e) underleaves scarce and vary in form from 1–3 celled papillae, to subulate to bilobed, and f) larger underleaves associated with branching frequently present.

Separation. With leaves wider about the leaf middle, rounded leaf lobes, caducous perianths, and sparse development of underleaves, *G. inflata* is easily separated from other California liverworts. In its color and lax growth in boggy habitats, it can be confused with *Cladopodiella fluitans*, a liverwort not yet found in California. *Cladopodiella fluitans*, however, has a) frequent development of distinct subulate or lanceolate underleaves, with 1-celled slime-filaments on the lateral margins (vs. sparse development of underleaves, without slime-filaments in *G. inflata*), b) larger median leaf cells, 28–44 μm wide and 32–45 μm long (vs. median leaf cells 17–29 μm wide and 20–42 μm long), and c) non-caducous perianths (vs. caducous perianths).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. Sunny to shaded sites subject to seasonal flooding, such as pond and lake margins, bogs, and seepages. Elevation mostly from 2250 to 3350 m, but around 160 m in *Sphagnum* bogs of Mendocino Co.

Distribution. Gymnocolea inflata occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 10824* (UC), **MP**: Modoc Co. *Doyle 9671* (UC), **NC**: Mendocino Co. Kellman 2205 (CAS), **SN**: Mono Co. *Doyle 6814* (UC), **SNE**: Inyo Co. *Shevock 15338* (CAS).

Gymnomitrion Corda 1829
(Gymnomitraceae)

Gymnomitrion is a distinctive genus with a) erect shoots often in tightly appressed, compact tufts, b) bifid leaves closely over-lapping and appressed (like roof tiles) so that the stem is not visible, c) leaf margins usually with strongly thickened cell walls, and d) perianths lacking or vestigial.

Two species in California.

Species Key

1. Leaf lobe tips mostly acute; lobe margins entire to weakly crenulate toward the apex (but mostly smooth toward the base); lobe sinus usually open near the base. . . . . **G. concinnatum**
1. Leaf lobe tips mostly obtuse or rounded, occasionally apiculate; lobe margins crenulate from apex to base; sinus between lobes usually closed near base. . . . . **G. obtusum**

Gymnomitrion concinnatum (Lightf.) Corda

Distinctive features. Look for a) leaf lobe apices mostly acute ending in 1–2 superposed cells, b) lobe margins smooth or weakly crenulate near the apex, but smooth toward the base, and c) leaf lobe sinus acute and usually open.

Separation. Gymnomitrion concinnatum is morphologically variable and occasionally can be difficult to separate from *G. obtusum*. Look carefully at the leaf apices, sinuses and margins. In *G. concinnatum* a) the lobe apex mostly is acute (vs. lobe apex mostly is obtuse or rounded in *G. obtusum*, although some apices often are apiculate), b) lobe sinus open (vs. lobe sinus closed, the inner lobe margins touch or overlap near the lobe base), and c) the leaf margin near the lobe apex is entire or weakly crenulate (vs. leaf margin from the apex nearly to the leaf base is clearly crenulate).

Illustrations. Damsholt 2002; Frye and Clark 1943; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Shaded, humid rock outcrops and surface of boulders; Elevation from 115 to 1800 m.

Distribution. Gymnomitrion concinnatum occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Norris 10881* (UC).

Gymnomitrion obtusum Lindb.

Distinctive features. Plants of this species often occur in compact, whitish tufts. Look for a) leaf lobe apex mostly obtuse or rounded (a few lobe apices often can be apiculate), b) lobe margins distinctly crenulate to the lobe base, and c) lobe sinuses acute to rounded, and usually closed (bases of the lobe inner margins touch or overlap) just above the sinus base.

Separation. Gymnomitrion obtusum and *G. concinnatum* share many features and occasionally are difficult to separate. See *G. concinnatum* for separation from that species.

Illustrations. Damsholt 2002; Frye and Clark 1943; Paton 1999; Schofield 2002; Schuster 1974; Smith 1990.

Habitat. Shaded boulder and cliff surfaces. Elevation above 1100 m.

Distribution. Gymnomitrion obtusum occurs in Europe and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Jessup 7406* (SOU), **SN**: El Dorado Co. *Norris 58397* (UC).

Gyrothyra M. Howe 1897
(Gyrothyraceae)

Distinctive features of this genus include a) large underleaves bifid with lanceolate lobes, b) leaf cells with conspicuous trigones, c) rhizoids developing near differentiated cushions on stem tissue, and d) capsules dehiscing by 4 long helical valves.

A monotypic genus.

Gyrothyra underwoodiana M. Howe

Distinctive features. The shoots of this species are sparingly branched and usually light green in color. Look for a) rhizoids mostly from around reddish multicellular cushions on the ventral stem surface (a few rhizoids often arising from cushion cells), the cushions are colorless near the stem apex and conspicuously reddish in older stem areas, b) thin-walled leaf cells with conspicuous triangular to bulging trigones, c) oil-bodies gray, ellipsoidal, 2–4 per median leaf cell, d) underleaves large, divided more than 0.5 their length into 2 lanceolate segments, the tips of which usually terminate with 2–4 uniseriate cells (underleaves are easier to see at the shoot apex because of the dense growth of rhizoids in older stem regions), and e) sporophyte capsules dehiscing by 4 long, narrow helical valves.

Separation. With the combination of a) succubous leaves with thin walls and triangular to bulging trigones, b) underleaves large and deeply bilobed, c) rhizoids surrounding reddish cushions on mature stem areas, and d) helical valves on the sporophyte capsule, *G. underwoodiana* should not be confused with other liverworts. The presence of large underleaves separate this plant from similar sized species of *Jungermannia* (a genus without underleaves).

Illustrations. Clark and Frye 1928; Howe 1897b; Howe 1899; Schofield 2002.

Habitat. On shaded, moist bare soil of hillsides, and road and trail banks. Elevation from 50 to 1200 m.

Distribution. Gyrothyra underwoodiana occurs only on the Pacific Coast of North America, where it occurs from Alaska to California. Calif. Geographic Regions: **KR**: Del Norte *Doyle 11049* (UC), **NC**: Marin Co. *Yurky 16* (NY 245632), **SN**: Butte *Doyle 11409* (UC).

Herbertus Gray 1821
(Herbertaceae)

This genus is questionable for California. Both ABSH and UC have packets labeled *Herbertus hutchinsiae* (=*Herbertus aduncus* (Dicks.) Gray subsp. *aduncus*) with the following information: Dodds, St. Lake; Pine Crest, Calif.; E. Morse; 1934. Pinecrest and Pinecrest Lake are east of Sonora on Calif. Highway 108, Stanislaus National Forest, Tuolumne, Co. No other collection of *Herbertus* is known for California. This species is abundant in British Columbia, rare in Washington, and known from only three localities in northern Oregon (Christy and Wagner 1996). In a note in the UC collection packet, Dan Norris wrote "This is surely a mis-statement of locality". The species name has been confirmed, but the State of collection likely is in error.

Herbertus aduncus (Dicks.) Gray subsp. **aduncus**

Distinctive features. Shoots usually are in large brownish-green to yellowish-brown mats. Look for a) lateral leaves and underleaves of similar size and shape, c) leaves bifid 0.75 or more their length, the lobes up to 6 times longer than wide, and d) a vitta of somewhat elongate cells extending 0.3 to 0.6 the lobe length. Slime papillae, when present, are unicellular (not stalked).

Separation. With its large shoots and strongly bifid leaves, *Herbertus* is more likely to be mistaken for a moss than a liverwort.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1966; Smith 1990.

Habitat. No substrate was given. In the Pinecrest and Pinecrest Lake area, search for this plant on tree trunks, and shaded cliffs and boulders.

Distribution. Herbertus aduncus subsp. *aduncus* occurs in East Asia and northwestern North America. Calif. Geographic Regions: **SN?**: presence needs confirmation.

Jamesoniella (Spruce) F. Lees 1881
(Jungermanniaceae)

The Rick Dewey collection of *Jamesoniella autumnalis* (DC.) Steph., cited by A. Whittemore (in litt.), is not from California. This packet has no collection data or number. Dewey (personal communication) suggested that the plants came from a class at Humboldt State University; this possibility was confirmed by Dan Norris (personal communication). No herbarium specimen of *J. autumnalis* was located during the present study. This species could not be confirmed for California, but is retained in the key (see Damsholt (2002), Paton (1999), Schofield (2002), or Schuster (1969) for description and illustration).

Jungermannia L. 1753
(Jungermanniaceae)

Species of *Jungermannia* a) have succubous leaves that never are bilobed and seldom emarginate, b) lack underleaves, c) have rhizoids scattered on the stem, and on leaf bases in some species, d) lack gemmae in most species, and e) have cylindrical perianths that are smooth below, and plicate toward the mouth in most species. Perianths are at the stem apex or on a perigynium (a perigynium is a fleshy, tubular structure of stem origin that develops post-fertilization at the stem apex, surrounding the developing sporophyte, and bearing the perianth and female bracts. See Paton 1999: 276, 286, and 331 for illustrations.)

Nine species in California.

Species Key

Plants with perianths are more easily keyed to species than are vegetative only plants. However, most collections will consist only of vegetative plants. The first key is for plants with perianths. For vegetative plants, go directly to the second key.

1. Key to Plants with Perianths

1. Perianth cylindrical, smooth (not plicate), and abruptly contracted near the apex to a short tubular beaked mouth recessed in a shallow apical depression; leaves oblong, ± parallel-sided. . . . . **J. leiantha**
1. Perianth cylindrical, smooth below, plicate above, and gradually or abruptly contracted near the apex to a non-beaked or beaked mouth (if beaked, the beak not recessed in an apical depression); leaves various, but not oblong and ± parallel-sided. . . . . **2.**
2. Perigynium half as long or longer than the perianth; perianth emergent 0.5 or less its length beyond the female bracts. . . . . **3.**
2. Perigynium absent or very short; perianth usually long-emergent. . . . . **4.**
3. Leaves clearly bordered with thick-walled marginal cells (marginal leaf cells clearly differentiated from inner cells). . . . . **J. rubra**
3. Leaves not clearly bordered with thick-walled marginal cells (marginal leaf cells often not or little differentiated from inner cells). . . . . **J. hyalina**
4. Perigynium usually absent; perianth long-exserted above the female bracts, the bracts not sheathing the base of the perianth; perianth gradually narrowed to a non-beaked mouth; rhizoids from the stem only. . . . . **5.**
4. Perigynium usually present, but very low; perianth exserted above the female bracts by ½ to ¾ its length, the bracts sheathing the base of the perianth; perianth rather abruptly contracted near the apex to a short beaked mouth; rhizoids from both the stem and leaf base. . . . . **8.**
5. Dioicous. . . . . **6.**
5. Paroicous. . . . . **7.**
6. Plants usually blackish-green, 10 cm or more long; aromatic when fresh; leaves usually flacid, cordate to triangular and obtuse to broadly rounded at the apex. . . . . **J. exsertifolia** subsp. **cordifolia**
6. Plants usually olive- to yellowish-green, up to 4 cm long; not aromatic when fresh; leaves not flaccid, mostly ovate and broadly rounded at the apex. . . . . **J. atrovirens**
7. Median leaf cells mostly 17–28 μm wide × 25–30 μm long (or longer); perianths gradually narrowed to apex (fusiform), especially when young. . . . . **J. pumila**

7. Median leaf cells mostly 12–20 μm wide × 16–25 μm long; perianths widest near middle and rather abruptly rounded to apex. . . . . **J. polaris**
8. Leaves mostly reniform; rhizoids often in clusters from both stem and leaf base, with many closely appressed to the stem; in sun-forms the leaf margins, bracts and perianths often with pinkish, reddish, or purplish pigmentation. . . . . **J. confertissima**
8. Leaves nearly circular; rhizoids not in clusters with few from the leaf base and mostly oriented perpendicular to the stem; in sun-forms the leaves, bracts and perianths with brownish, never reddish coloration. . . . . **J. sphaerocarpa**

2. Key to Vegetative Plants

1. Leaves usually oblong and more-or-less parallel-sided; occasionally with attenuated gemmiferous shoots. . . . . **J. leiantha**
1. Leaves various, but not oblong and parallel-sided; gemmae and gemmiferous shoots always absent. . . . . **2.**
2. Leaves clearly bordered with thick-walled marginal cells (marginal leaf cells clearly differentiated from inner cells). . . . . **J. rubra**
2. Leaves not clearly bordered with thick-walled marginal cells (marginal leaf cells often not or little differentiated from inner cells). . . . . **3.**
3. Rhizoids (at least some) developing from leaf bases as well as stem tissue. . . . . **4.**
3. Rhizoids developing only from stem tissue. . . . . **6.**
4. Leaves obliquely inserted and nearly horizontal near the dorsal stem surface, usually long decurrent on the dorsal stem surface, and nearly semi-circular and widest near the base. . . . . **J. hyalina**
4. Leaves obliquely inserted but not nearly horizontal near the dorsal stem surface, not or short decurrent on the dorsal stem surface, and nearly circular or reniform and widest near the middle. . . . . **5.**
5. Leaves mostly reniform; rhizoids often in clusters from both the stem and leaf base, with many closely appressed to the stem; in sun-forms the leaf margins, bracts and perianths often with pinkish, reddish or purplish pigmentation. . . . . **J. confertissima**
5. Leaves nearly circular; rhizoids not in clusters, with a few from the leaf base and most oriented perpendicular to the stem; in sun-forms the leaves, bracts and perianths with brownish, never reddish coloration. . . . . **J. sphaerocarpa**
6. Shoots large, 2–12 cm long, usually blackish green; living plants strongly aromatic; leaves flaccid; rhizoids few, mostly near stem bases. . . . . **J. exsertifolia** subsp. **cordifolia**
6. Shoots usually less than 4 cm long, olive-green to blackish; living plants aromatic or not; leaves not flaccid; rhizoids numerous, nearly to the stem apex. . . . . **7.**
7. Plants small, less than 1 mm wide; median leaf cells 12–20 μm wide × 16–25 μm long. . . . . **J. polaris**
7. Plants larger, to 4.5 mm wide; median leaf cells 15–30 μm wide × 20–35 μm long or longer (At times, vegetative plants of the following two species can be impossible to separate.) . . **8.**
8. Typical, robust plants mostly with broadly ovate leaves; oil-bodies 2–3 per leaf cell; living plants aromatic. . . . . **J. atrovirens**
8. Typical, robust plants with somewhat elliptical leaves; oil-bodies 4–5 per leaf cell; living plants not aromatic. . . . . **J. pumila**

Jungermannia atrovirens Dumort.

Distinctive features. This dioicous species grows in yellowish-, olive-, to blackish-green populations. Look for a) shoots 0.5–4.5 mm wide, b) living plants aromatic, c) leaves often broadly ovate, d) median leaf cells thin-walled, mostly 15–25 μm wide and 20–33 μm long, e) leaf marginal cells mostly 10–15 μm wide, f) rhizoids from the stem surface, none from the leaf base, g) oil-bodies mostly 2–3 per leaf cell, and h) perianths oblong to cylindrical, plicate and narrowed toward the apex to a non-beaked mouth.

Separation. Jungermannia atrovirens and *J. pumila* share many characteristics and are most easily separated when reproductive: *J. atrovirens* is dioicous whereas *J. pumila* is paroicous. Because of morphological variability of vegetative plants, some populations of the two species can be impossible to identify with absolute certainty. Mature "typical" vegetative plants of *J. atrovirens* can be separated from those of *J. pumila* mainly by a) leaves often broadly ovate (vs. leaves rather elliptical in *J. pumila*), b) living plants aromatic (vs. living plants not aromatic), and c) oil-bodies 2–3 per median leaf cell (vs. oil-bodies mostly 4–5 per median leaf cell).

Illustrations. Damsholt 2002 (as *J. lanceolata*); Paton 1999; Schuster 1969; Smith 1990.

Habitat. On soil and rocks in wet places, such as stream banks where often seasonally submerged. Elevation from 115 to 2000 m.

Distribution. Jungermannia atrovirens occurs in Europe, Asia, Africa, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 11068* (perianths) (UC).

Jungermannia confertissima Nees

Distinctive features. This usually erect paroicous species often occurs in yellowish-green to green populations. The leaves of sun-forms, however, can be pink, reddish or purplish toward the margins (the leaf bases and stems are not reddish). Look for a) leaves reniform, obliquely to subtransversely inserted, b) median leaf cells mostly 25–35 μm wide × 25–42 μm long, c) marginal leaf cells 24–30 μm wide, d) rhizoids numerous, brownish, hyaline or occasionally purplish, often in clusters from stem and leaf bases, with many rhizoids closely appressed to the stem, and e) perianths of sun-forms usually reddish or purplish.

Separation. This species can be confused with *J. sphaerocarpa*, however, *J. confertissima* can be separated by a) leaves subtransversely inserted, reniform and concave (vs. leaves obliquely inserted, not reniform and little or not concave and often spreading in *J. sphaerocarpa*), b) rhizoids mostly appressed to the stem (vs. rhizoids mostly at right angles to the stem), and c) leaf margins and perianths occasionally with reddish or purplish pigmentation (vs. leaf margins and perianths brownish; rarely, if ever, reddish or purplish).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On shaded, damp stream banks and rocks. Elevation above 1100 m.

Distribution. Jungermannia confertissima occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Tulare Co. *Doyle 2855* (perianths) (UC).

Jungermannia exsertifolia Steph. subsp. ***cordifolia*** (Dumort.) Váňa

Distinctive features. This gray- to blackish-green dioicous species consists of large plants, up to 18 cm long. Look for a) living plants aromatic, b) leaf bases loosely sheath the stem, c) median leaf cells 20–30 μm wide × 30–60 μm long, with dark brown to blackish-brown walls, d) rhizoids hyaline to brownish, only from the stem, and e) perianths long-exserted, fusiform, plicate near the apex and narrowed to a non-beaked mouth.

Separation. With its large size, aromatic living plants, sheathing leaf bases, brown to blackish-brown leaf cell walls, and sparse development of rhizoids, *J. exsertifolia* subsp. *cordifolia* should not be confused with other California species of *Jungermannia*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Usually attached to rocks in or near swiftly flowing water, where it is seasonally submerged. Elevation from 1800 to 3050 m.

Distribution. Jungermannia exsertifolia subsp. *cordifolia* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 9314* (UC), **KR**: Trinity Co. *Doyle 6046* (perianths) (UC), **SC**: San Bernardino Co. *Howell 719* (CAS), **SN**: Nevada Co. *Norris 102605* (UC).

Jungermannia hyalina Lyell

Distinctive features. This species usually is green to yellow-green. Look for a) nearly semi-circular leaves about as wide as long, and widest at or near the leaf base, b) leaves usually clearly decurrent on the dorsal stem surface, c) median leaf cells 25–35 μm wide × 30–45 μm long, and marginal leaf cells 21–35 μm wide, d) rhizoids brownish to reddish (seldom hyaline), mostly from the stem, but some from the leaf base, e) leaf bases and the ventral sides of stems often reddish, f) stem epidermal cells thin-walled, 5–10 times as long as wide, and g) oil-bodies 2–5 per leaf cell.

Separation. This species can be confused with *J. confertissima* and *J. sphaerocarpa*. It is separated from both by nearly semicircular leaves that are widest at or near the leaf base (vs. reniform or nearly circular leaves that are widest near the leaf middle.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On mineral and peaty soil; drainages through meadows, along streams. Elevation from 1800 to 2500 m.

Distribution. Jungermannia hyalina occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **SN**: Fresno Co. *Doyle 10728* (male plants) (UC).

