A revision of Californian *Porella* (Hepaticae)

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Four species, *Porella bolanderi* (Aust.) Pears., *P. cordaeana* (Hüb.) Moore, *P. navicularis* (Lehm. & Lindenb.) Lindb., and *P. roellii* Steph. (Hepaticae) occur in California. All of them except *P. cordaeana* are endemic to Western North America. *Porella platyphylla* (L.) Pfeiff. and *P. platyphylloidea* (Schwein.) Lindb. do not occur in California. A key to the species, table of characters, and illustrations, descriptions and distribution maps are provided for every species.

Key words: California, Hepaticae, North America, Porella, taxonomy

Howe (1897), Barbour (1902) and Frye and Clark (1947) have studied North American Porella L., Schuster (1980) those of E North America. Hong (1983) published a key, discussion and distribution maps of the taxa of W North America. In spite of these studies, the distinguishing characters of the species seem to be poorly understood. In none of the studies above the IKI (iod kalium iod) reaction (see Nultsch & Grahle 1971) of the species has been tried, even though the reaction was used already by Müller (1954-57, see also Hattori 1967, 1976) for Porella. IKI turns the starch molecules violet, a method well known and widely used in vascular plant anatomy. This IKI reaction would make the separation of *Porella cordaeana* (Hüb.) Moore easy from the other taxa. When it comes to distinguishing *P. cordaeana* from *P. platyphylla* (L.) Pfeiff. outside California, where they both occur, the matter becomes somewhat more complicated.

Both of these species, and *P. platyphylloidea* (Schwein.) Lindb., turn violet by IKI, which reveals the close relationship between these taxa. The status of these three species should be carefully studied not only in North America but also in Europe and Asia. In the present paper, the characters of the four species occurring in California are clarified (Table 1).

In the present study 561 specimens collected in California were studied. Most of the specimens were collected by Daniel Norris, but 90 specimens were on loan from CAS. In addition some taxa preserved in H were studied. UC and LAM did not send the requested specimens to the senior author. Specimen citations are limited to ones representative of counties of distribution. The specimens from CAS are cited according to the herbarium code, all the other specimens without indication are preserved in H. The complete list is available from the senior author.

Key to Californian Porella

- Plants flaccid, not glossy or somewhat glossy; underleaves 1.2–2 X wider than ventral leaf lobes; underleaf and ventral leaf lobe margins less or not incurved; perianth mouth toothed, or entire if contracted

- 3. Very flaccid; leaf margins very deflexed; basal leaf margins toothed; ventral leaf lobe 2/5–3/5 of dorsal lobe width; underleaf bases usually toothed or laciniate; female branches without normal leaves .. P. bolanderi

Porella bolanderi (Aust.) Pears. (Figs. 1, 2)

List Canad. Hep. Geol. & Nat. Hist. Survey Canada 7. 1890. — *Madotheca bolanderi* Aust., Bull. Torrey Bot. Club 3: 14. 1872. — Type: USA. California, 1865 *Bolander*, Hb. Pearson ex Hb. Austin (BM!, holotype, isotypes S!, H-SOL!).

Dioicous. Plants in loose mats, not glossy, dark green to yellowish green, olive green or greyish green, shoots 2-4 mm wide. Stems prostrate to somewhat pendulous, 1.5-6 cm long, almost simple, once pinnate or occasionally 2-pinnate. Leaves densely imbricate, keel quite short to almost non-existent. Dorsal lobe of leaf obliquely ovate, widely spreading, somewhat adaxially concave, 1.5–3 mm long and 0.7-2.1 mm wide, $1.6-2.5 \times$ as long as the ventral lobe, the insertion line arching around the stem in a semicircle and ending at or only little above the level of keel base, not or little decurrent; apex widely to obtusely rounded, often somewhat deflexed; margins slightly incurved when moist, much more incurved when dry; postical margin undulate, base usually with one or more teeth or cilia; antical margin usually sinuate, more rarely somewhat toothed, especially at base, base arching 1/3 to 1 the stem width beyond the stem. Ventral lobe ovate-lanceolate to linear-lanceolate or rarely almost subulate, erect with the long axis almost parallel with the stem, distinctly adaxially convex, 0.4–1.2 mm long and 0.1–0.6 mm wide, the insertion line only little arching upward on the stem and descending to ca. 1/2-3/4 the stem width below keel base level, long decurrent; apex obtuse to acute; margin sometimes distinctly recurved, entire to sinuate, near the bases toothed to laciniate-toothed, near ventral base sometimes entire. Cells in the middle of dorsal lobe 20–38 µm, in the margin and apex $16-30 \mu m$, in the base $25-62 \mu m$, almost isodiametric, thin-walled, trigones rather small. Underleaves ovate, erect with usually recurved tip, adaxially convex, 0.4–1.3 mm long and 0.4–1 mm wide, ca. 2×the width of ventral lobe, a little wider than the stem, the insertion line arching up the stem for 1/2 to 3/4 the stem width, long decurrent on both sides; apex mostly recurved, acute to emarginate or somewhat 2-toothed but usually rounded; margin plane or recurved, often undulate, entire to sinuate, the bases usually with 2-3 teeth or laciniae. Male branches lateral, usually primary, oblong to almost linear, 2–4 mm long. Female branches very common on main shoot, lateral, short, without normal leaves, the underleaf adjacent to the female branches emarginate or 2-toothed at apex. Female bracts larger than the leaves, dorsal lobe acute to obtuse, ventral lobe acute to subulate-pointed, margins entire to toothed above and ciliate-caudate or cilate-laciniate at base; bracteoles free, large, ovate, commonly acute, toothed above, caudate or ciliate-laciniate toward base. Perianth broadly ovoid from a short obconic base, 1–2 mm long and 0.9–1.5 mm wide, dorsiventrally flattened, plicate especially ventrally, narrowed at mouth, mouth ca. 1/2 as wide as perianth, deeply 2-lipped, lips ciliate. The seta, sporangium, elaters and spores were described by Frye and Clark (1946).

Illustrations: Barbour 1902: 33, 36 (figs. 2 and 8), Frye & Clark 1946: 730.

Porella bolanderi is a fairly distinctive species: not glossy, usually not yellowish, very flaccid, curly with inflexed and deflexed leaves especially when dry (Table 1). It is rather small for a Porella. Branching is simple or sparse. In contrast to other local species, the margins of the dorsal lobes are basally toothed (note, however, that very small teeth can sometimes be found in P. cordaeana). Insertion of the ventral lobe on the stem continues distinctly below the keel base. Ventral lobes are short compared to dorsal lobe width. Underleaf bases are toothed or laciniate. Female branches are very numerous and without normal leaves, which causes the ventral side of plants to look disordered.