Jungermannia leiantha Grolle

Distinctive features. These paroicous plants, with shoots 2–2.5 mm wide, occur mostly in green to yellowish-brown patches. Look for a) leaves often nearly parallel-sided with rounded apices, b) median leaf cells 28–33 μm wide × 30–50 μm long, c) leaf cells thin-walled with small to bulging trigones, d) older leaves usually with brownish cell walls, e) oil-bodies granular, mostly 7–11 per leaf cell, f) rhizoids hyaline or pale brownish, g) underleaves absent, and h) perianth smooth (not plicate), abruptly contracted near the apex into a short, tubular beak that is recessed in a shallow depression.

Separation. The cylindrical perianth abruptly contracted near the apex into a short, tubular beak recessed in a shallow depression clearly separates *J. leiantha* from other members of the genus. Vegetative plants of *J. leiantha* are separated from *Mylia anomala* by the absence of underleaves (underleaves present in *M. anomala*).

Illustrations. Damsholt 2002 (as *J. subulata*); Frye and Clark 1943 (as *J. lanceolata*); Schuster 1969 (as *J. lanceolata*).

Habitat. Generally on moist decaying logs in seepages and near creeks, and on peaty substrates. Elevation from 200 to 3050 m.

Distribution. Jungermannia leiantha occurs in Europe and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Doyle 11102* (perianths) (UC), **KR**: Siskiyou Co. *Shevock 26194* (CAS), **MP**: Modoc Co. *Doyle 6687* (gemmae and perianths) (UC), **SN**: Tulare Co. *Doyle 7807* (perianths) (UC).

Jungermannia polaris Lindb.

Distinctive features. This small, paroicous plant occurs in yellowish- to dark- to blackish-green patches. Look for a) shoots less than 1 mm wide, b) leaves concave, broadly ovate to round, c) median leaf cells thin-walled 12–20 μm wide × 16–25 μm long, with small trigones, d) oil-bodies mostly 2–4 per leaf cell, and e) perianths nearly pyriform, smooth below and rounded and plicate from about the middle to a non-beaked mouth.

Separation. Both *J. polaris* and *J. pumila* are morphologically variable and some populations can be difficult to identify. Most of the time, *J. polaris* can be separated by one or more of the following a) shoots less than 1 mm wide (vs. shoots usually more than 1 mm and up to 3.5 mm wide in *J. pumila*), b) leaves broadly ovate to round (vs. leaves mostly elliptical), c) median leaf cells 12–20 μm wide × 16–25 μm long (vs. median leaf cells 17–28 μm wide × 25–35 μm long), and d) mature perianths mostly pyriform (vs. mature perianths usually fusiform).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Near streams. Elevation from 3000 to 3500 m.

Distribution. Jungermannia polaris occurs at high elevations in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Mono Co. *Doyle 10263* (perianths) (UC).

Jungermannia pumila With.

Distinctive features. Populations of this paroicous species vary from olive-to dark to blackish-green. Look for a) living plants non-aromatic, b) shoots 0.5–3.5 mm wide, c) leaves generally elliptical to ovoid, d) leaf cells thin-walled with no or only small trigones, e) median leaf cells 17–28 μm wide × 25–35 μm long, f) rhizoids from the stem surface, none from the leaf base, g) oil-bodies mostly 4–5 per leaf cell, and h) perianth usually somewhat fusiform and slightly flattened, narrowed and plicate toward the apex, with a non-beaked mouth.

Separation. Jungermannia pumila (paroicous) and *J. atrovirens* (dioicous) are definitively separated on the basis of sexuality. Vegetative plants, however, sometimes cannot be identified with certainty.

See *J. atrovirens* for a possible separation from that species. See *Jungermannia pumila* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On rocks near streams where it is seasonally submerged. Elevation from 2100 to 2600 m.

Distribution. Jungermannia pumila occurs in Europe, Asia, Africa, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 2040* (large aquatic form; perianths) (UC), **SN**: Madera Co. *Doyle 6915* (perianths) (UC).

Jungermannia rubra Gottsche ex Underw.

Distinctive features. These dioicous plants often grow in large patches. The shoots generally are green when actively growing and in damp shaded habitats, and reddish in exposed and drying habitats. Look for a) leaves usually bordered with thick-walled marginal cells usually slightly larger than the submarginal cells (**note**—the extent of wall thickening of marginal cells is variable), b) median leaf cells with distinct and often bulging trigones, c) rhizoids hyaline, and d) perianths plicate, reddish to purplish, with a beaked mouth.

Separation. Jungermannia rubra is separated from other species of *Jungermannia* by the following combination of features a) reddish shoot coloration, b) marginal leaf cells thick-walled, c) median leaf cells with distinct trigones, d) a perigynium present, and e) perianths reddish to purplish.

Illustrations. Frye and Clark 1943; Schofield 2002.

Habitat. Soil, occasionally on rocks; shaded banks, hillsides and cliffs; near sea-level to 2160 m; usually below 1110 m.

Distribution. Jungermannia rubra occurs in western North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10394* (UC), **CR**: Shasta Co. *Doyle 10985* (UC), **KR**: Trinity Co. *Norris 99804* (UC), **MP**: Modoc Co. *Doyle 9659* (UC), **NC**: Humboldt Co. *Doyle 10056* (UC), **SC**: Riverside Co. *Doyle 7336* (UC), **SN**: Yuba Co. *Doyle 9575*.

Jungermannia sphaerocarpa Hook.

Distinctive features. This paroicous species often occurs in green patches or olive-green to brownish patches in exposed sun-forms. Look for a) leaves nearly circular (orbicular) that are obliquely to sub-transversely inserted and widest near the leaf middle, b) leaves occasionally slightly bordered, with median leaf cells 22–32 μm wide × 30–40 μm long and marginal cells 16–24 μm wide, c) rhizoids hyaline to brownish, mostly from the stem, but a few from the leaf base, d) rhizoids mostly oriented perpendicular to the stem, and d) perianths and bracts without reddish or purplish coloration.

Separation. This species can be confused with *J. confertissima*. For separation, see discussion under that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On rocks and soil of creek banks. Elevation up to 3000 m.

Distribution. Jungermannia sphaerocarpa occurs in Europe, Asia, and North and South America. Calif. Geographic Regions: **SN**: Tuolumne Co. *Doyle 10316* (perianths) (UC).

Kurzia G. Martens 1870
(Lepidoziaceae)

This is a genus of small plants, less than 0.5 mm wide. Look for a) leaves transversely inserted on the stem, b) leaves divided nearly to base into 3–4 lobes, and c) underleaves smaller than the leaves and divided nearly to the base into 3–4 lobes.

One species in California.

Kurzia sylvatica (A. Evans) Grolle

Distinctive features. This is a very small plant and easily overlooked except when growing in mats. The brownish-green to yellowish-brown shoots are less than 0.4 mm wide. Look for a) leaves transversely inserted and usually overlapping, b) stem leaves symmetrically 3–4 lobed; the dorsal leaf

lobe equal in size to the ventral lobe, c) leaf lobes each with 2–3 superposed cells at the tip and 2–3 cells wide at the base, d) underleaves 3–4 lobed with 1–2 lobes markedly reduced in size to only one or two cells long, and e) oil-bodies usually absent from all leaf cells.

Separation. With its a) small size (less than 0.4 mm wide), b) leaves deeply divided into 3–4 lobes, c) leaf lobes uniseriate at the tip and 2–3 cells wide at the base, and underleaves lobed and smaller than the leaves, this species is easily separated from all other California liverworts. *Blepharostoma* and *Lepidozia* also have deeply divided leaves and underleaves, but *Blepharostoma* has leaf and underleaf lobes uniseriate to the base, and *Lepidozia* has leaves and underleaves divided for only 0.5 their length.

Kurzia sylvatica can be confused with *K. makinoana* (Steph.) Grolle, a species of East Asia that has not been collected in California. *Kurzia sylvatica* can be separated by a) stem leaves usually overlapping (vs. stem leaves usually somewhat remote in *K. makinoana*), b) stem leaves symmetrical, with the dorsal leaf lobe as large as the ventral leaf lobe (vs. stem leaves asymmetrical, with the dorsal leaf lobe smaller [often spinose] than the ventral leaf lobe), and c) underleaves asymmetrical with 1–2 lobes markedly reduced or aborted (vs. underleaves usually symmetrical or with only one lobe slightly smaller in size).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969.

Habitat. On shaded, moist, decaying logs and hummocks, especially in *Sphagnum* bog areas. Elevation from near sea-level to 35 m.

Distribution. Kurzia sylvatica occurs in Europe and North America. Calif. Geographic Regions: **NC**: Humboldt Co. *Doyle 10582* (UC); Mendocino Co. *Doyle 10502* (UC).

Lepidozia (Dumort.) Dumort. 1835
(Lepidoziaceae)

Plants of this genus are dark to yellowish-green and regularly 1–2 pinnately branched. Look for a) leaves 3–5-lobed, divided for 0.5 their length or less, b) underleaves 3–4-lobed, divided for less than 0.5 their length, c) oil-bodies 5–10 per leaf cell, and d) flagelliform branches present.

One species in California.

Lepidozia reptans (L.) Dumort.

Distinctive features. Mature shoots of this autoicous species are over 1 mm wide. Look for a) leaves on main stems divided up to 0.5 their length into 3–4 triangular lobes, with incurved lobe tips, b) the undivided leaf base 4–7 cells wide, c) underleaves divided up to 0.5 their length into 3–4 lobes, d) oil-bodies 10–16 per leaf cell, and d) flagelliform branches with small leaves.

Separation. This distinctive species is not easily confused with other California liverworts. See *Kurzia sylvatica* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. Shaded, damp decaying logs and stumps, and base of trees in redwood forests. Elevation from 25 to 200 m.

Distribution. Lepidozia reptans occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10369* (UC), **KR**: Del Norte Co. *Doyle 7722* (UC), **NC** Sonoma Co. *Doyle 10654* (UC).

Lophocolea (Dumort.) Dumort. 1835
(Geocalycaceae)

This genus is characterized by a) perianths terminal on the main stem or short lateral branch, b) succubous leaves, c) some or all leaves bilobed, d) underleaves bilobed, with lobes usually spreading, and e) rhizoids in clusters and restricted to the underleaf base.

Some researchers (e.g., Damsholt 2002; Schuster 1969) include *Lophocolea* within the genus *Chiloscyphus*. The traditional recognition of these two as separate genera is followed here, in part based on a) perianth terminal on the main stem or short lateral branch (vs. perianth usually terminal on a dwarf lateral branch in *Chiloscyphus*), b) leaves either bilobed throughout or at least some leaves

shallowly bilobed (vs. leaves entire or emarginate, c) underleaf lobes spreading, with rather large teeth on the lateral margins (vs. underleaves usually with somewhat parallel-sided lobes, with no or smaller, less conspicuous lateral teeth). See also Grolle (1995) for reasons to maintain *Lophocolea* and *Chiloscyphus* as separate genera.

Two species in California. This publication follows Smith (1990) and Paton (1999) in including *L. cuspidata* within the circumscription of *L. bidentata*.

Species Key

1. Leaves polymorphic, even on same shoot, entire, slightly indented or shallowly bilobed; lobe apices rounded to obtuse. . . . . **L. heterophylla**
1. Leaves clearly bilobed throughout; lobe apices acute to acuminate, terminated by 2–6 uniseriate cells. . . . . **L. bidentata**

Lophocolea bidentata (L.) Dumort.

Distinctive features. These dioicous or autoicous, whitish- to yellowish-green plants are 2–3.5 mm wide. Look for a) leaves distinctly bilobed with the lobe apices ending in 2–6 uniseriate cells, b) underleaves deeply bifid, up to 0.8 their length, and c) perianths terminal on long branches.

Separation. This species is not easily confused with other California leafy liverworts.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002 (as *L. cuspidata*); Schuster 1969; Smith 1990.

Habitat. Wet, humid habitats; usually on decaying wood and organic matter; occasionally on soil and base of trunks of living trees. Elevation from 25 to 1650 m; mostly below 850 m.

Distribution. Lophocolea bidentata occurs in Europe, Africa, Asia, and North America. Calif. Geographic Regions: **CC** San Francisco Co. *Shevock 19306* (CAS), **KR**: Trinity Co. *Doyle 4652* (UC), **NC**: Humboldt Co. *Doyle 11074* (UC), **SN**: Yuba Co. *Doyle 9585* (UC).

Lophocolea heterophylla (Schrad.) Dumort.

Distinctive features. This paroicous species usually occurs in green to yellowish-green patches. The shoots are 1–1.8 mm wide. As the name implies, this is a morphologically variable species. Look for a) leaves entire, emarginate, retuse, and/or shallowly bilobed often on the same stem (examine leaves from several areas of the population), b) underleaves bifid to below their middle, and c) perianths terminal on short branches.

Separation. The small shoot width, 1–1.8 mm, and polymorphic leaf apices separate this species from *L. bidentata*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Usually on shaded decaying logs and wood; occasionally on soil. Elevation from 20 to 1485 m; mostly below 760 m.

Distribution. Lophocolea heterophylla occurs in Europe, Africa, Asia, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10372* (UC), **CR**: Tehama Co. *Doyle 8764* (UC), **KR**: Del Norte Co. *Doyle 7748* (UC), **NC**: Humboldt Co. *Doyle 10070* (UC), **SN**: Yuba Co. *Dillingham 986* (CHSC).

Lophozia (Dumort.) Dumort. 1835
(Scapaniaceae)

This is a large, heterogeneous and often difficult genus. Species identification becomes easier with experience. As treated in this publication, plants included in *Lophozia* have a) leaves mostly obliquely inserted, b) leaves predominantly bifid (although a few species have both 2- and 3-lobed leaves on the same stem; and another species has 3–4-lobed leaves), c) leaves lacking uniseriate filaments on the ventral base, and d) gemmae angular, stellate or tetrahedral.

Because of environmentally-induced morphological variations that can blur lines among species, a combination of features often must be used to identifiy some specimens. Careful observations and

measurements on healthy, mature vegetative plants, gemmae, and perianths contribute to the security of correct species identification.

In this treatment we have not recognized *Leiocolea* as a genus distinct from *Lophozia*, as also reflected in Appendix II. However, recent studies such as that of Forrest et al. (2006) show that *Leiocolea* is phylogenetically quite removed from *Lophozia*. Four of the species treated here, namely, *L. bantriensis, L. collaris, L. gillmanii*, and *L. heterocolpos*, should perhaps be regarded as species of the genus *Leiocolea*, rather than *Lophozia*.

Eleven species plus one variety in California; one species to be described.

Species Key

1. Underleaves linear, subulate or lanceolate frequently to usually present on vegetative stems. **2.**
1. Underleaves absent, infrequent, or very small. . . . **6.**
2. Leaf lobes clearly rounded; median leaf cells isodiametric; oil-bodies 15–50 per cell. **L. obtusa**
2. Leaf lobes acute to subacute; median leaf cells slightly to much longer than wide; oil-bodies 2–10 per cell. . . . **3.**
3. Gemmae brown, on leaf margins of erect attenuated stems; median cells of mature leaves with large bulging trigones. . . . **L. heterocolpos**
3. Gemmae lacking and erect attenuated shoots not present; median leaf cells mostly with small to moderate trigones (rarely bulging). . . . **4.**
4. Paroicous; perianths usually rather long-beaked. . . . **L. gillmanii**
4. Dioicous; perianths mostly not or only short-beaked. . . . **5.**
5. Leaves clearly decurrent on the dorsal stem surface; median leaf cells 35–40 μm wide; mature shoots 3–4 mm wide. . . . **L. bantriensis**
5. Leaves not or slightly decurrent on the dorsal stem surface; median leaf cells 25–30 μm wide; mature shoots 1–2.8 mm wide. . . . **L. collaris**
6. Plants small, less than 1 mm wide; stems translucent; perianths smooth (not plicate), abruptly contracted near the apex to a distinct beak. . . . **L.**, sp. nov.
6. Plants larger, usually 1–3 mm wide; stems not translucent; perianths usually smooth below but plicate toward the mouth, not-beaked. . . . **7.**
7. Plants pale bluish-green; leaves near the shoot apex usually 3–5 lobed and often with marginal teeth; leaves rather opaque; oil-bodies 20–50 per leaf cell. . . . **8.**
7. Plants green, yellowish- to reddish-brown, or brown; leaves near the shoot apex usually 2-lobed; leaves seldom opaque; oil-bodies 4–24 per leaf cell. . . . **9.**
8. Leaves near the shoot apex usually spinose; leaf lobes broadly triangular; plants of higher elevation, usually over 2000 m. . . . **L. incisa** var. **incisa**
8. Leaves near the shoot apex not spinose; leaf lobes more narrowly triangular; plants of lower elevation, below 2000 m. . . . **L. incisa** var. **opacifolia**
9. Gemmae reddish-brown, reddish-purple or purple. . . . **10.**
9. Gemmae pale or yellow green. . . . **12.**
10. Leaf cell walls often strongly brownish; trigones of leaf cells distinct to moderately bulging; gemmae reddish-brown. . . . **L. sudetica**
10. Leaf cell walls colorless (but brownish, purplish-brown or tinged reddish in sun-exposed plants); trigones of leaf cells absent or small; gemmae vinaceous, purplish or brownish-purple. . . . **11.**
11. Paroicous; gemmae pyramidal to 5-angled; sun-exposed plants often with reddish to purplish pigmentation. . . . **L. excisa**
11. Dioicous; gemmae irregularly pyriform; sun-exposed plants often with brownish pigmentation. . . . **L. latifolia**
12. Leaves as long as or longer than wide; median leaf cells with large bulging trigones; perianth mouth with teeth 2–5 cells long. . . . **L. longiflora**
12. Leaves as wide as or wider than long; median leaf cells with concave to moderately bulging trigones; perianth mouth with teeth mostly 1–2 cells long. . . . **13.**
13. Leaves concave with incurved lobe margins and shallowly bilobed to 0.2 their length with wide, usually with crescentic sinuses. . . . **L. wenzelii**
13. Leaves flat or weakly concave, lacking incurved lobe margins and bilobed 0.2–0.3 their length with obtuse to rectangular sinuses. . . . **L. ventricosa**

Excluded. Lophozia obtusa (Lindb.) A. Evans. Based on *Howell 586* (CAS), Sutliffe (1942) reported *Lophozia (Leiocolea) obtusa* from Madera Co., Sierra Nevada. This specimen, as well as *Howell 603* (CAS) from Tulare Co., was mis-identified. No specimens of *L. obtusa* were located during this study.

It could not be confirmed for California. (Descriptions and illustrations of this species occur in Schuster 1969, Smith 1990, Paton 1999, and Damsholt 2002).

Lophozia bantriensis (Hook.) Steph.

Distinctive features. These green to reddish-brown to blackish plants are 3–4 mm wide × 2–5 cm long or longer. Look for a) underleaves lanceolate (rarely bilobed) with marginal teeth, b) leaves flaccid, often convex, divided to 0.25 their length into acute to obtuse lobes, c) median leaf cells usually thin-walled, 35–40 μm wide × 40–60 μm long with small to moderate trigones, c) oil-bodies brownish, 2–4 pale per cell, d) gemmae lacking, and e) perianths cylindrical below, abruptly contracted and often plicate near the apex to a nonbeaked or short beaked mouth (the perianth mouth often is somewhat obliquely positioned).

Separation. The consistent presence of underleaves easily separates this species from others in the genus, except for *L. collaris, L. gillmanii* and *L. heterocolpos*. See *L. heterocolpos* for separation from that species. *L. bantriensis* and *L. gillmanii* are nearly the same size, have similar leaf cell sizes and have similar underleaves. Vegetative shoots can be impossible to identify with certainty. The two species consistently differ only in sexuality—*L. bantriensis* is dioicous and *L. gillmanii* is paroicous.

Lophozia bantriensis and *L. collaris* both are dioicous and share similar leaf and underleaf form. *Lophozia bantriensis* can be separated by the larger median leaf cells 35–40 μm wide × 40–60 μm long (vs. median leaf cells 25–30 μm wide × 27–35 μm long in *L. collaris*).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On shaded moist soil near springs, marshes, stream banks, etc. Elevation from 2000 to 3200 m.

Distribution. Lophozia bantriensis occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 9763* (UC), **SN**: Mono Co. *Whittemore 1537A* (perianths) (CAS).

Lophozia collaris (Nees) Dumort.

Distinctive features. These often brownish dioicous plants are 1–2.8 mm wide and 0.8–3.5 cm long. Look for a) underleaves lanceolate, usually with 2–4 marginal filaments or slime hairs, b) median leaf cells 25–30 μm wide × 27–34 μm long, b) oil-bodies grayish, 2–5 per median leaf cell, c) gemmae lacking, and d) perianths cylindrical, abruptly contracted near the apex into a short beaked mouth, the mouth with elongate 1–2-celled teeth.

Separation. The consistent presence of underleaves separate this species from others in the genus, except for *L. bantriensis, L. gillmanii* and *L. heterocolpos*. *L. collaris* is separated from a) *L. heterocolpos* by sexuality (doicous) and absence of gemmae development (vs. paroicous and reddish-brown gemmae on specialized erect shoots), b) *L. gillmanii* by sexuality (dioicous) and smaller median leaf cell size, 25–30 μm wide (vs. paroicous and median leaf cell size 30–36 μm wide), and c) from *L. bantriensis* by smaller median leaf cell size, 25–30 μm wide (vs. median leaf cell size 35–40 μm wide).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On soil and rocks of creek banks. Elevation from 1450 to 3000 m.

Distribution. Lophozia collaris occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Nevada Co. *Whittemore 4157* (CAS).

Lophozia excisa (Dicks.) Dumort.

Distinctive features. These frequently fertile paroicous plants are variable in size and appearance. Shoots often have a pale green color, but in exposed sun-forms, the shoots often are tinged reddish or purplish. Shoots are 1.0–2.3 mm wide × 0.5–3 cm long. Look for a) leaves bilobed with broadly triangular lobes and somewhat crisped leaves near the shoot apex, b) leaves short decurrent on the dorsal stem surface, c) median leaf cells thin-walled, 20–32 μm wide × 28–40 μm long, with no or very small trigones, d) stems somewhat fleshy, e) oil-bodies 11–18 per leaf cell, f) underleaves absent (or rare), g) gemmae vinaceous to reddish-brown, bluntly angular to polyhedral with rounded thick-walled angles, and h) perianth plicate above and contracted to a non-beaked and shallowly lobed mouth, with a crenulate margin.

Separation. This species can be confused with *L. latifolia*, *L. sudetica* and *L. ventricosa*. See *L. latifolia* for separation from that species. See *L. sudetica* for separation from that species. *Lophozia excisa* can be separated from *L. ventricosa* by a) being paroicous (vs. dioicous in *L. ventricosa*), b) gemmae vinaceous to reddish-brown (vs. gemmae greenish), and c) leaves near the shoot apex somewhat crisped (vs. leaves near the shoot apex not crisped).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On organic matter. Elevation under 500 m.

Distribution. Lophozia excisa occurs in Europe, Asia, Antarctica, South Pacific, and North and South America. Calif. Geographic Regions: **NC**: Humboldt Co. *Boratynski 213* (CHSC).

Lophozia gillmanii (Austin) R. M. Schust.

Distinctive features. This paroicous species usually is pale- to deep- to blackish-green, 1–4 mm wide × 2–4 cm long. Look for perianths and determine whether the population is paroicous or dioicous. Look for a) underleaves subulate or lanceolate; search near the stem apex because they are small and often are obscured by the dense growth of rhizoids in older stem areas, b) median leaf cells usually 30–36 μm wide × 36–50 μm long, usually with coarse to strongly bulging trigones, c) gemma absent, and d) perianths cylindrical, abruptly contracted (but not plicate) near the apex into a rather elongate beaked mouth (the elongate beak can be easily broken off; observe perianths carefully to be sure that a "non-beaked" mouth is intact, rather than represented by broken perianth cells).

Separation. The consistent presence of underleaves separates this species from others in the genus, except for *L. bantriensis, L. collaris*, and *L. heterocolpos. Lophozia gillmanii* is separated from *L. heterocolpos* by a) gemma development absent (vs. gemmae on erect specialized branches in *L. heterocolpos*), and b) larger median leaf cells, 30–36 μm wide × 36–50 μm long (vs. median leaf cells 20–27 μm wide × 22–36 μm long). *Lophozia gillmanii* is separated from *L. bantriensis,* and *L. collaris* by being paroicous (vs. dioicous), and, additionally, from *L. collaris* by larger median leaf cells 30–36 μm wide (vs. median leaf cells 25–30 μm wide in *L. collaris*).

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. Soil of creek banks. Elevation above 1500 m.

Distribution. Lophozia gillmanii occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Tulare Co. *Doyle 7839* (UC).

Lophozia heterocolpos (Thed. ex. Hartm.) M. Howe

Distinctive features. These green (in shade) to warm brown (in sun) dioicous plants are 1.5–3.0 mm wide × 0.8–1.5 cm long. They have smooth cylindrical perianths that are abruptly contracted near the apex to a short beak and toothed mouth. Gemmae development is distinctive and some plants of a population usually have gemmae. Look for erect, somewhat stiff, slender gemmiferous shoots with brownish gemmae that develop mostly from brownish leaf margins. The 2-celled gemmae are smooth (not angular). Also look for a) leaf cells thin- to moderately thick-walled, usually with large convex, often confluent trigones, b) cell walls and trigones often a warm brown in color, c) median leaf cells 20–27 μm wide × 22–36 μm long, d) underleaves lanceolate (especially visible near the shoot apex), usually with cilia or slime papillae on the lateral margins, and e) 2–5 oil-bodies per leaf cell.

Separation. The consistent presence of underleaves separates this species from others in the genus, except for *L. bantriensis. L. collaris* and *L. gillmanii*. None of these three species, however, have the specialized erect gemmiferous shoots with smooth brownish gemmae that almost always are present in *L. heterocolpos*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Shaded soil in drainages, base of cliffs and near streams. Elevation from 1400 to 3350 m.

Distribution. Lophozia heterocolpos occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Siskiyou Co. *Doyle 9234* (UC), **MP**: Modoc Co. *Doyle 6685* (UC), **SN**: Alpine Co. *Doyle 8824* (UC).

Lophozia incisa (Schrad.) Dumort. subsp. **incisa**

Distinctive features. This distinctive dioicous species often can be recognized in the field with a 10 × handlens by the a) small size, 1–2 mm wide × 0.5–1 cm long, b) tendency to grow in pure dense patches, c) color opaque dark to bright green, and d) leaves near the stem apex crowded and wavy, giving a crisped appearance to the shoot. Also look for a) leaves with 2–5 asymmetric acute to apiculate lobes, b) median leaf cells nearly isodiametric, 30–35 μm wide × 30–40 μm long, the cells relatively thin-walled and without trigones, c) leaf margins often erose because of the frequent development of pale green, tetrahedral to polyhedral gemmae, d) oil-bodies 20–50 per leaf cell, e) underleaves absent on vegetative stems, f) perianth 5–6 plicate, contracted near the apex to a non-beaked lobulate mouth, the lobes with teeth 1–4 cells long, and g) spores 12–15 μm in diameter.

Separation. This species and both subspecies are not easily confused with other liverworts because of their a) size, b) opaqueness of the shoot, c) dark- to bright-green color, d) tendency to grow in dense patches, e) crisped appearance of shoot apices, f) leaves with 2–5 asymmetric acute to apiculate leaf lobes, g) oil-bodies 20–50 per leaf cell, and h) underleaves absent on vegetative stems.
See *L. incisa* subsp. *opacifolia* for separation from that subspecies.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. Usually on moist shaded decaying logs; also shaded seepages of rock outcrops and on peaty soil. Elevation from 60 to 1965 m.

Distribution. Lophozia incisa subsp. *incisa* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 11036* (UC), **NC**: Humboldt Co. *Mauer s.n.* (CHSC 20011).

Lophozia incisa (Schrad.) Dumort. subsp. **opacifolia** (Culm. ex Meyl.) R. M. Schust. and Damsh.

Distinctive features. Because of morphological variability of both subspecies of *L. incisa*, subsp. *opacifolia* often can be separated only with difficulty from subsp. *incisa.* Look for a) opaque shoots usually a bluish-green color, b) leaf lobes broadly triangular, each lobe ending in a short, blunt apical cell, c) perianth mouth entire or with a few scattered teeth, and d) spores 14.5–20 μm in diameter.

Separation. L. incisa subsp. *opacifolia* can be separated from subspecies *incisa* by a) plants bluish-green (vs. plants dark to bright green in subsp. *incisa*), b) leaf lobes broadly triangular, each ending in a blunt apical cell (vs. leaf lobes more narrowly triangular and apiculate), c) perianth mouth entire or sparsely dentate (vs. perianth mouth lobulate with teeth), and d) spores 14.5–20.0 μm in diameter (vs. spores 12–15 μm in diameter). In addition, subsp. *opacifolia* usually occurs at higher elevations (over 2000 m) than does subsp. *incisa* (under 2000 m).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Shaded moist soil and organic matter of creek banks. Elevation from 2210 to 3460 m.

Distribution. Lophozia incisa subsp. *opacifolia* occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Inyo Co. *Doyle 8836* (UC).

Lophozia latifolia R. M. Schust.

Distinctive features. These pale green (in shade) to purplish-brown (in sun) dioicous plants are 2.0–2.4 mm wide × 0.5–1.0 cm long. Look for a) gemmae purplish to deep purple and bluntly angular, in small clusters on tips of young leaves, b) leaves as wide as long with median cells 25–30 μm wide × 30–40 μm long, usually brownish walls, and small concave trigones, c) leaf lobes often with a reflexed sinus base and each lobe terminating in a single cell, d) oil-bodies 10–15 per leaf cell, e) underleaves absent, and f) perianths brownish or purplish with crenulate perianth mouths.

Separation. This species can be confused with *L. excisa. Lophozia latifolia* can be separated by a) dioicous (vs. paroicous in *L. excisa*, b) leaves usually brownish (vs. leaves usually reddish), and c) gemmae irregularly pyriform (vs. gemmae 3–5 polyhedral).

Illustrations. Schuster 1969.

Habitat. Peaty soil and rocks with moss. Elevation from 1500 to 3200 m.

Distribution. Lophozia latifolia occurs in Europe and North America. Calif. Geographic Regions: **SN**: Tulare Co. *Howell 784* (CAS).

Lophozia longiflora (Nees) Schiffn.

Distincttive features. This dioicous species appears to be restricted to decaying logs and stumps. Shoots are 1–3 mm wide × 1.5–5 cm long, pale green, but becoming reddish-brown to reddish with age and sun-exposure. Look for a) shoot apices usually slightly upturned, b) leaves bilobed about 0.2–0.3 their length, the lobes triangular, with acute apices, c) median leaf cells 20–30 μm wide × 24–35 μm long, with thin-walls and coarsely convex to confluent trigones, d) oil-bodies 5–10 per cell, the oil-bodies with numerous small spherules, e) gemmae green, polymorphic, and angular at the leaf tips, f) underleaves absent, and g) perianths often reddish, plicate above and contracted near the apex to a toothed/ciliate mouth, with teeth 1–4 cells long.

Separation. This species occasionally can be confused with *L. ventricosa. Lophozia longiflora* can be separated by the combination of a) coarsely convex to confluent trigones (vs. moderate to large trigones in *L. ventricosa*), b) oil-bodies 5–10 per cell (vs. oil-bodies 6–16 per cell), and c) perianth mouth ciliate/toothed with cells 1–4 cells long (vs. perianth mouth toothed with cells 1–2 cells long).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Damp decaying logs and stumps along streams, meadows, ponds, and lakes. Elevation from to 1500 to 3000 m.

Distribution. Lophozia longiflora occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Trinity Co. *Doyle 7539* (UC), **SN**: Plumas Co. *Dillingham 1034* (gemmae and perianths) (CHSC).

Lophozia sudetica (Nees ex Huebener) Grolle

Distinctive features. These polymorphic, deep-green to brownish, dioicous plants are 1.5–2.0 mm wide × 0.5–4.0 cm long. With age and sun-exposure, the stem ventral surface and leaf bases often are reddish. Rhizoids often are reddish at the base, but otherwise hyaline. Look for a) leaves roundish or circular, concave to canaliculate, divided to 0.2 their length into 2 very short, triangular lobes, b) leaf lobes usually incurved and separated by a broad, crescentic sinus, c) median leaf cells 18–20 μm wide × 24–25 μm long, and with thin, usually brownish walls, and small to moderately bulging trigones, d) oil-bodies spherical to elliptical, 6–9 per leaf cell, e) gemmae reddish-brown usually present, and f) perianths plicate above and contracted near the apex to a crenulate to denticulate, non-beaked mouth.

Separation. Lophozia sudetica usually can be separated from other species of the genus by the combination of a) leaves roundish, concave, and with a broad, shallow, crescent-shaped sinus, b) median leaf cells 18–20 μm × 24–25 μm, often with thin brownish walls and distinct to bulging trigones, and c) gemmae rust-brown to reddish-brown. *L. sudetica* and *L. wenzelii* have a similar leaf shape, but can be separated by a) gemmae reddish-brown (vs. gemmae light green in *L. wenzelii*), and b) smaller median leaf cells 18–20 μm × 24–25 μm (vs. median leaf cells 22–28 μm × 24–36 μm).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On rock, soil and occasionally organic substrates. Elevation from 1000 to 3500 m.

Distribution. Lophozia sudetica occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 10827* (UC), **SN**: El Dorado Co. *Doyle 11145* (UC).

Lophozia ventricosa (Dicks.) Dumort.

Distinctive features. These green to yellow-green dioicous plants are 1.0–2.2 mm wide × 1.0–2.5 cm long. Stems and leaf bases occasionally are reddish in sunny habitats. Look for a) leaves divided to 0.3 their length into 2 subequal lobes with somewhat acute apices, b) median leaf cells thin-walled, 20–30 μm wide × 22–38 μm long with distinct, but never bulging trigones, c) leaves generally 0.9–1.3 times as long as wide, d) gemmae green, and e) oil-bodies usually 6–16 per cell, each oil-body consisting of several minute spherules.

Separation. Thalli of *L. ventricosa* are morphologically variable. See *L. wenzelii* for separation from that species. See *L. excise* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1969; Smith 1990.

Habitat. On soil, rocks and decaying wood of stream banks and rock overhangs. Elevation from 1300 to 3600 m.

Distribution. Lophozia ventricosa occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: El Dorado Co. *Whittemore 4004* (CAS).

Lophozia wenzelii (Nees) Steph.

Distinctive features. Shoots of this dioicous, light- to yellow-green species, often tinged brownish to reddish-brown, are 1.2–2.0 mm wide × 1.0–5.5 cm long. Look for a) broad, concave leaves bilobed up to 0.2 their length, b) leaf lobes usually incurved, especially near the shoot apex, and the sinus often is shallow and crescentic, c) median leaf cells thin-walled 22–28 μm wide × 24–36 μm long, usually with small to moderate concave-sided trigones, d) oil-bodies spherical to ellipsoidal, mostly 4–10 per leaf cell, e) gemmae light green (rarely pinkish), quadrate to weakly polygonal, and f) perianths plicate, contracted near the apex to a lobulate, denticulate mouth.

Separation. Thalli of both *L. wenzelii* and *L. ventricosa* are morphologically variable and both have yellow-green gemmae; the two species occasionally can be difficult to separate. *L. wenzelii* usually can be separated by broadly orbicular, saucer-shaped leaves with incurved lateral margins and leaf lobes (vs. absence of clearly concave leaves with incurved margins and lobes in *L. ventricosa*). *Lophozia wenzelii* and *L. sudetica* have similar leaf shape; see that species for Separation

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Usually exposed wet to boggy habitats; along mountain streams and streamlets in meadows. Elevation from 1100 to 3550 m.

Distribution. Lophozia wenzelii occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Lassen Co. *Doyle 9802* (UC).

Marsupella Dumort. 1822
(Gymnomitriaceae)

This genus is distinguished by a) transversely inserted leaves in two rows b) leaves usually spreading away from stem—the stem is visible, c) cells of leaf margin living at leaf maturity, d) leaves bilobed up to 1/5 their length, the lobe margins smooth, e) leaf cells often with 2–3 large oil-bodies, f) perianths with a crenulate mouth and shorter than the surrounding female bracts, g) a sporophyte that develops within an erect tubular perigynium, and h) spores mostly 7–13 μm.

Marsupella can be confused with *Gymnomitrion*, from which it can be separated by a) marginal cells of mature leaves living (vs. marginal cells of mature leaves usually dead and whitish), and b) perianth short, but present (vs. perianth lacking or vestigial).

Five species reported in California.

Species Key

1. Leaves bilobed to 0.25 their length with the leaf sinus usually rounded to crescentic; leaf lobes obtuse to slightly pointed; dorsal leaf margins often recurved. . . . . **M. emarginata**
1. Leaves bilobed 0.25 to 0.5 their length with the leaf sinus acute to right angled; leaf lobes acute to broadly rounded; dorsal leaf margins not recurved. . . . . **2.**
2. Trigones in the leaf cells very small or absent. . . . . **M. bolanderi**
2. Trigones in the leaf cells distinct to bulging. . . . . **3.**
3. Leaf lobes broadly rounded to obtuse; dioicous. . . . . **M. sphacelata**
3. Leaf lobes acute; paroicous. . . . . **4.**
4. Plants small, less than 0.4 mm wide; leaf lobes erect. . . . . **M. sprucei**
4. Plants larger, 0.4–1.5 mm wide; leaf lobes somewhat lax. . . . . **M. sparsifolia**

Marsupella bolanderi (Austin) Underw.

Distinctive features. This small dioicous species is up to 0.2 mm wide and generally less than 6 mm long. Look for a) shoots reddish-green, reddish-brown or reddish-black, b) leaves bilobed up to 0.3 their length, the lobes acute to obtuse, c) leaf cell walls usually reddish or vinaceous, d) median leaf

cells 16–36 μm, with thin to thick walls and no or small trigones, e) cells of leaf margins 14–25 μm wide, margins often crenulate because of slightly bulging outer walls, and f) female bracts usually bordered with radially elongate marginal cells.

Separation. This species can be confused with small forms of *M. emarginata*. It can be separated by leaf cell walls with no or small trigones (vs. leaf cell walls with conspicuous large trigones in *M. emarginata*).

Illustrations. Frye and Clark 1943; Howe 1899.

Habitat. Moist shaded soil and surface of sandstone boulders, open areas, and under shrubs and trees on hillsides. Elevation from 65 to 850 m.

Distribution. Marsupella bolanderi is endemic to the western United States, from Washington to California. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8114* (perianths) (UC), **CR**: Shasta Co. *Kellman 2799* (CAS), **KR**: Siskiyou Co. *Howell 458* (CAS), **NC**: Mendocino Co. *Doyle 10419* (UC), **SC**: Santa Barbara Co.: *Doyle 4196* (perianths) (UC).