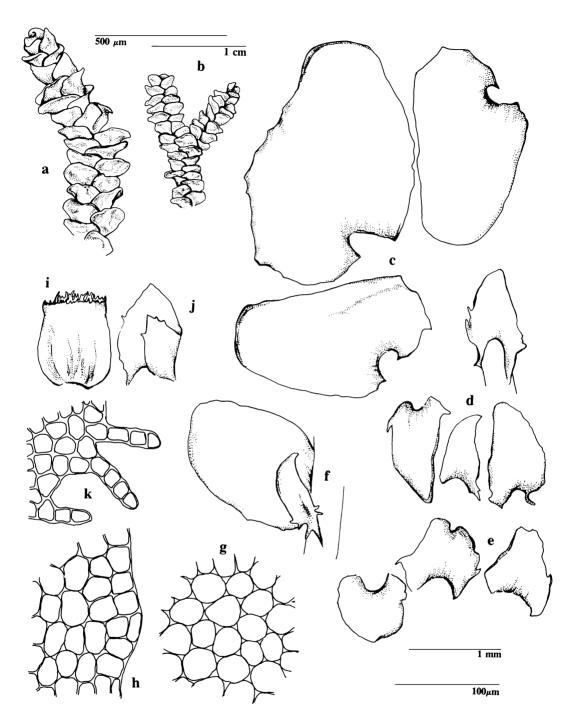


Fig. 1a–k. *Porella bolanderi* (Aust.) Pears. (from *Norris 58135*). — a: Dorsal habit in dry condition. — b: Dorsal habit in wet condition. — c: Dorsal leaf lobes. — d: Ventral leaf lobes. — e: Underleaves. — f: Dorsal and ventral leaf lobe. — g: Median cells of dorsal leaf lobe lamina. — h: Marginal cells of dorsal leaf lobe. — i: Perianth. — j: Female bract. — k: Perianth mouth. — The 100 μ m scale for g, h, k, the 1 mm scale for c–f, i, j, the 500 mm scale for a, and the 1 cm scale for b.



Fig. 2. Distribution of *Porella bolanderi* (Aust.) Pears. in California.

Porella bolanderi occurs at the altitudes 0–2 000 m. However, it is far more common at 100–750 m. Most often it grows on outcrops and boulders, including limestone, siliceous, serpentine or sandstone. The species is sometimes found on soil. If it grows as an epiphyte, it is most common on Quercus, but sometimes is found also on Aesculus, Umbellularia, Platanus or Acer macrophyllum. The species is most common in open oak forests. It is, however, met in other kind of forests, such as open Pseudotsuga-forest, open Abies magnifica or Sequoia sempervirens forests with scattered meadows, and Pseudotsuga-Quercus/Acer/Arbutus/Platanus-forests. It also occurs in other kinds of mixed conifer forests with Pinus coulteri and P. ponderosa.

Porella bolanderi is scattered in a large portion of California (Fig. 2). It occurs through the coastal part of the state, but is also encountered inland. Judging from the distribution in California, the species probably occurs also in Baja California. So far it is endemic to North America, known only from W North America (see map in Hong 1983).

Range in California (only selected specimens seen listed; number of studied specimens per county given in parentheses; total amount of specimens seen 66, see Fig. 2): BUTTE COUNTY (2): Oroville Dam Quad., 39°22′N 121°30′W, in

oak-digger pine woodland opposite spillway of Oroville Dam, on moist, diffusely lit base of oak, 1979 Norris 52578. CONTRA COSTA COUNTY (3): Berkeley, in campo Universitatis Californiae, ad corticem Quercus agrifoliae, Parks (Schiffner, Krypt. Exs. Ed. Mus. Hist. Nat. Vind. 3073). HUMBOLDT COUNTY (1): In douglas fir and tan oak forest on large sandstone outcrop ca. 1 mile SW of Eel Rock, Sec. 20, T2S, R4E, ca. 1 500 ft., on moist diffusely lit rock outcrop, 1980 Norris 56202. LAKE COUNTY (2): On boulders near road in Clear Lake State Park, 1968 Carmiggelt (3 spec.). LOS ANGELES COUNTY (4): Puddingstone Canyon, 2 mi. from San Dimas, 750 ft., 1943 Sweet 140 (CAS, 2 spec.). Santa Catalina I., on rock in deep canyon above White's Landing, 5 miles N of Avalon, 1953 Steere (CAS-505749). MARIN COUNTY (10): South Novato in oak woodlands along lower Fairway Drive, on bark at base of Aesculus californica, 1973 Jenkinson. MARIPOSA COUNTY (1): In live oak forest in steep-sided canyon of East Fork of Chowchilla River at Hwy 49, 37°28'N 119°44'W, 3 200 ft., on moist shaded boulder, 1978 Norris 51092. MENDOCINO COUNTY (7): Boonville Quad., 39°05'N 123°29'W, in riverine forest with redwood and oaks along Greenwood Ridge Road at Navarro River near entrance to Hendy Woods State Park, ca. 300 ft., on moist, diffusely lit bark of *Umbellularia*, 1979 Norris 53115. MONTEREY COUNTY (4): On very open oak forest on massive rock outcrop near Wagon Cave Campground, Sec. 26 RSE, T21S, ca. 1 500 ft., on fairly moist, rather shaded boulder, 1977 Norris 48541. NAPA COUNTY (1): In lawns with planted live oaks in Crane Park, St. Helena, on moist, diffusely lit bark of live oak, 1977 Norris 48236. ORANGE COUNTY (1): Upper Trabuco Cyn., Santa Ana Mts., steep shaded canyon, riparion of oak and bay laurel, 1 500 ft., on damp soil, 1975 Shevock 3990. RIVERSIDE COUNTY (3): In chaparral with live oaks in canyons near Ortega Oaks Campground, Cleveland National Forest, 33°37′N 117°25′W, on moist, diffusely lit boulder, 1981 Norris 58124: 58135. SAN BENITO COUNTY (1): Vancouver Pinnacles, alt. 1 100 ft., 1917 Abrams (CAS-505713). SAN BERNARDINO COUNTY (1): Bonita Creek, 100 yards below Bonita falls, San Bernardino National forest, along creek, in oak and bay laurel association, on damp soil, 1975 Shevock 4004. SAN DIEGO COUNTY (1): In oak and ponderosa pine forest ca. 1 mile N of Cuyamaca Grande State Park Hdgts, 32°58′N 116°34′W, ca. 4 800 ft., on fairly moist, rather sunny boulder, 1977 Norris 50731. SAN LUIS OBISPO COUNTY (2): In live oak and Coulter pine forest in deep canyon about 1.5 miles W of jct. roads to Black Mtn. and that to Navajo Camp, 35°22′N 120°21′W, ca. 2 300 ft., on moist, shaded soil in boulder crack, 1979 Norris 55267. SAN MATEO COUNTY (5): Along Flume Trail near Boulder Creek bridge, Filoli Center, just north of Woodside, shaded side of boulder in Ouercus agrifolia forest, 1994 Whittemore 4405 (CAS-788073). SANTA BARBARA COUNTY (1): Along road ca. 4 miles S of Solvang in Santa Ynez Mtns., 34°33′N 120°09′W, 200 m, in large oak forest with grassy clearings, 1982 Norris 68165. SANTA CLARA COUNTY (3): In madrone, douglas fir forest on steep north facing slopes above Uva Creek in Uva Canyon County Park S of San Jose,