Marsupella emarginata (Ehrh.) Dumort.

Distinctive features. This dioicous species usually occurs in dull green, brown, reddish-brown, or blackish patches. Shoots usually are 0.5–2.5 mm wide × 1.0–5.0 cm long. Look for a) dorsal leaf margins reflexed toward the base, b) leaves bilobed to 0.25 their length, with open sinuses, c) leaf lobes triangular, clearly wider than long, d) leaf lobe apices obtuse to slightly pointed, usually standing somewhat stiffly away from the stem, e) median leaf cells 13–25 μm wide, with slightly thickened walls and bulging, often confluent trigones, and f) marginal leaf cells 13–20 μm wide.

Separation. This species and *M. sphacelata* exhibit great morphological variation and often can be difficult to separate. *Marsupella emarginata* usually can be separated by a) leaves bilobed 0.2–0.25 their length (vs. leaves bilobed 0.3–0.6 their length in *M. sphacelata*, b) leaf dorsal margins reflexed toward the base (vs. leaf margins not recurved toward the base), c) leaf lobes clearly wider than long (vs. leaf lobes as long as or longer than wide), d) leaf lobes broadly triangular (vs. leaf lobes usually broadly rounded), and e) sinuses open (vs. sinuses acute and often nearly closed at the base). Perianth details are not helpful in separation of these two species. See *M. bolanderi* for separation from small shoots of *M. emarginata*.

Illustrations. Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1974; Smith 1990.

Habitat. On shaded, damp soil and rock of river banks, ravines and cliffs; occasionally on submerged rocks in creeks. Elevation from 200 to 2700 m.

Distribution. Marsupella emarginata occurs in Europe, Asia. and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Mueller 6895* (ABSH), **KR**: Del Norte Co. *Doyle 11029* (UC), **NC**: Humboldt Co. *Doyle 2188* (UC), **SN**: Fresno Co. *Shevock 22862* (CAS).

Marsupella sparsifolia (Lindb.) Dumort.

Distinctive features. These paroicous, brownish-green to purplish-black plants are 0.4–1.5 mm wide × 3 cm long. Look for a) leaves transversely inserted and somewhat distant on older stem areas, b) leaves bilobed to 0.25–3.5 their length, with open sinuses, c) leaf lobes broadly ovate to acute, d) median leaf cells 15–24 μm wide × 18–24 μm long, with large bulging trigones, d) marginal leaf cells 12–15 μm wide, and e) perianths with subtending antheridial bracts.

Separation. This paroicous species should not be confused with other California species of the genus.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. On damp to wet soil and rocks near streams and seepages in late snowmelt areas. Elevation above 2000 m.

Distribution. Marsupella sparsifolia occurs in Europe, Asia, South Africa, New Zealand, and North America. Calif. Geographic Regions: **SN**: Madera Co. *Howell 570* (as *M. sphacelata*) (TENN) (reported by Hong 1982; this specimen has not been examined).

Marsupella sphacelata (Gieseke ex Lindenb.) Dumort.

Distinctive features. Terrestrial populations are rigid, blackish-brown, and densely-leaved with leaf lobes tightly overlapping (the stem is not visible). Aquatic populations are lax, dull green to brownish, with leaves somewhat distantly spaced on the stem (the stem is visible). Look for a) leaves bilobed 0.25–0.6 their length, sinuses acute and often closed at the base, and with flat (not recurved) basal margins, b) leaf lobes as long as or longer than wide with broadly rounded apices, and c) median leaf cells 15–25 μm wide × 20–31 μm long, with distinct trigones.

Separation. See *M. emarginata* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Higher elevations; damp soil and rocks of creek and lake banks, and drainage channels where it often is periodically submerged in flowing water. Elevation from 1210 to 3600 m.

Distribution. Marsupella sphacelata occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Lassen Co.: *Doyle 6778* (UC), **KR**: Trinity Co. *Doyle 9351* (UC), **SN**: El Dorado Co. *Doyle 8797* (UC).

Marsupella sprucei (Limpr.) Bernet

Distinctive features. These easily overlooked small paroicous plants are 0.2–0.4 mm wide × 0.2–0.5 cm long. Shoots occur in small, dense, dark green, brownish to blackish populations, usually arising from stoloniferous branches. Look for a) leaves bilobed 0.25–0.35 their length with acute to rectangular sinuses, b) leaf margins flat (not reflexed) toward the base, c) leaf lobes triangular with apices acute to obtuse and often ending in 2 superposed cells, d) marginal leaf cells 8–18 μm wide, e) median leaf cells 12–18 μm wide × 15–26 μm long, with slightly thickened walls and mostly bulging trigones.

Separation. This small paroicous species is not easily confused with other California species of the genus.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Soil on and around rocks of higher elevations. Elevation above 1750 m.

Distribution. Marsupella sprucei occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Showers 2613B* (SFSU) (reported by Hong 1982; this specimen was not available for examination).

Mylia Gray 1821
(Jungermanniaceae)

Plants of this dioicous genus usually occur in green to brown mats. Look for a) succubous leaves with thin walls and large, bulging trigones. b) underleaves always present, and c) rhizoids often in dense tufts, especially from leaf and underleaf bases.

One species in California.

Mylia anomala (Hook.) Gray

Distinctive features. These are relatively large dioicous plants with shoots 2.5–3.0 mm wide. Look for a) succubous leaves with large median leaf cells 45–50 μm wide × 50–60 μm long, b) leaf cells thin-walled with large bulging trigones, c) oil-bodies 5–18 per mid-leaf cell, d) underleaves subulate to lanceolate (often obscured by dense rhizoid growth), e) rhizoid development mostly confined to underleaf and leaf bases, f) gemmae green, 2-celled, on the margins of lanceolate leaves, and g) perianths laterally compressed with a smooth to crenulate mouth.

Separation. With the combination of a) large size, b) large median leaf cells with large and bulging trigones, c) underleaves present, and d) laterally compressed perianths, *M. anomala* should not be confused with other California liverworts.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. Coastal; usually associated with *Sphagnum*. Elevation from near sea-level to 260 m.

Distribution. Mylia anomala occurs in Europe, Asia, and North America. Calif. Geographic Regions: **NC**: Humboldt Co. *Doyle 1332* (UC).

Nardia Gray 1821
(Jungermanniaceae)

Species of *Nardia* often occur in green to yellow-brown to reddish-brown patches. Leaf apices are rounded, emarginate or bilobed. Look for a) underleaves present, but often obscured by dense rhizoid growth or are small or ephemeral (search near shoot apices for underleaves), b) numerous rhizoids developing from both stem and leaf bases, and c) perianths shorter than and obscured by the female bracts.

Nardia can be confused with *Jungermannia* when the underleaves are missed. In *Jungermannia*, look for perianths short or long emergent beyond the female bracts (vs. perianths not emergent in *Nardia*).

Two species in California.

Species Key

1. Leaves on vegetative shoots entire to emarginate. . . . . **N. geoscyphus**
1. Leaves on vegetative shoots distinctly bilobed. . . . . **N. insecta**

Excluded. Nardia scalaris (Schrad.) Gray. Based on *Howell 388* (CAS), Sutliffe (1947) reported this species from Big Lagoon, Humboldt Co. However, *Howell 388* was mis-identified: it is *Gyrothyra underwoodiana*. No herbarium specimens of *N. scalaris* were found during this study. This species could not be confirmed for California.

Nardia geoscyphus (De Not.) Lindb.

Distinctive features. These paroicous plants are 0.8–1.5 mm wide and usually occur in somewhat opaque green, brown or reddish-brown patches. Look for a) leaves circular to reniform with rounded to emarginate apices (**note:** leaves on reproductive regions of the shoots are bilobed 0.1–0.2 their length, b) underleaves small, lanceolate to triangular, usually found near the stem apex, c) rhizoids hyaline, brownish or reddish, and d) oil-bodies grayish, granular, 2–3 per leaf cell.

Separation. Both *N. geoscyphus* and *N. insecta* are paroicous, have grayish granular oil-bodies, and have green to reddish to brownish coloration. *Nardia geoscyphus* can be separated by leaf apices rounded or emarginate on non-reproductive stem regions, and shallowly bilobed only on reproductive stem regions (vs. leaf apices uniformly bilobed 0.25–0.5 their length on both vegetative and reproductive regions of the stem in *N. insecta*).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On mineral soil of creek banks and drainages, and peaty soil of higher elevations. Elevation from 1400 to 2000 m.

Distribution. Nardia geoscyphus occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Tuolumne Co. *Doyle 11213* (UC).

Nardia insecta Lindb.

Distinctive features. This paroicous species usually occurs in grayish-green to reddish-brown patches. Look for a) leaves uniformly and deeply bilobed 0.25–0.5 their length on both vegetative and reproductive stem regions; b) leaf cells thin-walled, usually with bulging trigones, c) underleaves distinct, lanceolate to triangular and usually at nearly right angles to the stem (and often more easily seen when stems are viewed from the side with the compound microscope), d) rhizoids hyaline to reddish, and d) oil-bodies grayish, granular, 2–3 (up to 5) per leaf cell.

Separation. See *N. geoscyphus* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1969; Smith 1990.

Habitat. On soil of creek banks and drainages. Elevation 775 to 2000 m.

Distribution. Nardia insecta occurs in Europe and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Showers 3693* (SFSU), **SN**: Alpine Co. *Doyle 10803* (UC).

Plagiochila (Dumort.) Dumort. 1835
(Plagiochilaceae)

This is a genus of large, usually deep green, dioicous plants with succubous, obliquely inserted and long decurrent leaves. The adaxial leaf surface is concave near the leaf base and the dorsal leaf margin often is recurved. Gemmae are lacking and rhizoids generally are absent. Small inconspicuous underleaves usually are visible near the shoot apex.

A single species in California.

Plagiochila porelloides (Torr. ex Nees) Lindenb.

Plagiochila porelloides is a morphologically diverse species. Earlier, this species often was considered to be either a synonym (Howe 1899; Frye and Clark 1945), or a subspecies of *P. asplenioides* (Schuster 1980). Hong (1992) reported both *P. porelloides* and *P. satoi* S. Hatt. for California. However, *P. satoi* now is considered to be a synonym of the morphologically variable *P. porelloides* (So and Grolle 2000).

Distinctive features. These are rather large, green to dark green plants 2.0–5.6 mm wide × 1.5–7.0 cm long. Look for a) leaves ovate with the dorsal margin usually entire, recurved and markedly decurrent, b) ventral leaf margins usually dentate (but occasionally entire) with teeth usually 1–2 cells long and 1–2 cells wide at their base, and c) perianths laterally compressed and elongate with a smooth to ciliate-dentate mouth.

Separation. This distinctive plant is not easily confused with other species of leafy liverworts.

Illustrations. Damsholt 2002; Schofield 2002; Schuster 1980.

Habitat. Soil and rock faces of cliffs; damp soil of banks; decayed logs; trunks of trees; occasionally in seepages and periodically submerged at edges of creeks. Elevation from 50 to 1800 m.

Distribution. Plagiochila porelloides occurs in Europe and North America. Calif. Geographic Regions: **KR**: Del Norte Co. *Doyle 7725* (UC), **NC**: Humboldt Co. *Norris 22359* (UC), **SC**: Los Angeles Co. *Kingman 808* (ABSH).

Pleurocladula Grolle 1979
(Cephaloziaceae)

Species of this genus have a) epidermal cells large, thin-walled and colorless (hyalodermis) surrounding smaller interior cells viewed in stem cross-section, b) bifid leaves nearly transversely inserted, and c) large underleaves often only slightly smaller than the leaves. The presence of distinct underleaves easily separates this genus from somewhat similar appearing species of *Cephalozia* (e.g., *C. pleniceps*).

Excluded. Pleurocladula albescens (Hook.) Grolle. Based on *Howell 510* and *Howell 515*, Sutliffe (1941) reported this species from California. During this study, examination of *Howell 515* (CAS), from Ouzel Creek, Tulare Co., Sierra Nevada, found only *Anthelia juratzkana* and very poorly preserved plants of *Lophozia* sp.; no plants with a hyalodermis or distinct underleaves were found. Unfortunately, *Howell 510*, from Reflection Lake, Tulare Co., Sierra Nevada, was not located. Hong (1988b) reported *P. albescens* from California, but no collection was cited and he did not enter it on his distribution map. *Pleurocladula albescens* occurs in Europe, Asia, and North America. It is rare in Oregon. Although this genus could not be confirmed for California, the above description of the genus should aid in its identification. Look for it in margins of wet meadows, seepages and drainages in Arctic/Alpine elevations. See Damsholt (2002), Paton (1999), or Schofield (2002) for Illustrations

Porella L. 1753
(Porellaceae)

Once seen, this distinctive genus is easily recognized in the field. Plants usually grow as large mats on tree trunks and shaded rock outcrops, less commonly on soil. Look for a) leaves complicate-bilobed with incubous dorsal lobes, b) ventral lobes much smaller than the dorsal, but never forming water-sacs as in *Frullania*, c) underleaves not lobed, and d) perianths mostly dorsiventrally flattened, especially above the middle.

The genus is dioicous and male and female plants usually occur in separate mats. Search carefully for both female plants with perianths and male plants with antheridial branches. Not only are details of the perianth mouth helpful in species identification, but collection of both female and male plants result in complete species documentation.

Although the genus is easy to identify, species determination of vegetative plants can be difficult because of morphological variability. There are two iodine tests that can be used to separate the polymorphic *P. cordaeana* from the other California species of the genus. (1) Piippo and Norris (1996) described the use of iodine potassium-iodide, IKI. (IKI might be obtained from the Botany or Biology Department of a nearby university or college. **USE WITH CARE—IKI IS A POISON**). (2) David Wagner (personal communication) recommended the use of emergency drinking water germicidal tablets (e.g., Coghlan's or Potable Agua). A concentrated solution (2–3 tablets dissolved in 10 cc of water) works quickly and uniformly. A neutralizing agent can be purchased with Potable Agua.

For examination, remove with tweezers one or two (fresh or dry) mature leaves from a stem and put the leaves in a small drop of IKI or germicidal solution on a microscope slide. Leaves of *P. cordaeana* quickly darken and become nearly black as observed with the high power of the dissection microscope. Add a coverslip for a detailed examination of leaf cell contents under the compound microscope. A region of the leaf cells of *P. cordaeana* will have a violet coloration with IKI or a bluish coloration with the germicidal tablet solution. Leaf cell contents of the other California species lack this violet or blue coloration.

The intensity of the coloration is variable, apparently depending upon the physiological condition of the plant at the time of collection, rather than the age of the herbarium specimen. For example, *Howe s.n.* (May 7, 1892) (ABSH) of *P. cordaeana* from Marin County still gave an intense violet color reaction with IKI. Cells of young leaves near the shoot apex often stain less intensely, and some not at all.

Four species in California.

Species Key

In the following key, start at 1. when IKI or germicidal solution is used; start at 2. when not used.

1. Leaf cell contents darken and have a violet or blue coloration. . . . . **P. cordaeana**
1. Leaf cell contents do not darken and do not have a violet or blue coloration. . . . . **2.**
2. Cells of mature leaves with large and bulging trigones; underleaves about the same width as the ventral lobes; perianth mouth wide and usually entire when mature, but short-ciliated or toothed when young; perianth apex usually transversely recurved, giving the perianth a truncated appearance. . . . . **P. navicularis**
2. Cells of mature leaves with minute, small or moderate trigones; underleaves only slightly to much wider than ventral lobes; perianth mouth wide and coarsely dentate, or narrow and smooth or ciliated; perianth apex obliquely or not recurved. . . . . **3.**
3. Ventral lobes not or only short decurrent; perianth mouth wide and coarsely toothed; taste peppery in fresh material. . . . . **P. roellii**
3. Ventral lobes long-decurrent; perianth mouth narrow and smooth or ciliated; taste aromatic, not peppery, in fresh material. . . . . **4.**
4. Underleaves on mature stems usually distant, apices rounded; cells of dorsal lobes with small to medium trigones; perianth mouth usually smooth. . . . . **P. cordaeana**
4. Underleaves on mature stems usually overlapping, apices acute; cells of dorsal lobes usually with minute trigones; perianth mouth ciliated. . . . . **P. bolanderi**

Excluded. Porella platyphylla (L.) Pfeiff. The reports by Clark and Frye (1936), Frye and Clark (1946) and Hong (1983) of this species in California were based on the *Frye 2121*, March 27, 1934 collection from a rock wall in a gorge near Salyer, Trinity County (WTU). In the WTU specimen packet, David Wagner had placed an annotation label, dated April 1990, with the corrected identification of *P. roellii* Steph. *Frye 2121* was examined during this study and was found to have perianths typical of *P. roellii*, confirming Wagner's identification. Moreover, all herbarium specimens from California that had been labeled *P. platyphylla* and examined in this study were mis-identified. *Porella platyphylla* could not be confirmed for California.

Porella bolanderi (Austin) Pearson

Distinctive features. This species is most easily identified by perianth characteristics. Look for a) perianth ventral surface weakly to strongly 2–5 plicate, b) perianth usually narrowed at the apex to

0.3 or less of the width of the perianth, and c) a ciliate perianth mouth with uniseriate filaments 2–6 cells in length.

Vegetative plants are variable in morphology. The plants are irregularly branched, once to twice pinnate, with shoots 2–4 mm wide and up to 6 cm long. The dorsal lobes are dark to olive-green and not glossy. In drier habitats, the dorsal lobes are closely to tightly imbricate, and the margins often are slightly upturned. In more humid habitats and young plants, the lobes are more remote and flat. Margins of the dorsal lobes of plants from drier habitats often have several rows of dead, colorless cells, which contrast sharply with the living cells. Look for a) one or more teeth often on the basal margin of the dorsal lobe, b) underleaves long decurrent and, on mature branches, usually overlapping, c) underleaf tip recurved and usually acute, and d) underleaf margins toothed to laciniate toward the base.

Caution. The plants often occur in large mats. Growing through the mats usually are narrower shoots that have dorsal, ventral and underleaf morphologies similar to those of *P. cordaeana.* However, these shoots usually can be traced back as branches from mature stems of *P. bolanderi.* Occasionally, some of the first–formed underleaves on these narrow shoots have bifid tips, mimicking the underleaves of *Frullania.*

Separation. New growth, young plants, plants growing in humid or wet habitats, and narrow branches growing through mats can be confused with the highly polymorphic *P. cordaeana.* The IKI or germicidal solution test is the quickest and most accurate method to separate these two species; the cell contents of *P. bolanderi* do not react with IKI or germicidal solution (vs. appearance of a violet or blue color in *P. cordaeana*). *Porella bolanderi* also can be separated by the a) perianth distinctly plicate, especially ventrally (vs. perianth not plicate in *P. cordaeana*) and b) perianth mouth ciliate (vs. perianth mouth smooth or toothed).

Illustrations. Frye and Clark 1946; Howe 1899, Piippo and Norris 1996.

Habitat. On trunks of angiosperms, shaded boulders and rock outcrops; occasionally on shaded soil of canyon walls. Elevation from near sea-level to 1500 m, but mostly below 800 m.

Distribution. Porella bolanderi is endemic to western North America. Calif. Geographic Regions: **CC**: Contra Costa Co. *Shevock 24516* (CAS), **CR**: Shasta Co. *Doyle 2904* (UC), **NC**: Humboldt Co. *Norris 84073* (UC), **SC**: Ventura Co. *Sagar 957* (SFV), **SN**: Tulare Co. *Doyle 6977* (UC).