ca. 1 000 ft., on fairly moist, diffusely lit bark of oak, 1977 Norris 48599. SANTA CRUZ COUNTY (1): In cut-over redwood forest with scattered grassy meadows on campus of the University of California, Santa Cruz, 37°59.5'N 122°0.3'W, 700 ft., on moist, diffusely lit bark of oaks, 1980 Norris 55658. SHASTA COUNTY (3): In douglas fir, tan oak, and big-leaf maple forest in deep steep walled ravine in extensive limestone outcrop along Hwy. 299 ca. 24 miles E of Redding, on moist, diffusely lit boulder, 1972 Norris 21572, 21573. SISKIYOU COUNTY (1): On dry, sunny siliceous rock along road in canyon live oak forest, south fork of Salmon River at West Fork, 41°09'N, 123°13'W, 1968 Norris 10103. STANISLAUS COUNTY (1): Knights Ferry, 1923 Eastwood (CAS-119231). TRINITY COUNTY (5): In open red fir forest with scattered grassy meadows in area of granitic outcrops near Browns Meadows, 41°3′N 122°58′W, ca. 6 000-6 600 ft., on very moist, shaded soil and rocks along river, 1972 Norris 23155. VENTURA COUNTY (2): In incense cedar, bigcone douglas fir forest in canyon of Potrero John Creek near Hwy. 399, 34°35.5′N 119°16′W, ca. 3 750 ft., on moist, diffusely lit north face sandstone cliff, 1979 Norris 55522, 55523. YUBA COUNTY (1): Along Hwy. 20 near Timbuctoo, 39°13′N 121°19′W, 60 m, on moist, diffusely lit boulder in open oak forest, 1981 Norris 67495. — Additionally reported from the following counties: Alameda, Glenn, Placer, and Sonoma (Howe 1897, Hong 1983).

Total range: California, Utah, Oregon (Frye & Clark 1946, Hong 1983). — Map: Hong 1983: 147 (fig. 1).

Porella cordaeana (Hüb.) Moore (Figs. 3–5)

Proc. R. Irish Acad., Ser. 2, 2: 618. 1876. — *Jungermannia cordaeana* Hüb., Hepaticol. Germanica 291. 1834. — *Madotheca cordaeana* (Hüb.) Dum., Bull. Soc. R. Bot. Belgique 13: 25. 1874. — Type: Germany. Vogesen, am Kalmit bei Kaiserslaufern, *Hübener* (not seen).

Dioicous. Plants in loose mats or wefts, somewhat glossy to lustreless, yellowish green, sordid or bright dark green, yellowish, olive or grayish brown, turn violet with IKI, shoots 3-4 mm wide. Stems prostrate or procumbent, 3–10 cm long, irregularly 1–2-pinnate, branches numerous with branched plants somewhat fan-shaped. Leaves approximate to imbricate, keel very short or almost lacking. Dorsal lobe of leaf widely obliquely ovate, widely spreading, nearly flat, 1–2.4 mm long and 0.8–2.4 mm wide, 2.5–3.5 × as long as the ventral lobe, the insertion line arching upward on the stem in a semicircle or even higher curve and ending between the level of keel base and a stem width above it, antically decurrent; apex sometimes slightly reflexed, rounded; margins entire or sinuate, postical portion of dorsal margin often somewhat toothed. Ventral lobe obliquely ovate or nar-

rowly triangular, erect-spreading, adaxially convex, 0.4–1.1 mm and 0.2–1.1 mm wide (including the decurrent portion), the insertion line curving down the stem and ending 1-2 stem widths below keel base level, very long decurrent; apex acute; margin widely recurved, postical margin more recurved than the antical one, entire, undulate, the base and decurrent part often toothed. Cells in the dorsal lobe 23–43 µm, those near keel only little smaller, near the base 28–50 µm long and 22–33 µm wide, at the margins 15–25 µm, the cells in the outermost marginal row may be somewhat elongate, cells isodiametric, thin-walled, trigones minute to small, cuticle smooth. Underleaves roundish-quadrate, erect, distant to approximate, rarely imbricate, adaxially convex, 0.3–0.7 mm long and 0.4–1.1 mm wide (with the decurrent portion), ca. $2 \times$ the width of ventral lobe, the insertion line curving up stem in a long arch for more than a stem width; apex rounded; margin plane or slightly recurved, entire or sinuate but at base toothed and undulate-crispate. Male plants usually in separate patches, male spike comprising a short lateral branch. Female branches very short and modified, lateral, without normal leaves. Female bracts much smaller than the leaves, keel long; dorsal lobe ca. $2 \times$ as long as the keel and $1.2-1.5 \times$ as long as the ventral lobe, ventral lobe acute to obtuse, bracteole free. Both lobes of the modified leaves beneath the bracts often somewhat toothed at base. otherwise entire or merely sinuate. Perianth broadly ovoid, 2–3 mm long and ca. 2 mm wide, dorsiventrally compressed especially at mouth, 2-lipped with the one sinus much deeper than the other, slightly curved toward the ventral side, lips entire or sometimes somewhat sinuate-toothed. Seta, sporangium, elaters and spores were described by Frye and Clark (1946).

Illustrations: Macvicar 1926: 414, Buch 1936: 100 (fig. 8) as *Madotheca cordaeana*, Frye & Clark 1946: 732, Müller 1954–57: 1217 (fig. 471) as *M. cordaeana*, Smith 1990: 249 (fig. 109: 7–13).

Porella cordaeana is often fan-shaped, very variable both in size and in colour, depending on the habitat (Table 1). Some plants are dark green especially when growing in wet conditions, but they are usually yellowish green to brownish. Often the plants seem jointed especially in dry habitats. Ventral leaf lobes are small with their bases typically undulate and very long-decurrent, apices usually more obtuse than those of *P. bolanderi* and *P. roellii*. Under-

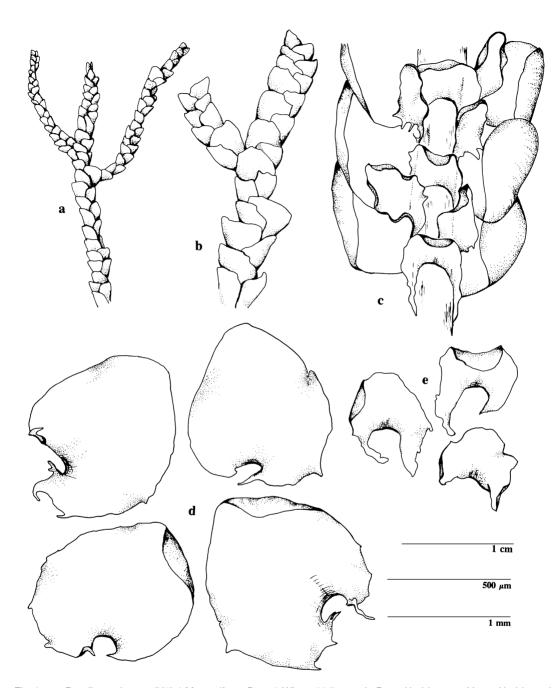


Fig. 3a–e. *Porella cordaeana* (Hüb.) Moore (from *Dorn & Winter 299*). — a, b: Dorsal habits. — c: Ventral habit. — d: Dorsal leaf lobes. — e: Underleaves. — The 1 mm scale for c–e, the 500 μ m scale for b, and the 1 cm scale for a.

leaf bases are undulate-crispate. Dorsal leaf lobes are almost flat. The perianth mouth differs from that of other Californian *Porella* species, in being contracted.

The plants turn violet with IKI, some specimens more so than others. This is an extremely good char-

acter in California where the other IKI-reactive species *Porella platyphylla* and *P. platyphylloidea* do not occur. This IKI reaction of *P. cordaeana* has apparently been overlooked because of Müller (1954), who wrote that the species "zeigt nicht immer die Saponarinreaktion mit Jod". The first author studied

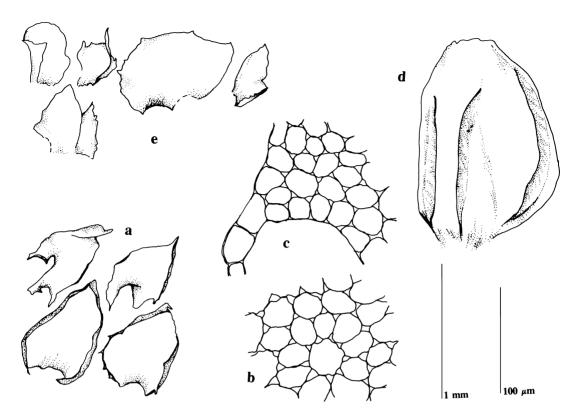


Fig. 4a–e. *Porella cordaeana* (Hüb.) Moore (from *Dorn & Winter 299*). — a: Ventral leaf lobes. — b: Median cells of dorsal leaf lamina. — c: Marginal cells of dorsal leaf lobe. — d: Perianth. — e: Female bracts. — The 100 μ m scale for b, c, and the 1 mm scale for a, d, and e.

a lot of N European material and found a distinct IKI reaction. Every specimen from California having typical characters of *P. cordaeana* turned violet with IKI.

In the material studied by the first author, *Porella cordaeana* has often been misnamed as *P. platyphylla* or *P. platyphylloidea*. Formerly it has been named even as *P. navicularis* var. B. *Thuja* Nees, and this has been a major factor in the misunderstanding of the genus. The status and distinctive characters of *P. platyphylloidea* (sometimes considered conspecific with *P. platyphylla*) are given and discussed by Frye and Clark (1946), Schuster (1980) and Hong (1983).

Porella cordaeana occurs only in W North America, even though it occurs in all of Europe. However, the status of *P. cordaeana* and its relationships with *P. platyphylla*, which occurs both in Europe and North America, need to be studied. European floras (Macvicar 1926, Buch 1936, Müller 1956, Smith 1990) distinguish the two species on the following bases: in *P. platyphylla* ventral leaf

lobe 1/5 of dorsal lobe and ca. 2/3 of the width of underleaf, underleaves 2–3 × the stem width, and their decurrent portion not undulate, and perianth mouth toothed or ciliate; in *P. cordaeana* ventral leaf lobe 1/9 of dorsal lobe and less than 1/2 of the width of underleaf, underleaves hardly wider than stem, and their decurrent portion undulating, and perianth mouth almost entire. However, Schuster (1980) claims that even these discriminating characters vary making distinction of the taxa difficult.

Porella cordaeana occurs at altitudes 0–2 250 m in California. The species is most common at 750–2 000 m, with the result that most inland and high elevation specimens of Porella are P. cordaeana. It is most common in N California, being specially common in northwestern parts of the state (Fig. 5). The species is almost confined to boulders and outcrops, both dry ones and those along rivers. Outcrops may also be limestone, serpentine or siliceous. The species is rare on logs or soil. When it occurs on trees, they are Sambucus,

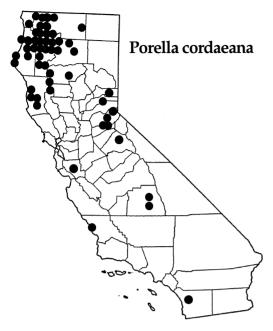


Fig. 5. Distribution of *Porella cordaeana* (Hüb.) Moore in California.

Acer macrophyllum, Quercus, Corylus, Holodiscus or Umbellularia. Porella cordaeana is most common in open or rich mixed conifer forests. Tree species are very diverse, e.g. Pseudotsuga, Quercus chrysolepis, Lithocarpus, Calocedrus, Chamaecyparis, Castanopsis, Abies concolor, Pinus lambertiana, P. ponderosa, P. jeffreyi, Acer macrophyllum etc. Sometimes it occurs in deciduous forests or in open (alpine) (sub)scrub or grassy meadows.

Range in California (only selected specimens seen listed; number of studied specimens per county given in parentheses; total number of specimens seen 166, see Fig. 5): DEL NORTE COUNTY (23): In very rich mixed conifer forest in river canyon, along trail from Wilderness Falls to Doe Flat, 41°51'N 123°39'W, 41°50′N 123°41′W, on moist, diffusely lit outcrop along river, 1 200 m, 1982 Norris 67750. EL DORADO COUNTY (6): In mixed conifer forest along South Fork of American River at Bridal Veil Falls Campground, 120°29'W 38°46'N, ca. 3 200 ft., 1981 Norris 58374. GLENN COUNTY (4): On serpentine mountain top and adjacent scree slopes at Black Butte, 39°43′N 122°52′W, on fairly moist shaded reces in outcrop, 1976 Norris 47971, 47980. HUMBOLDT COUNTY (39): In very open forest of incense cedar on barren granitic slopes on headwaters of Oregon Creek N of Trinity Summit Guard Station, 41°05'N 123°29′W, on moist, diffusely lit granite outcrop, no direct rainfall, 5 600-6 000 ft., 1977 Norris & Creek 50091, 50108, 50150. In very large, old-growth mixed conifer forest along small creek on Long Ridge near headwaters of Bunch Grass Creek ca. 0.9 miles N of Big Hill Rd., on moist shaded

boulder, Sec. 1, T8N, R5E, ca. 4000 ft., 1976 Norris 47805. MARIPOSA COUNTY (1): Yosemite Mts./Sierra Nevada, in small ravine above Wawona, primitive rocks, wet, ca. 1 460 m, on rock, 1981 R. & I. Duell 2116/2, MENDOCINO COUNTY (7): In open oak forest with grassy meadows along South Fork of Eel River in Branscomb Reserve of the Nature Conservancy, N of Branscomb, Secs. 20 & 21, R16W, T22N, on moist to submerged, diffusely lit boulder, 1 200-1 400 ft... 1976 Norris 47220. MODOC COUNTY (1): In lava field with Arctostaphylos and scattered Pinus ponderosa near Mayfield Ice Caves, Sec. 8, T40N, R4E, moist, on shaded recess, 1972 Norris 22511. PLACER COUNTY (9): On moist, rather shaded boulder beside stream on north-facing slope with Acer macrophyllum, Calocedrus, and Alnus along road to Bowman Lake ca, 2 miles N of Hwy, 20, 39°20'N 120°39'W, 1500 m, 1991 Norris 77015, 77016. SAN DI-EGO COUNTY (1): Smith Mt., 1897 Parish 3891 (CAS-503030). SAN LUIS OBISPO COUNTY (1): In Eucalyptus forest and adjacent sand dunes, along road through Montana De Oro State Park, W of San Luis Obispo, Sec. 3, T31S, RIOE, 35°16′N 120°53′W, 50 m, 1982 Norris 68197. SANTA CLARA COUNTY (3): At Big Basin Way (Hwy. 9) ca. 1 mile WSW Saratoga in the Santa Cruz Mts. in Platanus racemosa stream forest, on prim. rocks ca. 10 m, 1981 R. & I. Duell 2158/1. SHASTA COUNTY (5): In douglas fir, canyon live oak forest along Coffee Creek at East Fork of Coffee Creek, Sec. 30, T38N, R8W, on fairly dry, sunny rocks, ca. 3 500 ft., 1972 Norris & Hermann 22593. SIERRA COUNTY (1): Salmon Lake Camp., wet rocks in rill, 6 800 ft., 1921 Surtiffe (CAS-119307). SISKIYOU COUNTY (40): On moist, diffusely lit seepage on granite outcrop in Abies forest above Big Boulder Lake, W of Carrville, 41°03'N 122°47′W, ca. 1 900 m, 1989 Norris & Streimann 74788, 74808. On moist, diffusely lit base of granitic outcrop in mixed conifer forest along trail to Long Gulch, Klamath National Forest, SW of Callahan, 41°13′N 122°55′W, ca. 1 900 m, 1989 Norris 74872. TEHAMA COUNTY (10): In very open alpine scrub on east-facing slopes of Anthony Peak, 39°51'N 122°57′W, on moist, diffusely lit rock along stream, ca. 6 500– 6 900 ft., 1979 Norris 55038; on moist, rather shaded outcrop, 1979 Norris 55029. TOULUMNE COUNTY (1): Yosemite, trail to Nevada Falls, under boulders, 1923 Eastwood (CAS-119332). TRINITY COUNTY (30): In open red fir forest with scattered grassy meadows in area of grannitic outcrops near Browns Meadows, 41°3′N 122°58′W, ca. 6000– 6 600 ft., on moist to submerged shaded rocks along river, 1972 Norris 23161. On moist, diffusely lit rock, north fork of the Trinity River, 1973 Dorn & Winter 299. TULARE COUNTY (2): In Sequoiadendron forest at Belknap Grove, 36°08′N 118°36′W, on moist, diffusely lit rock outcrop, ca. 5 200 ft., 1977 Norris 50905. — Additionally reported from the following counties: Butte, Contra Costa, Fresno, Lassen, Marin, Napa, Nevada, Plumas, Sacramento, San Mateo, Santa Cruz, and Sonoma (Howe 1897, Frye & Clark 1946, Hong 1983).