Porella cordaeana (Huebener) Moore

Distinctive characteristics. This species is irregularly 1–2 pinnate, with the side branches narrower than the main branch; the main branches are 2.5–4.0 mm wide and up to 10 cm long. This is a highly polymorphic species. In wet or humid habitats, the plants usually are dark-green and not, or only a little, glossy; in drier or more exposed habitats, the plants usually are olive- to brownish-green to green, and somewhat glossy. The form of the ventral lobes and underleaves also is variable in different habitats. First, look for a positive response to IKI or germicidal solution. Also look for a) underleaves long decurrent with rounded apices, and not or only little overlapping on mature parts of main branches (however, on young or rapidly growing branches, the underleaves often overlap and the apices are somewhat acute), b) a perianth smooth, not plicate (occasionally there is a single central low longitudinal fold on the ventral surface of young perianths, which disappears with sporophyte development), c) a perianth that usually is obliquely recurved from below the middle to the apex, and d) a narrow perianth mouth less than 0.3 the width of the perianth, generally smooth, but occasionally sinuate with teeth on the sinuations.

Separation. Porella cordaeana can be difficult to separate from *P. bolanderi,* because of the morphological variability of the vegetative shoots of these two species. A positive IKI or germicidal solution test most easily separates *P. cordaeana* from *P. bolanderi* (and from other California species of *Porella*). In the absence of IKI or germicidal solution, see *P. bolanderi* for separation of that species.

Illustrations. Frye and Clark 1946; Piippo and Norris 1996.

Habitat. Both dry and humid environments; on boulders, rock outcrops and tree trunks; rarely on soil. Elevation from near sea-level to 2750 m, but more common below 2000 m.

Distribution. Porella cordaeana occurs in Europe, Asia, and North Africa, and apparently is restricted to the western part of North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 10894* (UC), **CR**: Tehama Co. *Doyle 8632* (UC), **KR** Siskiyou Co. *Lenz 1059* (UC), **MP**: Modoc Co.

Doyle 6688 (UC), **NC** Marin Co. *Howe s.n.* (May 7, 1892) (ABSH), **SC**: Los Angeles Co. *Smith 2* (CHSC), **SN**: Amador Co. *Norris 82870* (UC).

Porella navicularis (Lehm. and Lindenb.) Lindb.

Distinctive features. These are rather shiny, dark green, yellowish-brown or yellowish-green plants that usually occur in large mats. The shoots are more-or-less regularly bipinnate; the main branches 2.5–4.5 mm wide and up to 12 cm long. Look for a) median cells of the dorsal and ventral lobes (and cells of underleaves and perianths) with large bulging trigones on mature parts of the shoots, b) ventral lobes and underleaves of similar size, c) on female plants, a few small leaves on the short stem between the main branch and the perianth, d) a perianth flattened and non-plicate, only slightly narrowed at the apex, usually transversely recurved near the apex, giving the perianth a truncate appearance, e) a wide perianth mouth that usually is entire when mature, but often short-ciliate or toothed when young.

Separation. With a) large, bulging trigones in cells of the dorsal and ventral lobes, underleaves, and perianths, b) underleaves and ventral lobes of nearly the same width, and c) perianth apex recurved, *P. navicularis* is not easily confused with other California species of *Porella*.

Illustrations. Frye and Clark 1946; Howe 1899, Piippo and Norris 1996; Schofield 2002.

Habitat. Commonly on trunks and branches of angiosperms, especially *Quercus*; also on logs and rocks; less commonly on conifers. Elevation from near sea-level to 2400 m, but most often below 800 m.

Distribution. Porella navicularis is endemic to western North America and is especially common along the Pacific Coast from southeast Alaska to California. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10377* (UC), **KR**: Siskiyou Co. *Norris 67798* (UC), **NC**: Mendocino Co. *Doyle 9068* (UC).

Porella roellii Steph.

Distinctive features. The distinctive peppery taste of living plants is the easiest way to identify this species in the field. These are shiny, dark green to yellowish-brown plants. The shoots are 1–2 times pinnately branched; main branches are 1.5–2.2 mm wide and up to 8 cm long. Plants with perianths are easily identified. Look for a) a non-plicate perianth only occasionally slightly obliquely recurved, b) a perianth mouth wide (but usually slightly contracted), sinuate, with coarse teeth (1–4 cells long and 1–4 cells wide at the base) on the sinuations, and c) leaves 2–6 on the short stem between the perianth and the main branch.

On vegetative plants, look for a) trigones small to medium (occasionally large in very old leaf cells) in cells of the dorsal leaf lobe, and b) ventral lobes more-or-less parallel to the stem, especially on young branches, generally narrower than the underleaves, and not, or only little, decurrent, narrowed to an often obtuse or acute apex, and broadly rounded or with a blunt spur at the base.

Separation. The peppery taste is the easiest field-test to separate this plant from the other California species of the genus. Vegetative plants of herbarium specimens can be confused with *P. cordaeana*, but can be separated by a) lack of a violet or blue reaction with **IKI** or germicidal solution (vs. a violet or blue reaction in *P. cordaeana*), b) the ventral lobe little decurrent (vs. ventral lobe long decurrent), c) underleaves on mature stems clearly overlap (vs. underleaves on mature stems with little or no overlap), d) short branch between the perianth and the main branch with 2–6 normal leaves (vs. normal leaves on the short branch absent), and e) a perianth with a wide mouth (vs. a perianth narrowed toward the apex, with a narrow mouth).

Shoots of both *P. roellii* and *P. navicularis* have a shiny appearance and can be of similar color. However, *P. roellii* has a) mature leaf cells without large bulging trigones (vs. mature leaf cells with large bulging trigones in *P. navicularis*) and b) perianth apex only occasionally obliquely recurved (vs. perianth apex usually transversely recurved).

Illustrations. Frye and Clark 1946; Howe 1899, Piippo and Norris 1996.

Habitat. On rocks, boulders and tree trunks (especially angiosperms); less often on logs and soil; usually occurs in humid habitats, e.g., near streams in canyon bottoms and outcrops in narrow ravines. Elevation from near sea-level to 1800 m; more common below 1200 m.

Distribution. Porella roellii is restricted to western North America, from Alaska to California. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8886* (UC), **KR**: Trinity Co. *Doyle 7532* (UC), **NC**: Sonoma Co. *Mason 2519* (perianths) (UC); **SN**: Plumas Co. *Norris 52647* (UC).

Ptilidium Nees 1833
(Ptilidiaceae)

Plants of this brownish to reddish-brown genus occur in large or small patches. The incubous leaves are deeply bilobed, with each lobe divided 1–3 times. Slender cilia occur at the lobe tips and margins. The large underleaves also are bilobed and have ciliate margins.

One species in California.

Ptilidium californicum (Austin) Pearson

Distinctive features. These yellowish-brown to reddish-brown plants often grow in dense mats, but easily can be overlooked when small populations grow intermixed with moss. Look for a) leaves 3–4 lobed with filamentous lobe apices and margins, decurrent on the dorsal stem surface, b) leaf cells medium-thick to thick-walled with bulging trigones, c) underleaves about 0.5 the size of the leaves, with ciliate margins, and d) perianths plicate and narrowed to a ciliate mouth.

Separation. A very distinctive plant; when once seen it is difficult to confuse with any other California liverwort.

Illustrations. Frye and Clark 1943; Howe 1899; Schofield 2002.

Habitat. Usually on trunks of *Abies concolor, A. magnifica*, and *Pseudotsuga menziesii*; less frequently on snags and decaying conifer logs. Elevation from 420 to 1878 m.

Distribution. Ptilidium californicum is endemic to coastal western North America, from Alaska to California. Calif. Geographic Regions: **CR**: Shasta Co. *Williams 72799b* (UC), **KR**: Siskiyou Co. *Ziegler JRZ005* (UC), **NC**: Humboldt Co. *Norris 57738* (NY).

Radula Dumort. 1833
(Radulaceae)

Plants of this genus have complicate-bilobed leaves with the dorsal lobe larger than the ventral lobe. Look for a) ventral lobes usually flattened and appressed to the dorsal lobe, b) underleaves absent, c) oil-bodies large, brownish, plate-like, 1 (occasionally to 3) per dorsal lobe cell, d) rhizoids restricted to a small area at the base of the ventral leaf lobe, and e) truncate perianth mouth.

Radula is similar to *Frullania* and *Porella* in its complicate-bilobed leaves with the dorsal lobe larger than the ventral lobe. It is easily separated from both genera by a) underleaves absent, b) rhizoids developing at the base of the ventral lobe, and c) oil-bodies large, plate-like, usually only 1 per mature dorsal lobe cell.

Two species in California.

Species Key

1. Dorsal lobe inner margin adnate to the stem, the apical region not extending across the stem; cells in the middle of the dorsal lobe 9–18 μm long; gemmae absent; rhizoids scarce to absent; large oil-body nearly filling the cell lumen; dioicous. . . . . **R. bolanderi**
1. Dorsal lobe inner margin not adnate to stem, the apical region usually extending across the stem; cells in the middle of the dorsal lobe 15–30 μm long; gemmae occasionally present on leaf margins; rhizoids abundant; oil-body filling only about 0.5 of cell lumen; monoicous. . . . . **R. complanata**

Radula bolanderi Gottsche

Distinctive features. These dioicous plants usually occur in light- to gray-green patches. Look for a) the dorsal leaf lobe inner margin adnate to the stem, the apical region not extending beyond the stem, b) median dorsal lobe cells 9–18 μm long, c) mature dorsal lobe cells usually with 1 large oil-body nearly filling the cell lumen, d) rhizoids infrequent, e) gemmae absent, f) male plants with conspicuous "catkin-like" antheridial branches, g) female plants with perianths terminal on main branches, and h) spores 38–58 μm in diameter.

Separation. Radula bolanderi is readily separated from *R. complanata* by a) the dorsal lobe inner margin adnate to the stem (vs. the dorsal lobe inner margin not adnate to the stem in *R. complanata*), b) a single large oil-body nearly filling the cell lumen (vs. the single oil-body filling about 0.5 the cell lumen), c) rhizoids infrequent (vs. rhizoids abundant), d) gemmae absent (vs. gemmae frequently present), e) dioicous (vs. usually paroicous), and f) spores 38–58 μm (vs. spores 26–40 μm).

Illustrations. Clark and Frye 1928.

Habitat. Most commonly on trunks and branches of angiosperms, but occasionally on young *Pseudotsuga, Sequoia,* and *Calocedrus*; less frequently on soil, logs and boulders. Elevation from 15 to 1200 m; mostly below 400 m.

Distribution. Radula bolanderi is endemic to western North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 8919* (UC), **KR**: Trinity Co. *Norris 77258* (UC), **NC**: Marin Co. *Howe 3* (as *R. spicata)* (male and female) (NY).

Radula complanata (L.) Dumort.

Distinctive features. Plants of this paroicous species usually occur in yellowish- to dark-green patches. Look for a) the dorsal lobe inner margin not adnate to the stem, the apical region extending beyond the stem, b) median dorsal lobe cells 15–30 μm long, c) mature dorsal lobe cells with 1 oil-body filling about 0.5 the cell lumen, d) rhizoids frequent, e) gemmae occasionally present on the leaf margins, f) perianths terminal on short or main branches, g) male bracts conspicuous below the perianths, and h) spores 26–40 μm in diameter.

Separation. See *R. bolanderi* for separation from that species.

Illustrations. Frye and Clark 1946; Damsholt 2002; Paton 1999; Schofield 2002; Schuster 1980.

Habitat. Usually on trunks and branches of angiosperms; also on *Taxus* and young *Pseudotsuga*; less commonly on rocks and boulders; Elevation from near sea-level to 1850 m.

Distribution. Radula complanata occurs in Europe, Asia, North Africa, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 10388* (UC), **KR**: Siskiyou Co. *Doyle 9272* (gemmae) (UC), **NC**: Humboldt Co. *Norris 56311* (UC), **SC**: Santa Barbara Co. *Norris 102064* (UC), **SN**: Fresno Co. *Shevock 14498* (UC).

Scapania (Dumort.) Dumort. 1835
(Scapaniaceae)

Leaves of this genus are complicate-bilobed with the dorsal lobe slightly or greatly smaller than the ventral lobe. The leaves of most species are keeled at the fold. Look for a) epidermal and subepidermal cells of the stem (usually referred to as cortical cells) pigmented and thick-walled, surrounding thinner-walled medullary cells, b) underleaves absent, c) gemmae ellipsoidal, ovoid or pyriform, 1–2 celled, and d) perianths dorsiventrally flattened with a truncate mouth.

Caution. Several species of this genus exhibit considerable morphological plasticity. In addition, the color, size and form of juvenile plants can differ greatly from mature ones. Healthy, mature, robust parts of plants must be used for identification purposes.

Ten species plus one variety in California.

Species Key

1. Dorsal leaf lobe nearly the same size as the ventral lobe (subequal); both lobes with generally similar orientation to the stem. . . . . **2.**
1. Dorsal leaf lobe clearly smaller than ventral lobe (unequal); dorsal lobe generally more spreading from the stem than the ventral lobe. . . . . **3.**
2. Small plants, 1–2.7 mm wide, 1–2.2 cm long; basal part of leaf more-or-less appressed to and sheathing the stem; leaf margins entire; leaf fold not or scarcely keeled; gemmae generally dark brown to reddish. . . . . **S. cuspiduligera**
2. Larger plants, 2–4.5 mm wide, 1–7 cm long; basal part of leaf not appressed to or sheathing the stem; leaf margins usually finely denticulate; leaf fold weakly to clearly keeled; gemmae green (seldom pink or purplish-red). . . . . **S. subalpina**
3. Ventral leaf lobe not decurrent, or short decurrent to little more than level of attachment of the keel to the stem. . . . . **4.**

3. Ventral leaf lobe long decurrent beyond the level of attachment of the keel. . . . . **7.**
4. Leaves with broad ventral lobes (often nearly as wide as long); ventral lobes abruptly narrowed to the base; plants more than 2 cm in length. . . . . **S. irrigua**
4. Leaves with narrow ventral lobes (clearly longer than wide); ventral lobes gradually narrowed to the base; plants small, 2 cm or less in length. . . . . **5.**
5. Leaves usually bordered with 1–4 rows of uniformly thick-walled cells. . . . . **S. curta**
5. Leaf margins with thin-walled cells, or if bordered, then walls not uniformly thickened. . . **6.**
6. Ventral lobe apices usually broadly rounded; perianth mouth entire or with a few, scattered teeth. . . . . **S. scandica**
6. Ventral lobe apices mostly acute and apiculate; perianth mouth laciniate with large, close teeth. . . . . **S. mucronata**
7. Plants small, less than 2.5 mm wide. . . . . **S. umbrosa**
7. Plants large, more than 2.8 mm wide. . . . . **8.**
8. Dorsal lobe margin teeth strongly developed, larger and more widely spaced than those on the ventral lobe; dorsal lobe basal margin usually with branched (often antleroid) cilia. . . . . **S. bolanderi**
8. Dorsal lobe margin either entire or toothed, teeth, when present, generally similar in size and spacing, or smaller and fewer than on the ventral lobe; dorsal lobe basal margin entire, toothed or with unbranched cilia. . . . . **9.**
9. Dorsal lobes clearly decurrent on stem; thick-walled pigmented epidermal cells interrupted on the ventral stem surface by thinner-walled cells viewed in stem cross-section. **S. americana**
9. Dorsal lobes not (or only slightly) decurrent on stem; thick-walled pigmented epidermal cells not interrupted by thinner-walled cells in stem cross-section. . . . . **10.**
10. Leaf margins dentate, with conspicuous teeth on the keel. . . . . **S. undulata** var. **oakesii**
10. Leaf margins entire to dentate, but lacking teeth on the keel. . . . **S. undulata** var. **undulata**

Excluded. 1) *Scapania evansii* Bryhn. Clark and Frye (1936) reported this species from Califonia, based on a collection by Frye. However, WTU has no California specimen of *S. evansii*. No herbarium specimen of this species was located during this study. *Scapania evansii* could not be confirmed for California.

2) *Scapania glaucocephala* (Taylor) Austin. Based on *Howe 58* (UC) collected in Russian Gulch, Mendocino Co., Howe (1897a) and Hong (1980) reported this species from California. Howe (1899, p. 153–154) later changed his mind and referred to *Howe 58* as "an abortive, gemmiferous condition of *Scapania umbrosa*". In 2000, Alan Whittemore annotated this specimen as "probably depauparate *S. umbrosa*". Examination of *Howe 58* during this study confirmed the determinations by Howe and Whittemore. No herbarium specimens of *S. glaucocephala* from California were located during this study. This species could not be confirmed for California.

3) *Scapania nemorea* (L.) Grolle (= *S. nemorosa* (L.) Dumort). Early bryologists, e.g., Howe (1896), reported *S. nemorea* from California but the western North American plants were shown by Evans (1930) to be *S. americana*. No herbarium specimens of *S. nemorea* from California were located during this study. The species could not be confirmed for California.

Scapania americana Müll. Frib.

Amakawa (1967) has shown that *Scapania granulifera* A. Evans is conspecific with *S. americana*. Specimens examined during this study support that conclusion.

Distinctive features. Plants in green to golden-brown to purplish-red tufts or patches. Look for a) dorsal and ventral lobe margins ciliate or dentate, the dorsal lobe usually with fewer and shorter teeth (1–3 cells long) than the ventral lobe (1–5 cells long), b) dorsal lobes with unbranched teeth at their base, c) dorsal and ventral lobes distinctly decurrent, d) leaf surfaces often roughened with large (granulifera-type) or small wart-like or elongate papillae (the number and size of papillae is variable between and within populations), e) in stem cross-section, a deeply pigmented, thick-walled epidermis interrupted on the ventral side by 2–4 cells with thinner walls and little to no pigmentation f) gemmae 2-celled, golden-brown to reddish, and g) perianth mouth with ciliate lobes.

Separation. This species occasionally can be confused with *S. bolanderi*. See *S. bolanderi* for Separation

Illustrations. Evans 1930.

Habitat. Primarily on soil and rocks of outcrops and banks; seldom on wood. Elevation from 40 to 2275 m, mostly below 1000 m.

Distribution. Scapania americana is endemic to western North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 6065* (perianths) (UC), **KR**: Del Norte Co. *Doyle 9760* (perianths) (UC), **NC**: Marin Co. *Howe 21* (UC), **SN**: Tulare Co.: *Laeger 1936* (CAS).

Scapania bolanderi Austin

Distinctive features. This species grows in large greenish to yellow-green mats or as small shoots with other bryophytes. Look for a) dorsal and ventral lobes coarsely dentate, with teeth forming broad triangles, b) the ventral lobe spreading widely from stem axis, the margins often broadly recurved, with smaller and more frequent teeth than on the dorsal lobe, c) the dorsal lobe base usually with branched, multicellular cilia, resulting in an antleroid appearance, d) the dorsal lobe not or little decurrent, but the ventral lobe clearly decurrent, e) in stem cross-section, a deeply pigmented, thick-walled epidermis interrupted on the ventral side by 2–4 cells with thinner walls and little to no pigmentation, f) gemmae green, and g) perianth mouth coarsely lobed.

Separation. Scapania bolanderi and *S. americana* are the only California species with a strip of thinner-walled cells that interrupt the thick-walled epidermis on the ventral side of the stem. *S. bolanderi* can be separated from S. *americana* by: a) leaf teeth that form broad triangles and have blunt apices (vs. leaf teeth elongate triangles with slender apices in *S. americana*); b) dorsal lobes with distinctly fewer and coarser teeth than ventral lobes (vs. dorsal lobes with somewhat similar teeth as on ventral lobes); c) basal portion of dorsal lobe ciliate, the cilia usually branched, antleroid (vs. basal portion of dorsal lobe entire to short-dentate not ciliate or antleroid); and d) green gemmae with hyaline cell walls (vs. gemmae with golden-brown cell walls). In addition, *S. bolanderi* nearly always occurs on organic substrates (but exceptions occur, as in *Doyle 7846* [UC]) (vs. *S. americana* commonly occurring on inorganic substrates).