Total range: North America (Frye & Clark 1946, Hong 1983): Canada: Alberta, British Columbia. USA: Alaska, California, Colorado, Idaho, Montana, Nevada, New Mexico, Washington. Europe, N Africa, Asia. — Map: Schofield & Crum 1972 (map 28).

Table 1. Comparison of the characters of *Porella bolanderi* (Aust.) Pears., *P. cordaeana* (Hüb.) Moore, *P. navicularis* (Lehm. & Lindenb.)Lindb., and *P. roellii* Steph.

characters	P. bolanderi	P. cordaeana	P. navicularis	P. roellii
colour	not glossy; dark or grayish green or olive	glossy; variable, yellow- ish green, dark green, brownish	glossy; yellowish green to brownish	glossy; green to yellowish brown
colour reaction with IKI	no reaction	violet	no reaction	no reaction
plant size	1.5–6 cm long	3–10 cm long	4-12 cm long	4-8 cm long
branching	simple or sparsely 1–(2)-pinnate	irregularly and abundantly 1–2- pinnate, often fan-shaped	abundantly (1–)2- pinnate	irregularly and fairly abundantly 1–2(-3)-pinnate
stem	flaccid	fairly flaccid to rigid	rigid	fairly flaccid
dorsal leaf lobe size	$1.6-2.5 \times as long$ as ventral lobe	$2.5-3.5 \times$ as long as ventral lobe	$2-3 \times$ as long as ventral lobe	1.7–2.3 × as long as ventral lobe
leaf margins	very downflexed; basal half of an- tical leaf margin toothed	almost flat, those of ventral lobes recurved and undu- late; basal half of antical leaf margin toothed	distinctly and regularly down- flexed; margins entire	downflexed;margins entire
ventral leaf lobe shape	ovate- or linear- lanceolate	obliquely ovate to narrowly triangular	oval to ovate	ovate to lingulate
ventral leaf lobe size	2/5–3/5 of dorsal lobe width	2/5 of dorsal lobe width	2/5–1/2 of dorsal lobe width	2/3–3/4 of dorsal lobe width
insertion of ven- tral lobe to stem	little arching; end- ing distinctly below keel base (1/2–3/4 of stem width)	curving down the stem ending distinct- ly below keel base (1–2×stem width)	little arching; end- ing near the level or somewhat below keel base (1/2 of stem width)	semicircular; ending near keel base leve
underleaf size	2 × width of ventral lobe	2×width of ventral lobe	$1-1.2 \times$ width of ventral lobe	$1.2-1.8 \times$ width of ventral lobe
underleaf bases	usually toothed or laciniate	toothed, and undu- late-crispate	entire	rarely toothed
leaf cells	almost isodiametric; trigones rather small	almost isodiametric; trigones minute to small	cells at base of ventral margin thick- walled and small; trigones large and bulging	almost isodiametric; trigones moderate
female branch	without normal leaves	without normal leaves	few small leaves at base	2–6 leaves at base
female bracts	larger than leaves	smaller than leaves	smaller than leaves	larger than leaves
perianth mouth	wide; ciliate	contracted; entire to toothed	wide; entire when mature	wide; toothed

Porella navicularis (Lehm. & Lindenb.) Lindb. (Figs. 6–8)

Acta Soc. Sci. Fennica 9: 337. 1869. — *Jungermannia navicularis* Lehm. & Lindenb. in Lehm., Pugillus 6: 38. 1834. — *Madotheca navicularis* (Lehm. & Lindenb.) Nees, Naturges. Eur. Leberm. 3: 176. 1838. — Type: USA. "West coast, hb Hooker" (W-5717!, holotype, isotypes in BM!, S!).

Jungermannia recondita Lehm. & Lindenb. in Lehm., Pugillus 6: 38. 1834. — *Madotheca recondita* (Lehm. & Lindenb.) Gott. et al., Syn. Hep. 274. 1845. — Type: USA. "West coast. hb. Hooker" (not seen).

Madotheca douglasii Tayl., London J. Bot. 5: 379. 1846. — Type: USA. "North-west coast of America, Douglas, Hook. Herb." (not seen).

Dioicous. Plants in dense coarse mats, glossy, yellowish green to brown, most often yellowish; shoots 1.5–3 mm wide. Stems prostrate or somewhat pendulous, tip often ascending, 4–12 cm long, 1–2-pinnate, more often 2-pinnate, secondary branches usually 0.5–1.5 cm long, gradually narrowing toward tip. Leaves densely imbricate, keel very short to wanting. Dorsal lobe widely spreading, obliquely ovate to oblong-ovate, adaxially concave, 1.2–2.5 mm long and 1–1.8 mm wide, $2-3 \times$ as long as the ventral lobe, the insertion line arching up the stem in a semicircle but ending only about half the stem width above the keel base level, antically distinctly decurrent; apex incurved, rounded; margin antically slightly arching beyond the stem, entire except the base, postical base slightly undulate-crispate, antical base sometimes laciniate on decurrent portion. Postical lobe oval to ovate, rounded at postical base, adaxially convex, 0.4–1 mm long and 0.4–0.8 mm wide, the insertion line only little arching upward on the stem and ending from about the keel base level to half the stem width below it, decurrent; apex commonly recurved when dry, obtuse or rarely subacute; margin recurved, entire. Cells in the middle of dorsal lobe 17–38 µm, very similar throughout except those in the base of the ventral margin that are thickwalled and only 10–17 µm, in the apex and margins 13–20 µm, thin-walled between trigones, trigones large and bulging. Underleaves imbricate,s fairly large, erect-spreading, adaxially convex, oblongquadrate, 0.4–1 mm long and 0.3–0.9 mm wide, the insertion line arching semicircularly up the stem and extending downward on both sides forming fairly long decurrent basal angles; apex sometimes recurved, rounded; margins entire. Male branches short and lateral, 1.5–2.5 mm long. Male bracts very similar to leaves but smaller. Female branches very short and lateral with a few smaller leaves at base. Female bracts free, very similar to the leaves but smaller, dorsal lobe obtuse and entire, ventral lobe usually acute and entire to toothed; bracteoles larger than underleaves, free, entire. Perianth broadly obovoid from an obconic base, 3–5 mm long and 2.2–4 mm wide, tip quite clearly dorsiventrally compressed and strongly bent toward the ventral side; mouth very wide, deeply 2-lipped, lips somewhat ciliate-toothed when young but usually entire when mature. Seta, sporangium, elaters and spores were described by Frye and Clarke (1946).

Illustrations: Barbour 1902: 35 (fig. 6), Frye & Clark 1946: 727.

Porella navicularis is a glossy, rigid and usually very large species (Table 1). Typically it is yellowish green or yellowish brown and abundantly branched. Both dorsal and ventral leaf lobes and underleaves have regularly incurved and entire margins, and underleaf and ventral lobe apices are obtuse. Underleaves and ventral lobes are similar in size and shape making the ventral habit very regular-looking especially in branches. Leaf cells are distinctive: larger and more bulging trigones than in the other species, but at the postical margin near the keel the cells are clearly thick-walled and small. Female plants are often rich with perianths, which are large and easily visible. Perianth mouth bends ventrally and when mature is toothless.

Porella navicularis occurs in California at altitudes 0-1700 m, being most common within 50-750 m. The species is most common in northwestern California extending to San Francisco Bay area and somewhat to the south very near the coast (Fig. 8). The species is an epiphyte, even though it occurs on other substrates as well. Most commonly it is on Quercus, especially on Q. chrysolepis and Q. gambelii and Lithocarpus, but also on Alnus, Acer macrophyllum, Umbellularia, and sometimes on *Pseudotsuga*, *Castanopsis*, *Taxus*, Aesculus, Fraxinus, Cornus nuttallii, Cupressus, Corylus, Sambucus, Azalea, Holodiscus and Amelanchier. More rarely the species occurs on rocks, boulders and cliffs, which can occasionally be siliceous, serpentine, limestone or phyllite. It also grows on logs and wood and only rarely on soil.

Porella navicularis is common in Pseudotsuga forests, where may be tan oaks (Lithocarpus) or canyon live oaks (Quercus chrysolepis), or Umbellu-

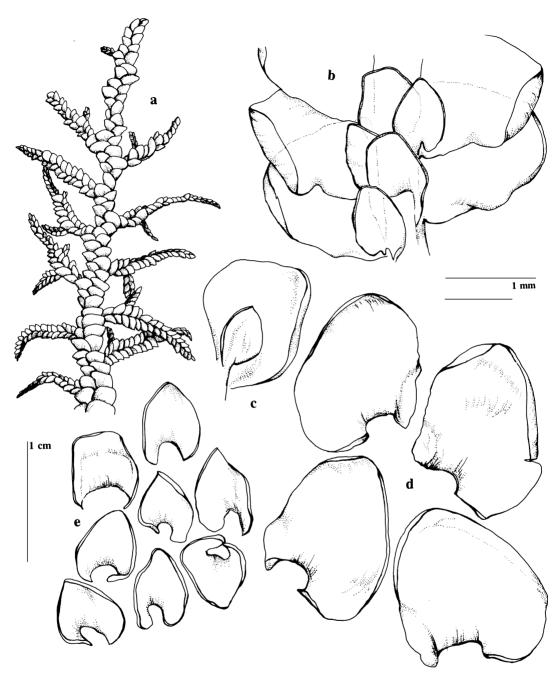


Fig. 6a-e. *Porella navicularis* (Lehm. & Lindenb.) Lindb. (from *Norris 8212*). — a: Dorsal habit. — b: Ventral habit. — c: Dorsal and ventral leaf lobe. — d: Dorsal leaf lobe. — e: Ventral leaf lobes and underleaves. — The longer 1 mm scale for b, d, e, the shorter 1 mm scale for c, and the 1 cm scale for a.

laria, Alnus, Arbutus, Abies, Thuja, Calocedrus, Acer macrophyllum, Castanopsis and Chamaecyparis and various species of Pinus. It occurs in other kind of mixed conifer forests and it is fairly common in

mixed redwood forests. It is also common in open oak forests. More rarely it is met in forests composed either of *Alnus*, *Salix*, *Arbutus*, *Umbellularia* or other kind of deciduous trees.

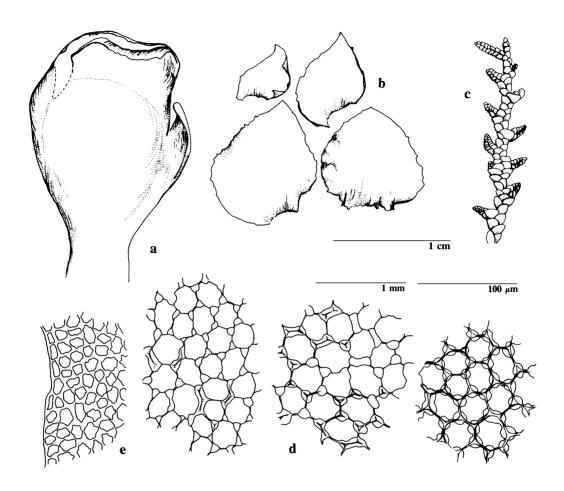


Fig. 7a–e. *Porella navicularis* (Lehm. & Lindenb.) Lindb. (a, b, d and e from *Norris 8212*, c from *Norris 67293*).

— a: Perianth. — b: Female bracts. — c: Male branch. — d: Median cells of dorsal leaf lobe lamina. — e: Marginal cells of basal dorsal leaf lobe. — The 100 μm scale for d, e, the 1 mm scale for a, b, and the 1 cm scale for c.

Range in California (only selected specimens seen listed; number of studied specimens per county given in parentheses; total number of specimens seen 214, see Fig. 8): DEL NORTE COUNTY (26): In Quercus chrysolepis and Pseudotsuga forest with dense understory of Arctostaphylos along Myrtle Creek at Smith River, on moist, diffusely lit bark of *Umbellularia*, 41°48′N 124°03′W, 100 m, 1981 Norris 67293. In Pinus lambertiana, Pseudotsuga and *Pinus attenuata* forest with understory of *Garrya*, Castanopsis and Quercus chrysolepis on windswept ridge ca. 6.5 miles from Big Flat on the Gasquet-Orleans Rd., 41°36′N 123°52′W, on moist, diffusely lit bark of *Quercus*, ca. 1 600 m, 1989 Norris 74139. GLENN COUNTY (1): Deep shade of cañon-bottom, near stream on rocks, Snow Basin Creek, W of Plaskett Meadows, 1944 Howell 644 (CAS-453415). HUMBOLDT COUNTY (82): On bark of Arbutus menziesii in rather undisturbed Pseudotsuga for-