Illustrations. Evans 1930; Howe 1899; Schofield 2002.

Habitat. Primarily on shaded trunks of hardwoods and softwoods; also on logs, burned stumps, soil and rock outcrops. Elevation from 30 to 3000 m; mostly below 800 m.

Distribution. Scapania bolanderi occurs on the Pacific Coast of Asia and North America. Calif. Geographic Regions: **CC**: San Mateo Co, *Doyle 10378* (UC), **KR**: Del Norte Co. *Doyle 10598* (UC), **NC**: Humboldt Co. *Shevock 16728* (CAS), **SN**: Tulare Co.: *Doyle 7846* (UC).

Scapania curta (Mart.) Dumort.

Distinctive features. These small polymorphic plants usually are less than 2.5 mm wide and up to 1.5 cm long. The plants often have a vinaceous ventral surface. Look for a) leaves margined with a border of 1–4 uniformly thick-walled cells, b) median leaf cells thin-walled, 20–23 μm wide × 21–24 μm long, with small trigones, c) ventral lobe apices mostly rounded, margins entire (sometimes with a few 1-celled teeth near the apex), bases often vinaceous; and not, or only little, decurrent, d) dorsal lobe apices not directed toward the shoot apex and not decurrent, e) large dorsal lobe over 0.65 the area of the ventral lobe, f) gemmae greenish, 2-celled, and g) perianth mouth with few scattered 1–2-celled teeth.

Separation. In size and morphological variability, *S. curta* occasionally can be difficult to separate from *S. mucronata* and *S. scandica*. Usually, it can be separated from *S. mucronata* by a) leaves with a border of uniformly thick-walled cells without trigones (vs. leaves not bordered with thick-walled cells without trigones in *S. mucronata*), b) teeth occasionally present near the lobe apices (vs. teeth never present near the the lobe apices), c) shoots often with a reddish coloration, especially in sun forms (vs. shoots often with a brownish coloration, but never reddish), and d) perianth mouth sparsely toothed (vs. perianth mouth laciniate with large close teeth).

Both *S. curta* and *S. scandica* have broadly rounded ventral lobes and a perianth mouth with a few scattered teeth. *Scapania curta* can be separated by a) leaf with a distinct 1–4-celled marginal border of uniformly thick-walled cells (vs. leaf marginal border absent, or, if present, a 1–2-celled border, but not uniformly thick-walled in *S. scandica*), and b) a large dorsal lobe over 0.65 the area of the ventral lobe (vs. a dorsal lobe 0.5–0.65 the area of the ventral lobe).

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. On mineral and peaty soil and wood along streams. Elevation from 2050 to 3450 m.

Distribution. Scapania curta occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Inyo Co. *Doyle 8742* (perianths) (UC).

Scapania cuspiduligera (Nees) Müll. Frib.

Distinctive features. This is a small pale-, whitish-, yellowish-, or brownish-green plant, 1.0–2.7 mm wide × 0.6–2.2 cm long. Look for a) subequally bilobed leaves (the lobes similar in size and shape), smooth margins bordered with 1–3 rows of thick-walled cells, and evenly rounded lobe apices, b) leaf without a sharp keel and with the leaf base sheathing the stem, c) dorsal leaf lobe usually upturned, giving the shoot a crisped appearance, d) leaf cells often with large trigones, e) gemmae frequent, forming dark brown to reddish-brown clusters near the shoot apex, f) ventral leaf lobes clearly decurrent, and g) perianth mouth smooth (rarely with a few teeth).

Separation. This species can resemble small shoots of *S. subalpina*. See that species for separation

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Usually on damp or wet rock and cliff outcrops, mostly on basic substrates. Elevation above 1750 m.

Distribution. Scapania cuspiduligera occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Shasta Co. *Doyle 9878* (brownish gemmae) (UC), **SN**: Mono Co. *Doyle 9813* (brownish gemmae) (UC).

Scapania irrigua (Nees) Gottsche, Lindenb. and Nees

Distinctive features. This is a moderately-sized yellowish-green to brown plant, up to 4 mm wide. Look for a) ventral lobes broadly reniform to cordate, almost as wide as long, often with acute apices and abruptly narrowed to the base, b) ventral leaf lobes not decurrent or seldom decurrent to below the level of insertion of keel, c) dorsal leaf lobes with a pointed apex and not decurrent, d) cells of leaf margins thin-walled to slightly thickened, the marginal cells not differentiated from the interior cells, e) leaves with smooth margins (but teeth occur near apices with gemmae), f) gemmae green, 2-celled, slender and often in large clusters at the shoot apex, and g) perianth mouth dentate to short ciliate, 1–4 cells long.

Separation. Robust, mature plants should not be confused with other California species of *Scapania*. Look for mature shoots to study because juvenile or poorly developed plants can be mistaken for *S. scandica* or *S. curta*.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Often around standing or slow flowing water, but rarely submerged; on soil in meadows and on logs; sunny rocky banks of lakes, ponds, bogs, pools, and seepages; Elevation up to 2660 m.

Distribution. Scapania irrigua occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: Nevada Co. *Whittemore 4159* (MO).

Scapania mucronata H. Buch

Distinctive features. These are small green to brown plants, mostly less than 2.5 mm wide. Look for a) marginal cells of both the dorsal and ventral lobes more-or-less isodiametric, 14–20 μm in diameter, b) leaf lobe marginal cells mostly thin-walled, not forming a distinct border, and usually with large bulging trigones, c) ventral lobe apices apiculate, d) leaf margins smooth except near gemmae development, e) oil-bodies present in marginal cells, e) gemmae green to reddish, 2-celled, common, and g) perianth mouth mostly laciniate with tapering teeth (2–5 cells wide at the base and several cells long).

Separation. This species can be confused with *S. curta* and *S. scandica*. *Scapania mucronata* can be separated from *S. scandica* by a) apiculate ventral lobe apices (vs. ventral lobe apices rounded in *S. scandica*), and b) perianth mouths mostly laciniate with large close teeth (vs. perianth mouth smooth or with a few scattered teeth). See *S. curta* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. On shaded soil, boulders and rock cliff faces. Elevation above 1000 m.

Distribution. Scapania mucronata occurs in Europe, Asia, and North America. Calif. Geographic Regions: **KR**: Trinity Co. *Doyle 7557* (UC), **MP**: Modoc Co. *Doyle 6670* (gemmae) (UC).

Scapania scandica (Arnell & H. Buch) Macvicar

Distinctive features. This is a small pale green to reddish-brown plant mostly less than 2.5 mm wide and up to 1.5 cm long. Look for a) leaf lobe margins usually entire except when gemmiferous, then with a few scattered spinose teeth near places of gemmae development, b) median leaf cells 16–19 μm wide × 18–24 μm long, c) marginal leaf cell walls usually thin or slightly thickened, with trigones (**note:** the marginal 1–2 rows of cells occasionally have non-uniformly thickened walls), d) the ventral lobe not, or only slightly, decurrent and the lobe apex usually is broadly rounded, e) the dorsal lobe not, or only slightly, decurrent and the lobe apex usually sharply pointed (apiculate), and f) the perianth mouth smooth or with a few scattered 1–2-celled teeth.

Separation. See *S. curta* for separation from that species. See *S. mucronata* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. On shaded soil and rocks, occasionally decaying logs. Elevation from 350 to 2000 m.

Distribution. Scapania scandica occurs in Europe, Asia, and North America. Calif. Geographic Regions: **CR**: Tehama Co. *Doyle 9413* (UC), **SN**: El Dorado Co. *Doyle 11119* (perianths) (UC).

Scapania subalpina (Nees) Dumort.

Distinctive features. These are small to large plants, 2.0–4.5 mm wide × 1–6 cm long often occurring in silt- or sand-encrusted loose tufts. The leaves usually are whitish to pale green; the stem is green to reddish-brown and blackish when mature. Look for a) dorsal and ventral leaf lobes subequal and usually distally rounded, although older leaves sometimes are more unequally bilobed than those near the shoot apex, b) margins of both lobes usually finely denticulate, occasionally smooth, c) the ventral lobe usually flat and long decurrent, d) the dorsal lobe flat to erect, nearly transversely inserted and the free margin extending across and beyond the stem, e) gemmae pale green, but pinkish to purplish-red in sun forms, and f) perianth mouth entire or finely dentate.

Separation. Small shoots of this species can resemble shoots of *S. cuspiduligera*; they can be separated by a) leaf lobe margins generally with fine marginal teeth (vs. leaf lobe margins smooth in *S. cuspiduligera*), b) larger size, shoots up to 4.5 mm wide (vs. shoots less that 2.7 mm wide), and c) keel well-developed (vs. keel not or only weakly developed). *S. subalpina* is nearly as variable in color, size and form as *S. undulata* and the two species often are difficult to separate. For separation, see discussion under *S. undulata* var. *undulata*.

Illustrations. Damsholt 2002; Evans 1923; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Often near running water, but rarely permanently submerged; attached to rocks or on soil of damp ledges, banks of creeks, cascades, springs, and seepages. Elevation from 2600 to 3500 m.

Distribution. Scapania subalpina occurs in Europe, Asia, and North America. Calif. Geographic Regions: **SN**: El Dorado Co. *Doyle 11125* (UC).

Scapania umbrosa (Schrad.) Dumort.

Distinctive features. These small distinctive plants are up to 2.5 mm wide × 1.8 cm long. Shoots are whitish- or yellowish-green, or pale reddish-brown often with a purplish tinge. Growth is erect with decurved shoot tips, especially when dry. Look for a) dorsal and ventral lobes narrow, gradually tapering, and with acute apices, b) lobe margins coarsely serrate (rarely smooth), c) dorsal lobe closely lying over the ventral lobe, the lobe apex usually pointing nearly directly toward the shoot apices, transversely inserted, and not decurrent, c) ventral lobes decurrent to well below the level of insertion of the often distinctly winged keel, d) gemmae in dark- to reddish-brown clusters, and e) perianth mouth sinuate with smooth or occasionally finely dentate margins.

Separation. Scapania umbrosa is not easily confused with other species of *Scapania* (except juvenile *S. bolanderi*, which never is reddish). Distinctive are the a) erect growth, b) strongly decurved shoot apices of dry plants, c) narrow leaf lobes gradually tapering and coarsely serrate, and d) dorsal lobe tip usually pointing toward the shoot apex.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Usually on damp decaying logs; also on shaded rocks and soil of paths and cliff faces; 15 to 1450 m; mostly below 600 m.

Distribution. Scapania umbrosa occurs in Europe and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 6062* (perianths) (UC), **KR**: Trinity Co. *Snodgrass 82* (DAV), **NC**: Humboldt Co. *Norris 23509* (UC), **SN**: Yuba Co. *Doyle 9588* (UC).

Scapania undulata (L.) Dumort. var. **undulata**

This species is widespread in California and remarkably variable in shape, size and coloration. Often there is little resemblance between the flaccid and undulate forms to the very rigid and non-undulate forms; yet there are intermediates between these extremes. This extreme polymorphism has led to much taxonomic confusion. Additional studies are needed to separate environmental from genetic variation.

Distinctive features. Plants are up to 5 mm wide × 20 cm long, and often form large mats or turfs. Leaves are green in shade forms, reddish-purple in the sun, and have smooth to dentate margins. Look for a) keels 0.25–0.5 of the length of the ventral lobe and without teeth, b) ventral lobes flat and long decurrent, c) dorsal lobes flat or occasionally convex, 0.35–0.65 the size of the ventral lobes, and transversely inserted or occasionally short-decurrent, d) leaf cells never with bulging trigones, and e) perianth mouth entire (usually when the leaf margins are entire) or dentate (usually when the leaf margins are dentate).

Separation. This species is most likely to be confused with *S. subalpina*. "Typical" plants of *S. undulata* can be separated from "typical" *S. subalpina* by a) unequal lobes, the dorsal lobe 0.35–0.65 the size of the ventral lobe (vs. dorsal and ventral lobes subequal, the dorsal lobe 0.75 the size of the ventral lobe in *S. subalpina*), b) dorsal lobes of well-developed leaves lying closely over the ventral lobe (vs. dorsal lobes flat to erect to squarrose), c) a shorter keel, 0.25–0.5 the length of the ventral lobe (vs. keel 0.5 the length of the ventral lobe), and d) leaves pale to dark green to reddish, to blackish (vs. leaves commonly pale to whitish-green). However, because of vegetative and perianth mouth variability, there can be times when species identification will be in doubt.

Illustrations. Damsholt 2002; Paton 1999; Schuster 1974; Smith 1990.

Habitat. Very wide range of habitats from submerged or near water-level of flowing water and cascades, to exposed summer-dry exposures; on sandy and gravelly soil, rocks, boulders, and wood. Elevation from near sea-level to 3300 m.

Distribution. Scapania undulata var. *undulata* occurs in Europe, North Africa, Asia, and North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 847* (UC), **CR**: Shasta Co. *Doyle 9318* (UC), **GV**: San Joaquin Co. *MacFadden 324* (ABSH), **KR**: Siskiyou Co. *Shevock 20103* (CAS), **MP**: Modoc Co. *Doyle 9674* (UC), **NC**: Mendocino Co. *Doyle 8028* (perianths) (UC), **SC**: Riverside Co.: *Doyle 7450* (UC), **SN**: Fresno Co. *Shevock 18353* (CAS).

Scapania undulata (L.) Dumort. var. **oakesii** (Austin) H. Buch

Distinctive features. Shoots of var. *oakesii* vary from greenish, to brownish, to reddish. Shoots are 3–4 mm wide and 1.0–2.5 cm long. The presence of a conspicuous single or double row of teeth on the keel is the single most definitive feature of this variety. (**Caution:** teeth on the keel often are absent or scarce on leaves of weak stems and plants growing in wet conditions, such as during the cloudy, rainy part of the growing season. On some shoots, teeth on the keel will be present on some leaves and absent on others.) Also look for a) the dorsal lobe base often with one or more coarse teeth, b) the ventral lobe base often with teeth extending down to the decurrent strip, and c) perianth mouth denticulate.

Separation. Variety *oakesii* can be separated from var. *undulata* primarily by: a) smaller size, shoots to 4 mm wide × 2.5 cm long (vs. shoots to 5 mm wide × 20 cm long in var. *undulata*, b) keel of vegetative shoots with a conspicuous single or double row of teeth (vs. keel lacking teeth), c) dorsal lobe base often with several large teeth (vs. dorsal lobe base usually without teeth), d) teeth on the ventral lobe often extending down to the decurrent strip (vs. base of the ventral lobe usually without teeth), and e) perianth mouth denticulate (vs. perianth mouth entire or distantly toothed). Variety *oakesii* can be separated from small plants of *S. americana* by a) the presence of teeth on the keel (vs.

keel without teeth in *S. americana*), and b) a longitudinal strip of thin-walled cells in the epidermis of the ventral stem surface absent (vs. a longitudinal strip of thin-walled cells in the epidermis of the ventral stem surface present).

Illustrations. Howe 1899; Schuster 1974.

Habitat. On soil, sandstone boulders and organic matter; 30 to 2230 m.

Distribution. Scapania undulata var. *oakesii* occurs in North America. Calif. Geographic Regions: **CC**: San Mateo Co. *Doyle 750* (perianths) (UC), **KR**: Del Norte Co. *Frye 77* (WTU), **NC**: Mendocino Co. *Doyle 9035* (UC).

HORNWORTS

The hornwort gametophyte is a dorsiventral thallus lacking air-chambers and ventral scales. Diagnostic features include: a) a single large chloroplast in young cells of the apical meristem (examine the apical meristem region because some California hornworts have two or more chloroplasts in cells of older parts of the thallus), and b) a sporophyte consisting of a cylindrical capsule, a foot embedded in gametophytic tissue and a meristematic region (called an intercalary meristem) between the foot and capsule. The intercalary meristem adds new cells to the base of the capsule, resulting in a) spore mother cell differentiation occurring near the capsule base, b) meiosis and spore development occurring in the capsule middle and c) mature spore discharge occurring from the dehisced capsule apex – all occurring at the same time in a capsule.

Some California hornworts develop tubers that serve as a means to survive unfavorable conditions, such as variable rainfall and drought. Tubers are localized thickened areas containing cells filled with food-reserve. Because many tubers develop on a single thallus, tubers also are a means for population increase. The tubers can develop a) on thallus margins, b) at apices of very short to long branches, and c) on stalks on the ventral midrib region. The presence, location and size of mature tubers can aid in species identification. **Note:** tubers that develop at apices of very short branches can appear to be marginal in origin.

In California, there are 3 genera, 7 species and 1 species to be described in a subsequent publication. (The genus to which the new species to be described belongs has not yet been determined.)

GENUS KEY

1. Spores blackish; thallus with large mucilage- or air-filled cavities, margins often crisped; cells of antheridial walls in four tiers. . . . . **Anthoceros**
1. Spores yellow, but spores of some species turning gray-brown (fuscous) when fully mature; thallus lacking large mucilage- or air-filled cavities, margins rarely crisped; cells of antheridial wall irregularly arranged, never in four tiers. . . . . **2.**
2. Spores matured in the field mostly yellow; chloroplast with a conspicuous central pyrenoid or, if lacking conspicuous pyrenoid, with marginal tubers; antheridial chambers usually with 2 or more antheridia. . . . . **Phaeoceros**
2. Spores matured in the field gray-brown (fuscous); chloroplasts with an indistinct central pyrenoid; tubers ventral and stalked; antheridial chambers usually with 1 (seldom 2) antheridium. . . . . **Phymatoceros**

Anthoceros L. 1753
(Anthocerotaceae)

Plants of this monoicous genus usually have rather highly dissected margins with crisped margins, and the thallus dorsal surface with lamellae of variable lengths. The length of the antheridial body is important in identification of some species. Use living plants to look for antheridial chambers because they are indistinct in dry plants. The black spores usually look grayish under the compound microscope.

Three species in California.

SPECIES KEY

1. Dorsal thallus surface with numerous lamellae; distal spore face with short spines on a complex basal reticulum; proximal spore face with numerous, irregular papillae on

a simple basal reticulum, with a narrow strip devoid of papillae near the center of the triradiate ridge. . . . . **A. fusiformis**

1. Dorsal thallus surface with few to several low, short lamellae; distal spore face with short or long spines on a simple- or non-reticulate base; proximal spore face without papillae, the surface smooth with shallow to deep depressions (alveolae) that extend to the triradiate ridge. . . . . **2.**
2. Thallus dorsal surface with few or no lamellae; antheridial body (without stalk) 100–150 μm long; distal spore face with long spines, often with sharp apices. . . . . **A. punctatus**
2. Thallus dorsal surface with many low lamellae; antheridial body (without stalk) 50–90 μm long; distal spore face with low spines, often with rounded apices. . . . . **A. agrestis**

Anthoceros agrestis Paton

Distinctive features. Thalli of this monoicous species form rosettes that are less than 1.5 cm in diameter. Look for a) thalli shallowly divided into linear lobes with low lamellae on the dorsal surface usually radiating away from the rosette center, b) antheridial body 50–90 μm long, c) capsules usually to 2 (seldom to 3) cm long, d) spores 40–55 μm in diameter, e) distal spore face usually with short, unbranched spines with rounded apices, and f) proximal spore face with shallow to deep depressions (alveolae) that extend to the triradiate ridge. Mature sporophytes from April through May.

Separation. See *A. punctatus* for separation from that species.

Illustrations. Damsholt 2002; Paton 1999.

Habitat. Gravelly soil, often thin soil over granite slabs; usually shaded slow-to-dry areas in and around chaparral, coastal scrub, and margins of seepages. Elevation from 30 to 1365 m.

Distribution. Anthoceros agrestis occurs in Europe, Asia, Africa, and North America. Calif. Geographic Regions: **CC**: San Luis Obispo Co. *Doyle 5734* (UC), **SC**: San Diego Co. *Doyle 7142* (UC).

Anthoceros fusiformis Austin

Distinctive features. A. fusiformis is widespread in California and will be the hornwort species most commonly encountered. The thallus often forms a rosette of (usually) strap-shaped, overlapping branches with crisped margins. Look for a) dorsal thallus surface with numerous lamellae of variable lengths (young plants, especially, have numerous lamellae and a compact crisped appearance, and resemble gametophytes of the horsetail *Equisetum*), b) capsules with mature spores usually from 4 to over 10 cm long, c) spores mostly 42–58 (up to 62) μm in diameter, d) distal spore face with low, unbranched spines on a complex basal reticulum, and e) proximal spore face with coarse irregular papillae on a basal reticulum, the papillae do not extend to the triradiate ridge, resulting in a narrow strip on both sides of the triradiate ridge devoid of papillae and alveolae. Mature sporophytes from late March through August.

Separation. This species is separated from the other California species of *Anthoceros* by the a) large thalli with numerous dorsal lamellae, b) distal spore face with short spines on a complex reticulum and c) papillose proximal face with papillae that do not extend to the triradiate ridge.

Illustrations. Howe 1899.

Habitat. Easily disturbed summer-dry soil along trails, road banks, hillsides, landslides; exposed areas near seepages or shaded by shrubs or trees; seldom on rocks with moss. Elevation from 7 to 2340 m (the latter from Shasta Co., Doyle 9386, [UC]), but more common below 1200 m.

Distribution. Anthoceros fusiformis occurs in the Pacific Coast of Japan and North America. Calif. Geographic Regions: **CC** Santa Cruz Co. *Doyle 8155* (UC), **CR**: Shasta Co. *Doyle 9386* (UC), **GV**: Sutter Co. *Norris 103801* (UC), **KR**: Siskiyou Co. *Doyle 9217* (UC), **NC**: Lake Co. *Doyle 9078* (UC), **SC**: Riverside Co. *Doyle 7437* (UC), **SN**: Yuba Co. *Doyle 9601* (UC).

Anthoceros punctatus L.

Based on T. C. Frye collections from near Alton, Humboldt Co., Clark and Frye (1936) reported *Anthoceros punctatus* for California. WTU has two Frye collections (neither with collection number) both collected 30 July 1930 from near Alton. Examination of these collections determined that they

contained a mixture of *Anthoceros fusiformis* and *Phaeoceros carolinianus;* no thalli of *A. punctatus* were located. Although the Clark and Frye report could not be confirmed, *A. punctatus* subsequently has been confirmed for California.

Distinctive features. Living plants often are aromatic when crushed. Thalli usually form rosettes 1–3 cm in diameter. Look for a) dorsal thallus surface with few or no lamellae, b) antheridial body 100–150 μm long, c) capsules up to 10 cm long, d) spores 45–56 μm in diameter, e) a distal spore face with numerous, often sharp-pointed spines, the spines single or with 2–4 spines united at the base, and f) a proximal spore face with shallow to deep depressions (alveolae) extending to the triradiate ridge. Mature sporophytes from May through August.

Separation. Anthoceros punctatus can be separated from *A. agrestis* by a) usually forming larger rosettes, 1–3 cm in diameter (vs. thallus rosettes 0.5–1.5 cm in *A. agrestis*), b) lamellae on the dorsal thallus surface fewer and less distinct (vs. lamellae on the dorsal thallus surface many and low), c) antheridia 100–150 μm long (vs. antheridia 50–90 μm long), and d) sporophyte capsules up to 10 cm long (vs. capsules usually less than 3 cm long). Antheridial size is the surest way to separate these two species because small plants of *A. punctatus* can resemble large plants of *A. agrestis. Anthoceros punctatus* has been reported only from coastal Humboldt and Mendocino Counties; *A. agrestis* has been found in primarily coastal central and southern California. The distribution of both species needs additional field-work.

Illustrations. Paton 1999; Schofield 2002 (as *Aspiromitus punctatus*); Smith 1990.

Habitat. Damp, shaded, disturbed silty soil in garden plantings, along creek banks and shaded banks of seepages and drainages. Elevation from 8 to 75 m.

Distribution. Anthoceros punctatus occurs in Europe, Asia, North Africa, and North, Central, and South America. Calif. Geographic Regions: **NC**: Humboldt Co. *Doyle 11379* (UC) and Mendocino Co. *Doyle 10449* (UC).

Phaeoceros Prosk. 1951
(Notothyladaceae)

Thalli of this genus are light to dark green, frequently and irregularly branched, seldom with crisped margins, and without lamellae on the dorsal thallus surface. Thallus morphology is extremely variable, even in the same species when growing in different microhabitats (wet or dry, exposed or shaded, early or late in the growing season). Look for a) flat thallus branches that lack dorsal lamellae, b) antheridia 2–4 (occasionally more) per antheridial chamber, and c) spores that are yellow or brownish-yellow at maturity.

Vegetative plants of some species of this genus can be confused with vegetative plants of *Aneura, Pellia, Riccardia*, and *Blasia. Phaeoceros* can be separated a) from *Aneura, Pellia* and *Riccardia* by the presence of cyanobacteria colonies in the thallus and a single chloroplast in cells of the thallus apex (vs. absence of cyanobacteria and several chloroplasts in cells of the thallus apices of *Aneura, Pellia* and *Riccardia*), and b) from *Blasia* by unlobed thallus margins and a single chloroplast in cells of the thallus apex (vs. distinctly lobed thallus margins and several chloroplasts in cells of the thallus apex of *Blasia*).

Three species in California.

Species Key

1. Capsules short, less than 0.6 cm long; pseudoelaters mostly single cells, each cell only slightly longer than wide. . . . . **P. hallii**
1. Capsules long, up to 8 cm long; pseudoelaters often 2–4-celled, each cell usually longer than wide. . . . . **2.**
2. Chloroplasts sharply angular and with a conspicuous central pyrenoid; tubers lacking; distal spore face with numerous spines. . . . . **P. carolinianus**
2. Chloroplasts bluntly angular, or spherical, or dumbbell-shaped, or elongate, and without a conspicuous central pyrenoid; tubers common, marginal or apical; distal spore face with large crescentic to rounded warts. . . . . **P. pearsonii**

Phaeoceros carolinianus (Michx.) Prosk. ***s. l.***

Vegetative thalli and spores of *Phaeoceros carolinianus* are morphologically variable. In this publication, the species is used in a broad, inclusive sense. (See Schuster 1992b for a discussion of *P.*

carolinianus, P. mohrii, and *P oreganus*.) The vegetative thalli of California plants fall mostly within two groups: a) large thalli growing in and at the margins of permanently wet habitats, and b) smaller, more compact thalli growing in seasonally dry habitats. These differences are difficult to quantify; moreover, exceptions do occur.

Spore marking details have been used to separate populations into species. Features used include a) the number of spines across the distal spore face, b) the presence or absence of tubercles in the triangular facets between the triradiate ridge on the proximal spore face, c) tubercle distribution, clustered in the center or scattered, in the facets of the proximal spore face, d) the presence or absence of vermiculae on the distal and/or proximal spore face, and e) the width of the spore wing tissue. The details of spore markings of California populations do not fall within discrete groups. In fact, variation often occurs a) in the same population, b) in spores from the same capsule (be careful not to observe only spores that fit what you would like see), and c) spores from the same population at different times of the year. Perhaps J. Proskauer was correct: he considered the small California plants as variants belonging to the same species (personal communication). After studying this diversity and finding no clear-cut separation of variants, we are inclined to accept his judgement and refer all of these variants to *P. carolinianus*.

Distinctive features. Thalli of this strap-shaped dichotomously branched species are deep to dark green. Thallus branches and margins usually are flat, but are undulate in seepages and splash of creeks. Look for a) thalli without definite midribs, about 7–13 cells thick in the thallus mid-region, gradually thinning to 2–3 cells thick at the margins in thallus cross-section, b) tubers are not known in California plants, c) capsules up to 8 cm long, when mature splitting into two twisted valves or on one side only, d) spores yellow at maturity, 35–56 μm in diameter, e) the distal spore face with numerous short spines, and f) the proximal spore face with none, or few to many, rounded tubercles scattered or localized in the center of the facet between the triradiate ridge. Mature sporophytes from late March through October.

Separation. With its large angular chloroplast with a visible central pyrenoid, lack of tuber development, yellow spores with a spinose distal face and rounded tuberculate proximal face, this species should not be confused with other California hornworts.

Illustrations. Howe 1899 (as *Anthoceros carolinianus*); Schofield 2002 (as *Anthoceros carolinianus*).

Habitat. Shaded or open areas, permanently wet areas, such as seepages, splash of creeks, cascades and waterfalls; generally in slow to dry areas. Elevation from 6 to 1200 m.

Distribution. Phaeoceros carolinianus occurs in Europe, Asia, Africa, Australia, and North America. Calif. Geographic Regions: **CC**: Monterey Co. *Doyle 10390* (UC), **CR**: Tehama Co. *Doyle 8625* (UC), **DMoj**: Inyo Co. *Laeger 2623a* and *2594* (UC), **KR**: Del Norte Co. *Doyle 7735* (UC), **NC**: Mendocino Co. *Doyle 11376* (UC), **SC**: Riverside Co. *Doyle 7309* (UC), **SN**: Placer Co. *Doyle 11364* (UC).

Phaeoceros hallii (Austin) Prosk.

This hornwort has interesting sporophyte capsule behavior. The intercalary meristem between the foot and the capsule seems to have limited activity, resulting in a short capsule even when moisture conditions appear to be appropriate for continued cell division. The capsules often are indehiscent even when fully mature and dried naturally in the field. Field-dried capsules often are shriveled with sharp longidudinal ridges and appear immature. Dissection, however, can reveal mature spores from capsule apex to base.

Distinctive features. This is a distinctive species with thin, irregularly branched, green to light-green thalli with narrow branches mostly less that 2.5 mm wide. Look for a) a midrib region of the main branch 7–9 cells thick and a wing 1–2 cells thick in thallus cross-section, b) dry plants often with the thallus margins turned up, giving the appearance of a wide midrib, c) tubers flattened, disk-shaped, dark-green to greenish-black, usually less than 1.3 mm wide, occasionally marginal, but mostly at the apices of main or short lateral branches, d) capsules numerous, often in twos or clusters, but each with a separate involucre, e) mature capsules yellow to light-brown, less than 6 mm high, f) capsules cylindrical when fresh, but spindle-shaped and longitudinally ridged when dry, g) capsules indehiscent, or dehiscent late on one side only, h) mature spores lemon-yellow to light brown, 44–63 μm in diameter; the distal spore face with 20–35 rounded to elongate warts or low, branched ridges; the proximal spore face usually with more than 20 small, rounded papillae in the center of each facet on a matrix of interwoven fibrils between the arms of the triradiate ridge, and i) pseudoelaters mostly

unicellular, short rectangular and only slightly longer than wide. Mature sporophytes from May through August.

Separation. The gametophytes, sporophytes, and spores of this species are not easily confused with other species of the genus.

Illustrations. Frye and Clark 1947.

Habitat. Shaded soil and rocks, often with moss; slow-to-dry margins of seepages, creek banks, and humid mouse runs in tunnels under grass. Elevation from 210 to 1350 m.

Distribution. Phaeoceros hallii occurs on the Pacific Coast of North America, from Washington to California. Calif. Geographic Regions: **KR**: Trinity Co. *Doyle 8545* (UC), **MP**: Modoc Co. *Doyle 8649* (UC), **SN**: El Dorado Co. *Doyle 11363* (UC).

Phaeoceros pearsonii (M. Howe) Prosk.

Distinctive features. Plants in different microhabitats are variable in vegetative morphology and spore characteristics. In shaded, moist, slow-to-dry habitats, the thallus is green to dark green, up to 5 mm wide, and the fully mature spores usually are yellow to brownish, without secondary wall deposition, and without papillae on the proximal face. In more exposed habitats, a) the thallus is a lighter green, more highly branched and often less than 3 mm wide, and b) fully mature spores are dark brown to brownish-black (fuscous), with secondary wall deposition, and usually with few to several papillae on the proximal face.

Look for a) thalli mainly without a distinct broad central midrib region, 6–11 cells thick in the center and gradually thinning to 3–4 cells thick at the margins, in thallus cross-section , b) mature cells of the ventral thallus surface and interior tissue with angular, spherical, dumbbell-shaped, or multiple chloroplasts, c) chloroplasts without conspicuous pyrenoids, d) tubers large, flat, dark green to blackish, 2.5 mm or more wide when mature, both marginal and apical (occasionally at the apices of thin, nearly colorless branches, but never ventral in position), e) capsules up to 6 cm long, d) fully mature spores yellow, brown or brownish-black, 36–48 μm in diameter, f) the distal spore face mostly with 5–13 crescentic warts as viewed under the compound microscope or mostly round warts as viewed with the scanning electron microscope (there is a slight morphological difference between hydrated and dehydrated spores), g) the proximal spore face with interwoven fibrils and no, few or several clustered or scattered papillae, and h) pseudoelaters 1–4 cells long, and 3–8 times as long as wide. Mature sporophytes from April through June.

Separation. The combination of a) relatively large thallus, b) chloroplasts without a conspicuous central pyrenoid, c) cells of the ventral thallus surface and interior tissue with angular, spherical, dumbbell-shaped, or multiple chloroplasts, d) large marginal and apical tubers, and e) spores with 5–13 crescentic or round warts on the distal spore face separate this species from other species of the genus.

Illustrations. Howe 1899.

Habitat. Shaded soil; usually slow-to-dry summer-dry habitats; creek banks, hillsides, and road banks. Elevation from 5 to over 5000 m; mostly below 2000 m.

Distribution. Phaeoceros pearsonii occurs on the Pacific Coast of North America, from Washington to California. Calif. Geographic Regions: **CC**: San Luis Obispo Co. *Doyle 5726* (UC), **CR:** Shasta Co. *Malachowski s.n.* (CHSC 11613), **KR:** Siskiyou Co. *Doyle 5934* (UC), **NC**: Mendocino Co. *Doyle 11378* (UC), **SC**: Los Angeles Co. *Wilson 3730* (SFV), **SN**: Amador Co. *Doyle 8449* (UC).

Phymatoceros Stotler, W. T. Doyle and Crand.-Stotl. 2005
(Notothyladaceae)

Plants of this genus have a) chloroplasts that vary within thallus tissue from somewhat angular, to spindle-shaped, to somewhat rounded, to dumbbell-shaped, b) 1 (seldom 2) antheridium per antheridial chamber, and c) spores that are yellow when immature, but become fuscous when matured in the field; the darkening of the spore is correlated with the late deposition of secondary wall material on the spore surface.

P. bulbiculosus (Brot.) Stotler, W.T. Doyle and Crand.-Stotl.

Distinctive features. This species has separate female and male plants and some populations consist only of male or female plants. In the absence of sexual reproduction, the persistence of these

populations is made possible by the development of tubers. Tuber germination occurs soon after the onset of winter rains, and sex organ development begins early in young tuberlings, usually in late November to late December. Male plants are smaller than the female plants, generally less than 1 mm wide. Male plants develop a cluster of antheridia and then become vegetative and initiate development of long-stalked ventral tubers.

Female plants generally are up to 2.5 mm wide. This larger thallus, with or without sporophytes, usually is what is noticed in the field and collected. The thallus is somewhat grayish-green and often with slightly raised wing margins. The broad midrib region is 10–16 cells thick, and gradually thins to 3–5 cells thick at the wing margin, in thallus cross-section. Stalked ventral tubers develop early on female thalli without sporophytes. Plants with sporophytes develop a thickened cushion on the ventral thallus surface below the sporophyte foot; stalked ventral tubers develop later.

For *P. bulbiculosus* look for a) thalli with ventral tubers, b) erect to slightly bent capsules generally less than 2 cm tall, c) the capsule apex orange- to brownish-black, turning black as the capsules mature; the capsule usually splits on one side only, d) immature spores yellowish; mature spores brownish-black (fuscous), 47–67 μm in diameter, e) the distal spore face with a central raised elevation with thick, low circular and/or elongate ridges, and f) the proximal spore face smooth (no papillae). Fully mature sporophytes from April through June.

Separation. This is our only hornwort species that has stalked tubers on the ventral thallus surface.

Illustrations. Howe 1899 (as *Anthoceros phymatodes*); Crandall-Stotler, Doyle, and Stotler 2006.

Habitat. Shaded soil in slow to dry, summer-dry habitats. Hillsides, creek banks, road and trail banks, and margins of sloping meadows. Elevation from 15 to 650 m.

Distribution. Phymatoceros bulbiculosus occurs in Europe, and North and South America. Calif. Geographic Regions: **CC**: Santa Cruz Co. *Doyle 8384* (UC), **KR**: Shasta Co. *Doyle 9124* (UC), **NC**: Sonoma Co. *Doyle 10657* (UC), **SN**: Mariposa Co. *Doyle 8208A* (UC).

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APPENDIX I

GLOSSARY

Definition of Terms as Used in this Publication.

(See Stearn 1992, *Botanical Latin* and Magill 1990, *Glossarium Polyglottum Bryologiae* for additional definitions)

Abaxial—The surface of the leaf facing away from the axis of the stem.
Acuminate—Gradually narrowed to a slender point in leaves or leaf lobes.
Acute—Sharp pointed apex or sinus of leaves; at an angle of less than 90°.
Adaxial—The surface of the leaf facing toward the axis of the stem.
Adnate—The fusion of unlike parts to one another, such as a leaf margin to the stem.
Alveolate—With usually rounded, shallow to deep depressions.
Anterior—Toward the stem apex.
Antheridiophore—A stalk that elevates the antheridia above the thallus surface in some complex thalloid liverworts.
Antheridium (pl. **antheridia**)—Multicellular male reproductive organ in which sperm develop.
Archegoniophore—A stalk that elevates the archegonia above the thallus surface in some complex thalloid liverworts.
Archegonium (pl. **archegonia**)—Multicellular female reproductive organ, usually differentiated into a base (venter) containing an egg, and neck.
Areola (pl. **areolae**)— Angular-shaped spaces, walled by lamellae, on the surface of spores.
Auriculate—Having small ear-like lobes at the base of a leaf or underleaf.
Autoicous—Antheridia and archegonia develop on separate branches of the same gametophytic plants.

Botryoidal—Spherical clusters, like a bunch of grapes.
Bract—In leafy liverworts, a modified leaf associated with either a male or female inflorescence.
Bracteole—In leafy liverworts, a modified underleaf associated with either a male or female inflorescence.