est on Wilder Ridge ca. 5 miles S of Honeydew, 40°12′N 124°05′W, 1967 Norris 8041; on bark of big-leaf maple, 1967 Norris 8056. In open oak forest on grassy slope near Schoolhouse Peak, Sec. 24, T9N, R2E, on moist, diffusely lit bark of oak, ca. 3000 ft., 1973 Norris 24271. Tish Tang Valley near Hoopa Primitive rocks, ca. 500 m around campground on bark, 1981 R. & I. Duell 217/la (Exs. n. 505-USA 1981). On moist, sunny bark of big leaf maple, 1969 Norris 10306. In cutover forest on talus slope along Slide Creek, Sec. 23, T1ON, R1E, on base of stump, ca. 2 300 ft., 1967 Norris 8212. MARIN COUNTY (20): In wet second-growth forest with Alnus and Sequoia along creek near Five Brooks Trailhead, Point Reyes National Sea Shore, 37°59'N 122°45.5'W, on moist, diffusely lit bark of Alnus, 100-300 ft., 1984 Norris 71849. Mt. Tamalpais, in cortice *Pseudotsugae taxifoliae*, Parks (Schiffner, Krypt. Exs. Ed. Mus. Hist. Nat. Vindobon. 3175). MENDOCINO COUNTY (24): On bark of Lithocarpus in second-growth Pseudotsuga forest along Hwy. 101 near Laytonville, 39°42′N 123°29′W, 1967 Norris 8380. In riverine forest with redwood and oaks along Greenwood Ridge Rd. at Navarro River near entrance to Hendy Woods State Park, Sec. 11, T14N, R15W, 39°05'N 123°29'W, on moist, diffusely lit bark of oak, ca. 300 ft., 1979 Norris 53129. PLUMAS COUNTY (1): In riverine corridor forest along chipps creek at Hwy. 70 W of Belden, 39°59'N 121°15'W, on moist, diffusely lit outcrop, 1 300 m, 1984 Norris 69993. SAN MATEO COUNTY (6): Santa Cruz Mts., Mc Donald Co. Park near Hwy. 84, Seguioa sempervirensforests in Little Creek valley, primitive rocks/loam ca. 150 m s.m., on bark, 1981 R. & I. Duell 2155/5. SANTA CLARA COUNTY (2): Santa Cruz Mts., at Big Basin Way (Hwy. 9) ca. 4.5 miles W of Saratoga in decidous forests above creek, primitive rocks ca. 500 m, on bark, 1981 R. & I. Duell 2182/4. SANTA CRUZ COUNTY (9): In cut-over redwood forest with scattered grassy meadows on campus of the University of California, Santa Cruz, 37°59.5′N 122°03′W, on moist, diffusely lit bark of oak, ca. 700 ft., 1980 Norris 55668. SISKIYOU COUNTY (13): In canyon live oak of douglas fir forest along Elk Creek at Malone Creek south of Happy Camp, Sec. 13, T15N, R7E, on moist, diffusely lit thin soil over boulder, ca. 1 600 ft, 1978 Norris 52205. SONOMA COUNTY (8): In willow thicket on gradual slope near ocean, along California Hwy. 1 at Wright's Beach near Bodega Bay, 1969 Norris & Gantt 1-3. TRINITY COUNTY (17): In open oak forest along New River between Denny and Mills Creek, 40°57'N 123°23'W, on moist, diffusely lit bark of canyon live oak, ca. 1500 ft., 1973 Norris 23931. On moist, diffusely bark of Quercus qambelii in heavily fogprone ridge with Quercus chrysolepis, Arbutus, and Pseudotsuga on serpentine in old scree area of large boulders along Hennessy Ridge Rd. ca. 1 mile W of eastern border of Six Rivers National Forest, 40°50′N 123°32′W, 1 000 m, 1991 Norris 77260. — Additionally reported from the following counties: Alameda, Lake, San Joaquim, and Sierra (Hong 1983).

Total range: North America: Canada: British Columbia. USA: Alaska, California, Idaho, Montana, Oregon, Washington. Mexico?, Guadalupe Island? (Frye & Clark 1946, Hong 1983).

Porella roellii Steph. (Figs. 9–11)

in Röll, Bot. Centralbl. 45: 203. 1891. — *Madotheca roellii* (Steph.) Steph., Spec. Hep. 4: 255. 1910. — Type: USA. "Washington, Kitchelos Lake Cascades, 1888 *Röll* (G!, holotype, isotype: BM!).

Dioicous. Plants in loose mats or wefts, somewhat glossy or not, green to yellowish brown or olive brown; shoots distinctly complanate, 1.5–2.1 mm wide. Stems prostrate to procumbent, 4–8 cm long, rather flaccid, irregularly 1–2-pinnate, rarely 3-pinnate, the branches less than 1 cm long, rather numerous, often attenuate and reflexed at tip. Leaves

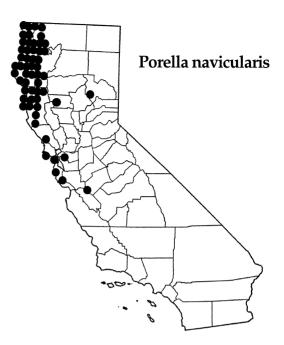


Fig. 8. Distribution of *Porella navicularis* (Lehm. & Lindenb.) Lindb. in California.

densely imbricate, keel very short or non-existent. Dorsal lobe obliquely ovate, widely spreading, somewhat adaxially concave, 0.9–1.7 mm long and 0.7–1.5 mm wide, $1.7-2.3 \times$ as long as ventral lobe, the insertion line arching upwards on the stem semicircularly, not decurrent; apex often incurved, obtuse to rounded, very rarely apiculate; margins somewhat incurved, entire to sinuate, antical margin widely arching and reaching the farther edge of the stem or passing beyond the stem width, postical margin may be somewhat undulate-crispate. Ventral lobe ovate to oblong-ovate to somewhat lingulate, erect to erectspreading but almost parallel with the stem, flat to somewhat adaxially convex, 0.5-0.7 mm long and 0.2–0.4 mm wide, the insertion line arching little or semicircularly and usually ending near the keel base level, little decurrent; much narrowed to the obtuse to sometimes acute apex; margins usually entire above, very rarely toothed, postical base usually toothed, antical base often with one long tooth. Cells in the middle portion of dorsal lobe 17–30 µm, in the median margin and apex 10–25 µm, in the base 20–42 µm, in the postical basal margin slightly smaller than in the median margin, isodiametric except in the base, thin-walled, trigones moderate.

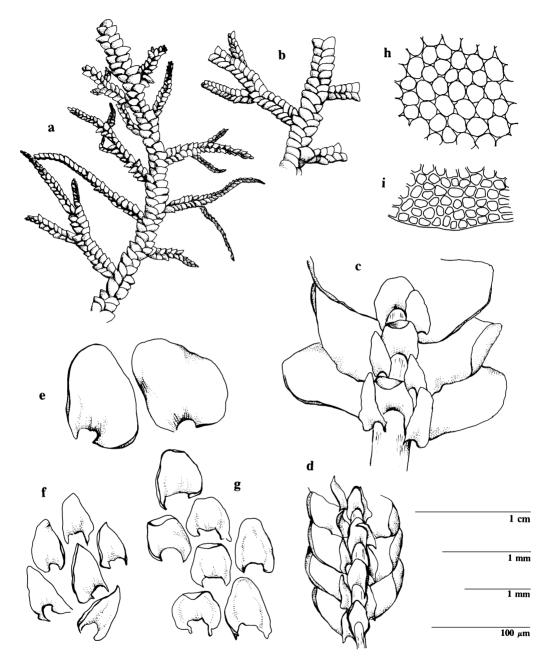


Fig. 9a–i. *Porella roellii* Steph. (from *Norris 9888*). — a: Dorsal habit in dry condition. — b: Dorsal habit in wet condition. — c: Stem from ventral side. — d: Branch from ventral side. — e: Dorsal leaf lobes. — f: Ventral leaf lobes. — g: Underleaves. — h: Median cells of dorsal leaf lobe lamina. — i: Marginal cells of dorsal leaf lobe. — The 100 µm scale for h, i, the longer 1 mm scale for c, e, f, g, the shorter 1 mm scale for d, and 1 cm scale for a and b.