Caducous—Detaching; in liverworts, referring to leaves and perianths that detach along pre-determined lines.
Canaliculate—Longitudinally channeled or grooved.
Capsule—The part of the sporophyte in which spores develop; the sporangium.
Carpocephalum — In complex thalloid liverworts, the female receptacle that bears sporophytes at the apex of the archegoniophore
Chlorenchyma—A tissue with chlorophyll-containing cells.
Ciliate—Having long hair-like processes.
Cismontane—The area west of the Sierra Nevada-California Cascade crest.
Columella—In hornworts, a central column of non-spore-producing tissue surrounded by spore-producing tissue.
Complicate—Leaf lobes folded face-to-face (e.g., as in *Porella* and *Scapania*).
Conic/conical—Cone-shaped, with a cylindrical base and rounded apex.
Connate—Fusion of like parts to one another, such as the tips of pseudoperianth segments in *Asterella.*
Connivent—Convergent; brought close together without fusion.
Cordate—Heart-shaped.
Cortex — In the leafy liverworts, often used for the differentiated outer layer (=epidermis): layers of stem cells that surround the non-differentiated central cells (=medulla).
Cortical—Of the cortex or outside.
Crenate—Edge scalloped with rounded teeth.
Crenulate—Slightly or minutely crenate.

Decurrent—Referring to an extension of leaf tissue down the stem below the point of insertion of the leaf on the stem.
Decurved—Broadly curved downwards or backwards towards the ventral stem surface or substrate.
Dentate—With sharp straight teeth of one or more cells in length (see serrate).
Denticulate—With minute or small teeth.
Dichotomous—Apical branching, with paired branches at least initially of equal size.
Dioicous—Antheridia and archegonia on separate gametophytes; separate male and female gametophytic plants.
Distal—In spores, the face away from the center of the tetrad of developing spores; the free outer face.
Dorsal—The morphologically upper surface of a plant; the side opposite the presence of underleaves, scales or rhizoids, or away from the substrate.
Dorsiventral—Flattened and having a distinct dorsal (top) and ventral (bottom) side.

Elaters—In sporophyte capsules, the elongate cells with helical bands of wall thickening; (see pseudoelaters).
Elliptical—Oblong with convex margins of equal length.
Emarginate—Leaf with a shallow notch at the apex; notch deeper than retuse (see retuse).
Emergent — Partly protruding, such as the extent to which the perianth protrudes beyond bracts in *Nardia.*
Epidermis — The outer cell layer of a stem or thallus (see cortex)
Explanate—Open or flattened, as in the ventral lobe of some species of *Frullania.*

Flagelliform—A branch that is either leafless or with small leaves.
Foveolate — With small pits or shallow depressions.
Fuscous—Dull- or grayish-brown.

Galeate— Term applied to specialized helmet-shaped ventral lobes in some species of *Frullania.*
Gametophyte—The haploid, gamete-producing growth phase of the bryophyte life history.
Gemma (pl. **gemmae**)—Specialized unicellular or multicellular asexual reproductive bodies.

Gemma-receptacle—Specialized structure in which gemmae develop.
Geniculate—Bent abruptly, like a knee.
Glaucous—Bluish-gray or whitish in color.
Granulate (granular, granulose)—Covered with very fine projections.
Guard cells—The pair of specialized epidermal cells that surround a pore (stoma) in the sporophyte capsule of many hornworts.

Hyaline -Translucent or nearly transparent.

Incubous—Leaf arrangement in which the front margin (toward the stem apex) of one leaf lies over the rear margin of the leaf in front of it in dorsal view (see succubous).
Incurved—A general term for curving inward or upward.
Inflexed—Abruptly bent upward.
Intercalary meristem—In hornworts, a localized region of active mitotic cell divisions located between the capsule and foot of the sporophyte.
Involucre—Strictly, a sheath of cells that grow upwards from the surface of the thallus or stem around one or more antheridia or archegonia.

Keel—A straight or curved fold or crease between the dorsal and ventral lobes of complicate-bilobed leaves; also, a ridge formed by a sharp longitudinal fold of a perianth.

Laciniate—The margin with narrow irregular lobes.
Lacunose—Having pits or depressions of variable shapes and sizes.
Lanceolate—Gradually narrowed and tapered from the base to a pointed lance-head-like apex; three or more times longer than wide.
Leaf—Lateral photosynthetic structure on stems of liverworts and mosses that is functionally analagous to the leaf of vascular plants.
Linear—Narrow with more-or-less parallel sides.
Lobule—A dimunitive lobe; often used to refer to the smaller dorsal or ventral segment of an unequally lobed leaf.
Lunate—Shaped like a crescent moon.

Marsupium—A specialized, fleshy, protective structure resulting from the downward growth of the stem apex into the substrate, carrying with it the developing sporophyte.
Medulla—The undifferentiated, central, non-cortical region of the stem in the leafy liverworts.
Meristem—Localized region of active mitotic cell division.
Midrib—The thickened, central region of thalloid liverworts, e.g., *Marchantia* and *Metzgeria*.
Monoicous—A general term to denote the development of antheridia and archegonia on the same gametophytic plant.
Monotypic—With only a single species.
Montane—Pertaining to mountains.
Mucilage hair—A short filament terminating in a cell that contains mucilage.

Nodose—With rounded, swollen knobs of cell wall thickening (as in nodose trigones of *Diplophyllum plicatum*).

Oblong—Of leaves, rectangular, with parallel sides and rounded at the apex.
Obovate—Egg-shaped in outline, with the widest part above the middle away from the stem.
Obtuse—Of leaves, blunt or rounded at the apex.
Oil-body—Translucent, opaque or colored oil-containing structure (organelle); **simple** if composed of a single unit; **compound** if composed of subunits.
Oil-cell — A cell with a single very large oil-body; common in the complex thalloid liverworts.
Orbicular—Nearly circular.
Ostiole — The opening or pore in the thallus through which sperm are released from an antheridium in some complex thalloid liverworts.
Ovate—Egg-shaped in outline (two-dimensional), with the widest part below the middle or near the base;.
Ovoid — An egg-shaped solid (three-dimensional).

Palmate—Lobes or branches radiating out as in fingers on a hand.
Papilla (pl. **papillae**)—Conical projections resembling nipples on a surface, as in papillose walls.
Parenchyma—Thin-walled tissue.
Paroicous—Male and female sex organs on the same gametophytic branch; antheridia develop immediately behind or below (away from apex) the archegonia.
Pegged rhizoids—Rhizoids with small, localized deposits of wall material (like pegs) on the inner wall surface.
Perennation—A means to persist for many years (as in tuber formation in hornworts).
Perianth—Strictly, a tubular sheath formed by the fusion of two or more modified leaves that surrounds a developing sporophyte of leafy liverworts.

Perigynium—A fleshy, tubular structure developed at the apex of a female branch after fertilization, surrounding the developing sporophyte.
Pinnate—Branches borne more-or-less regularly on either side of a stem.
Plicate—Longitudinal folds, like pleats.
Pore—An opening through the epidermis to the interior thallus tissue. 1) **compound pores:** pores surrounded by rings of superposed cells (like a barrel with open top and bottom) that project above the dorsal surface and below into the air-chamber, and 2) **simple pores:** pores surrounded by one or more concentric rings of non-superposed cells that project only above the dorsal surface.
Posterior—Away from the stem apex.
Proximal — In spores, the face toward the center of the tetrad of developing spores; the inner face.
Pseudoelater — In hornwort sporophyte capsules, multicellular or unicellular sterile cells with protoplasmic contents; false elaters (see elater).
Pseudoperianth—Strictly, a tubular sheath that develops post-fertilization from thallus tissue; each pseudoperianth surrounds a single sporophyte, e.g., *Asterella, Fossombronia.*
Punctate—With minute depressions or pits.
Pyriform—Pear-shaped.

Receptacle—Specialized sessile or stalked thallus tissue that bears sexual or asexual reproductive structures in some complex thalloid liverworts.
Recurved—Bent or curved downward in reference to the stem or thallus axis, or leaf margin.
Reflexed—Abruptly bent or curved downward or backward.
Reniform—Kidney-shaped; broadly rounded margins and a shallow sinus.
Repand—With an undulate, wavy or sinuate margin.
Reticulate—With a network-like pattern.
Retuse—A broad, shallow indentation in the otherwise truncate apex of a leaf (see emarginate).
Rhizoid—In liverworts and hornworts, a unicellular filament from the ventral surface of a stem or thallus and attaching the plant to the substrate. See also pegged rhizoids and smooth-walled rhizoids.

Secund—Leaf apices most or all turned to one side, such as the leaves of *Herbertus.*
Serrate—With teeth pointing toward the apex (see dentate).
Sexuality—See autoicous, dioicous, monoicous, paroicous.
Slime canals—Canals formed by the dissolution of end walls of files of cells that are filled with mucilage (slime).
Slime papilla—Ephemeral, thin-walled cell with swollen tip that exudes mucilage and protects the growing point.
Smooth-walled rhizoid—A rhizoid that lacks internal localized deposition (pegs) of wall material.
Spinose—Having large sharp-pointed teeth or spines.
Spinulose—Having small fine-pointed teeth or spines.
Sporangium — See capsule.
Sporophyte—The diploid, spore-producing growth phase of the bryophyte life-history.
Squarrose—Part of the leaf bent at an angle of 90 degrees or more from the rest of the leaf.
Stolon/Stoloniferous—A slender stem with or without minute leaves.
Stoma (pl. **stomata**; also called **stomate** and **stomates**)—A small pore surrounded by two guard cells leading into the photosynthetic tissue, as in the sporophyte capsule of many hornworts.
Subulate—Narrow and triangular, tapering from the base to an acute or long-acuminate apex.
Succubous—Leaf arrangement in which the rear margin of one leaf lies over the front margin of the leaf behind it in dorsal view (see incubous).
Superposed—Positioned one above the other.

Tetrad—The four haploid spores resulting from meiosis.
Thallus (pl. **thalli**)—A flattened gametophyte not differentiated into stem and leaf.
Transverse—Perpendicular to the long axis of the stem or thallus.
Trichome—A general term for an epidermal outgrowth, such as a hair or cilium.
Trigone—A cell wall thickening in the corners of cell lumens where three (or more) cells meet; of variable sizes and shapes, such as minute, large, concave, convex, bulging, and coalescent.
Triradiate ridge—Ridge on the inner face of a spore resulting from the attachment of the other three spores during spore development following meiosis.
Truncate—An apex (such as of a perianth) that ends or is folded abruptly, nearly at right angles to the main axis of the structure.
Tubercle—A small blunt (not sharp) swelling, nodule or protuberance.

Underleaf—Leaves on the morphological ventral side of the stem, as in many species of leafy liverworts.
Uniseriate—Cells in a single linear series.
Unistratose—A flat layer of cells, one cell in thickness.

Valves—Differentiated sections of the sporophyte capsule wall that separate during capsule dehiscence and spore discharge.
Ventral—The morphologically lower surface of a plant; the side bearing underleaves, scales or rhizoids, or adjacent to the substrate.

Vermiculae — Microscopic long, narrow worm-like structures.
Verrucose—Warty; with small wart-like projections.
Vinaceous—Purplish-red; wine colored.
Vitta—A row or band of longer and/or thicker-walled cells in the central part or base of a leaf and differentiated from the adjacent cells.

Wing—In vegetative plants of thalloid liverworts, the thallus tissue between the midrib region and the lateral margins. When present in spores, the area of the spore coat between the distal and proximal faces.

Appendix II

SYNONYMS

Various names historically have been applied to California liverworts and hornworts. This list of synonyms provides a crosswalk to names selected for this catalogue. The old names precede the currently accepted names.

Anthoceros carolinianus Michx. = *Phaeoceros carolinianus*
Anthoceros hallii Austin = *Phaeoceros hallii*
Anthoceros pearsoni M. Howe = *Phaeoceros pearsonii*
Anthoceros phymatodes M. Howe = *Phymatoceros bulbiculosus*
Aplozia Dumort. = *Jungermannia*
Aplozia riparia (Taylor) Dumort. = *Jungermannia atrovirens*
Aplozia sphaerocarpa (Hook.) Dumort. = *Jungermannia sphaerocarpa*
Asterella ludwigii auct. pl. = *A. gracilis*
Asterella violacea (Austin) Underw. = *A. bolanderi*
Calypogeia trichomanes auct. = *C. azurea*
Cephalozia affinis Lindb. ex Steph. = *C. lunulifolia*
Cephalozia lammersiana (Huebener) Carrington = *C. bicuspidata* subsp. *lammersiana*
Cephalozia media Lindb. = *C. lunulifolia*
Cephalozia turneri (Hook.) Lindb. = *Cephaloziella turneri*
Cephaloziella byssacea (Roth) Warnst. = *C. divaricata*
Cephaloziella byssacea var. *scabra* (M. Howe) R. M. Schust. = *C. divaricata* var. *scabra*
Cephaloziella limprichtii Warnst. = *C. stellulifera*
Cephaloziella papillosa (Douin) Schiffn. = *C. divaricata* var. *scabra*
Cephaloziella starkei (Funck ex. Nees) Schiffn. = *C. divaricata*
Cephaloziella subdentata Warnst. = *C. spinigera*
Chiloscyphus fragilis (Roth) Schiffn. = *C. pallescens* var. *fragilis*
Chiloscyphus latifolius (Nees) J. J. Engel & R. M. Schust. = *Lophocolea bidentata*
Chiloscyphus polyanthos (L.) var. *pallescens* (Ehrh. ex Hoffm.) Hartm. = *C. pallescens*
Chiloscyphus profundus (Nees) J. J. Engel & R. M. Schust. = *Lophocolea heterophylla*
Chilocsyphus rivularis (Schrad.) Loeske = *C. polyanthos* var. *rivularis*
Clevea Lindb. = *Athalamia*
Clevea hyalina (Sommerf.) Lindb. = *Athalina hyalina*
Fossombronia hispidissima Steph. = *Fossombronia longiseta*
Grimaldia Raddi = *Mannia*
Herbertus hutchinsiae auct. amer. = *Herbertus aduncus* var. *aduncus*
Jungermannia bolanderi Gottsche ex Underw. (non [Austin] Austin) = *J. confertissima*
Jungermannia danicola Gottsche ex Underw. = *J confertissima*
Jungermannia lanceolata auct. *sensu* Schrad. (non *J. lanceolata* L.) = *J. leiantha*
Jungermannia pendletonii (Pears.) A. Evans = *J. exsertifolia* subsp. *cordifolia* var. *pendletonii*
Jungermannia pumila With. var. *polaris* (Lindb.) Berggr. = *J. polaris*
Jungermannia riparia Taylor = *J. atrovirens*
Jungermannia schiffneri (Loitl.) A. Evans = *J. polaris*
Jungermannia tristis Nees = *J. atrovirens*
Kantia Lindb. = *Calypogeia*
Leiocolea alpestris (F. Weber) Isov. = *Lophozia collaris*
Leiocolea bantriensis (Hook.) Jörg. = *Lophozia bantriensis*
Leiocolea gillmanii (Austin) A. Evans = *Lophozia gillmanii*
Leiocolea heterocolpa (Thed.) H. Buch = *Lophozia heterocolpos*
Leiocolea obtusa (Lindb.) H. Buch = *Lophozia obtusa*
Leiocolea muelleri (Nees) Jörg. = *Lophozia collaris*
Lophozia alpestris auct. = *L. sudetica*
Lophozia baueriana Schiffn. = *Barbilophozia hatcheri*
Lophozia guttulata (Lindb. & Arnell) A. Evans = *L. longiflora*
Lophozia hatcheri (A. Evans) Steph. = *Barbilophozia hatcheri*
Lophozia hornschuchiana Macoun = *L. bantrienses*
Lophozia inflata (Huds.) M. Howe = *Gymnocolea inflata*

Lophozia latifolia R. M. Schust. = *L. jurensis*
Lophozia lycopodioides (Wallrich.) Cogn. = *Barbilophozia lycopodioides*
Lophozia muelleri (Nees) Dumort. = *L. collaris*
Lophozia opacifolia Culm. ex Meyl. = *L. incisa* subsp. *opacifolia*
Lophozia ovata (Dicks.) M. Howe = *Douinia ovata*
Lophozia porphyroleuca (Nees) Schiffn. = *L. longiflora*
Lunularia vulgaris Michx. = *L. cruciata*
Macrodiplophyllum plicatum (Lindb.) Perss. = *Diplophyllum plicatum*
Madotheca Dumort. = *Porella*
Madotheca cordaeana (Huebener) Dumort. = *Porella cordaeana*
Madotheca navicularis (Lehm. & Lindenb.) Dumort. = *Porella navicularis*
Madotheca roellii Steph. = *Porella roellii*
Marchantia alpestris (Nees) Burgeff = *M. polymorpha*
Marchantia aquatica (Nees) Burgeff = *M. polymorpha*
Marsupella sullivantii (De Not.) A. Evans = *M. sphacelata*
Metzgeria fruticulosa (Dicks.) A. Evans = *M. violacea*
Nardia hyalina (Lyell) Lindb. = *Jungermannia hyalina*
Nardia rubra (Gottsche) A. Evans = *Jungermannia rubra*
Neesiella Schiffn. = *Mannia*
Phaeoceros bulbiculosus (Brot.) Prosk. = *Phymatoceros bulbiculosus*
Phaeoceros laevis (L.) Prosk. subsp. *carolinianus* (Michx.) Prosk. = *P. carolinianus*
Plagiochila satoi S. Hatt. = *P. porelloides*
Plectocolea hyalina (Lyell) Mitt. = *Jungermannia hyalina*
Plectocolea rubra (Gottsche ex Underw.) H. Buch et al. = *Jungermannia rubra*
Porella rivularis (Nees) Trevis. = *P. cordaeana*
Prionolobus turneri (Hook.) Spruce = *Cephaloziella turneri*
Radula spicata Austin = *R. bolanderi*
Riccardia major Lindb. = *R. chamedryfolia*
Riccardia pinguis (L.) Gray = *Aneura pinguis*
Riccardia sinuata (Dicks.) Trevis = *R. chamedryfolia*
Riccia americana M. Howe = *R. lamellosa*
Riccia austini Steph. = *R. lamellosa*
Riccia crystallina auct. = *R. cavernosa*
Riccia lescuriana Austin = *R. beyrichiana*
Riccia minima L. = *R. sorocarpa*
Scapania bolanderi var. *americana* (Müll. Frib.) Frye & L. Clark = *Scapania americana*
Scapania granulifera A. Evans = *S. americana*
Scapania heterophylla M. Howe = *S. undulata* var. *undulata*
Scapania oakesii Austin = *S. undulata* var. *oakesii*
Scapania plicata (Lindb.) Potemkin = *Diplophyllum plicatum*
Solenostoma atrovirens (Dumort.) Müll. Frib. = *Jungermannia atrovirens*
Solenostoma cordifolium (Dumort.) Steph. = *Jungermannia exsertifolia* var. *cordifolia*
Solenostoma hyalinum (Lyell) Mitt. = *Jungermannia hyalina*
Solenostoma polaris (Lindb.) R. M. Schust. = *Jungermannia polaris*
Solenostoma pumilum (With.) Müll. Frib. = *Jungermannia pumila*
Solenostoma pumilum subsp. *polaris* (Lindb.) R. M. Schust. = *Jungermannia polaris*
Solenostoma rubrum (Gottsche ex Underw.) R. M. Schust. = *Jungermannia rubra*
Solenostoma schiffneri (Loitl.) A. Evans = *Jungermannia polaris*
Solenostoma sphaerocarpa (Hook.) Steph. = *Jungermannia sphaerocarpa*
Solenostoma triste (Nees) Müll. Frib. = *Jungermannia atrovirens*
Sphaerocarpos californica Austin = *S. texanus*

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ERRATA: PAGE 96
The first key Liverwort or Hornwort should be:
Liverwort: p. 96
Hornwort p. 185

The second key on that page should be:
Complex Thalloid Liverworts: p. 96
Leafy Liverworts: p. 133
Sphaerocarpoids: p. 119
Simple Thalloid Liverworts: p. 124