Underleaves ovate to ovate-lingulate, approximate, often recurved at apex, adaxially convex, 0.5–0.8 mm long, 0.4–0.8 mm wide, 1.2–1.8 × as wide as ventral lobe,

the insertion line arching up on the stem 1–2 stem widths, long decurrent on both sides; apex rounded, often recurved; margin recurved, usually entire or

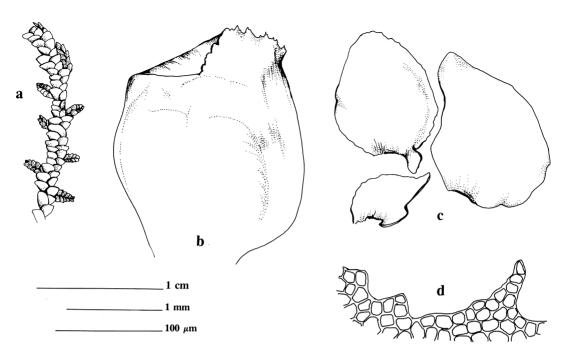


Fig. 10a–c. *Porella roellii* Steph. (a from *Norris 10167*, b–d from *Norris 9888*). — a: Male branch from dorsal side. — b: Perianth. — c: Female bracts. — d: Perianth mouth. — The 100 μ m scale for d, the 1 mm scale for b, c, and the 1 cm scale for a.

very rarely somewhat toothed in lower part, somewhat crispate toward base. Male branches very similar to the other branches, mostly on primary branches, usually with a few leaves at base. Female branches lateral, from the stem or larger primary branches, somewhat elongate, with 2-6 leaves at base, terminal. Female bracts very similar to leaves, somewhat larger, ventral and dorsal lobes not much united at base, the ventral one larger in proportion to the dorsal one than in the leaves, obtusely acute to rounded. entire or sinuate to somewhat toothed. Bracteole free. ovate, entire to toothed. Perianth broadly obovoid, 2.5-3.2 mm long and 2.1-2.8 mm wide, somewhat flattened dorsiventrally, not plicate, not or only little contracted at mouth, mouth not 2-lipped, not bent or hardly bent toward ventral side, sinuate and toothed over the sinuations. Seta, sporangium, elaters and spores were described by Frye and Clarke (1946).

Illustrations: Barbour 1902: 36 (fig. 7), Frye & Clark 1946: 725.

Because of its often large and wide underleaves (Table 1) *Porella roellii* has often been identified as *P. platyphylla*. The species is sometimes glossy, but much less so than *P. navicularis*. It is also more

flaccid than *P. navicularis*. Like *P. navicularis* it has abundant branching. Characteristic of *P. roellii* are the ventral leaf lobes especially on branches: large and lingulate with the outer (distal) bases with toothlike edge and pointed apices, conspicuously directed toward the branch apex.

Porella roellii occurs at altitudes 0-2 000 m in California, being most common below 1500 m and still more common below 1 000 m. The species occurs only in N California and is most common in northwestern corner of the state (see Fig. 11). The species occurs on rocks but more commonly on trees. Epilithic specimens have been collected on boulders, cliffs and rocks along stream, with the rock types including serpentine, sandstone, phyllite and siliceous. The species has been collected on Quercus, Acer macrophyllum, Alnus, Lithocarpus, Umbellularia, Arbutus, Baccharis and Salix. Occasionally it grows on soil or on logs. Porella roellii occurs in Pseudotsuga forests, Pseudotsuga-Lithocarpus forests, Pseudotsuga-Quercus chrysolepis forests, redwood forests and open oak forests usually composed of Quercus chrysolepis. It is also met in Abies forests, various mixed conifer forests and deciduous thickets.

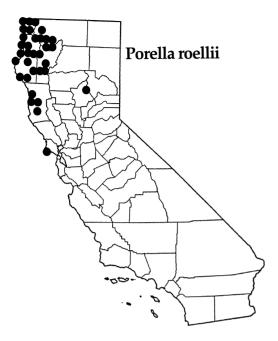


Fig. 11. Distribution of Porella roellii Steph. in California.

Range in California (only selected specimens seen listed; number of studied specimens per county given in parentheses; total number of specimens seen 112), see Fig. 11: DEL NORTE COUNTY (28): In mixed conifer forest with open serpentine areas near Doctor Rock, 41°32'N 123°46'W, on moist, shaded cliff, ca. 5 000 ft., 1977 Norris 50300. In redwood and sitka spruce forest along south side of Smith River in Jedediah Smith State Park W of Hiouchi Bridge, 41°49'N 124°05.5'W, on moist, sunny boulder, ca. 125 ft., 1981 Norris 67342, 67343, 67344. HUMBOLDT COUNTY (56): Lawrence Creek, ad truncos in silvis densis, Parks & Tracy (Schiffner, Krypt. Exs. Ed. Mus. Hist. Nat. Vindobon. 3074). On very moist, rather shaded boulder in bottom of canyon in Pseudotsuga forest along Bear Creek below Tolkan Recreation Area E of Shelter Cove, 40°04'N 123°59'W, 1973 Norris 23486. In virgin tan oak and redwood forest along Emerald Creek at junction with Redwood Creek Redwood National Park, 41°12'N 123°59.5′W, on moist, diffusely lit rock outcrop, ca. 200 ft., 1975 Norris 45825, 45823; On moist, diffusely lit bark of Lithocarpus, 1975 Norris 45824. MARIN COUNTY (3): In wet second-growth forest with Alnus and Sequoia along creek near Five Brooks Trailhead, Point Reyes National Sea Shore, 37°59'N 122°45.5'W, on moist, diffusely lit bark of Salix, 1984 Norris 71851. MENDOCINO COUNTY (9): In open oak forest in deep canyon along Covelo Rd. ca. 3.1 miles E of Longvale, on moist, rather shaded recess under boulder near stream, 1972 Norris 21713. PLUMAS COUNTY (1):

Pulga Quad., in canyon live oak forest in deep canyon on granitic outcrop ca. 2 miles below Cresta Power Station, 39°50'N 121°28'W, on moist, diffusely lit boulder, 1979 Norris 52647. SISKIYOU COUNTY (8): On moist, diffusely lit bark of oak in alder and maple forest on flat boggy soil, Butler Flat, Sec. 20, T11W, R7E, 1968 Norris 10167. TRINITY COUNTY (7): On moist, rather shaded boulder in open digger pine forest on shallow soil over serpentine outcrop ca. 2 miles from Junction City on road to Dedrick, 1972 Norris 21113. — Additionally reported from Shasta and Sonoma Counties by Hong (1983).

Total range: North America: Canada: British Columbia. USA: Alaska, California, Idaho, Montana, Nevada, Oregon, Washington (Frye & Clark 1946, Hong 1983).

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