

**TWO NEW SPECIES OF *MACRODIPLOPHYLLUM*
(SCAPANIACEAE, MARCHANTIOPHYTA)
ENDEMIC TO WESTERN NORTH AMERICA**

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ABSTRACT

Macrodiplophyllum rubrum D.H. Wagner, **sp. nov.**, and **Macrodiplophyllum flaccidum** D.H. Wagner, **sp. nov.**, are described from the northwest coast of North America. Previously confused with *Macrodiplophyllum plicatum* (Lindb.) Perss., they are separated by an array of distinctive morphological characters. Whereas *M. plicatum* is distributed in an arc around the North Pacific from British Columbia to Japan, *M. rubrum* is presently known only from California to northern British Columbia and *M. flaccidum* has been found from northern Oregon to southeastern Alaska.

In the course of preparing a treatment of *Macrodiplophyllum* for the liverwort volume of Flora of North America, the author detected two undescribed species in the herbarium of the University of British Columbia from among the three hundred and forty specimens filed under *M. plicatum* (Lindb.) Perss. The author had anticipated the presence of the first of these based on plants from southwest Oregon first found in 1997 and included in his identification guide to the liverworts of Oregon (Wagner 2014). These Oregon plants were initially identified as *M. plicatum* based on the keys in Godfrey (1977) and Hong (1980) but did not match the description found in Choi et al. (2012). Davison (1993) mentioned a discussion with Schofield about a distinctive form of *M. plicatum* in northern British Columbia and Alaska that deserved further study; this form proved to be the second species described here.

MACRODIPLOPHYLLUM RUBRUM D.H. Wagner, **sp. nov.** (Figures 1-5).

Plantae 20–70 x 2–4 mm, *ex lutescenti-viridi pallide olivaceo-virides*; *rami laterales, plerumque uti innovationes geminati gynoecia infecundata subtendentes*; *folia complicato-biloba, patentia, in parte distali pectinata, non imbricata, longitudine lobi dorsalis 0.45–0.7 longitudinis lobi ventralis. Lobus dorsalis non decurrens, sub angulo 42–54° ex axe caulis abiens, oblongus vel ligulatus, convexiusculus, apice rotundatus, base arcte caulem involvens et eum transiens, ad punctum carinae oppositum attingens. Lobus ventralis transverse insertus, linea insertionis valde arcuata, ad dimidium latitudinis caulis decurrent, ligulatus, apice rotundatus, valde convexus, saepe siccitate deflexus, margine basali limbo bene definito e cellulis pachyticho latitudine 2-5 cellularum, usque 1 mm supra insertionem attingens, dentibus gracilibus unicellularibus interdum recurvis spinosis arcte armata, limbo spinoso plerumque valde apice surculi rubro-tincto, aetate obscurante, cuticula verruculosa, carina subrecta, et ad marginem lobi anticam parallela, 0.45-0.7 partem longitudinis lobi. Corpora oleosa per cellulam 5-8 (-10), sphaerica vel elliptica, granulosa. Gemmae frequentes, ex sphaerico rotundae, polygonicae, 2(-4)-cellulares, pallide brunneolae. Dioica, androecia ignota; gynoecia terminalia, interdum perianthiis praesentibus, ore lobulato-ciliato, lobulis ramosis, gracilibus, apice argutis, longitudine ex 6–10(-20) cellulis composita.*

TYPE: USA. Oregon. Coos Co.: Cherry Creek Research Natural Area, ca. 20 mi SE of Coos Bay, streamside terrace, on *Thuja plicata* trunk, 43° 13' 10" N, 123° 56' 5" W, elev. 640 ft (195 m), 13 Jun 2016, *D.H. Wagner m3014* (holotype: OSC; isotypes: CAS, E, F, H, MO, NY, UBC, VBGI, WTU).

Plants 20–110 x 2–4 mm, ascending to erect, in tufts or scattered among other bryophytes, yellowish green to pale olive green; stems 440–520 x 320–350 μm , one layer of outer cortical cells thick walled, olive green at apex, dark brown to black below, branches lateral, frequently producing paired innovations subtending unfertilized gynoecia; leaves squarrose, imbricate-sheathing at base, spreading, distally pectinate, not imbricate; dorsal to ventral lobe length ratio 0.45–0.7, keel nearly straight and parallel to antical lobe margin, 0.5–0.75 of lobe length; dorsal lobe subtransversely inserted, insertion line weakly arched, not decurrent, angled 42–54° from stem axis, oblong to narrowly rectangular, slightly convex, apex rounded, usually dentate or eroded by gemma formation, lobe base reaching across stem and tightly wrapped around opposite side, 1.1–1.5 x 0.6–0.7 mm; ventral lobe transversely inserted, insertion strongly line arched, decurrent to half the stem width, midline angled 55–85° from stem axis, narrowly rectangular, apex rounded, strongly convex, often deflexed when dry, 2.0–2.6 x 0.8–1.2 mm, apex dentate or eroded by gemma formation, basal margin with a well defined strip of 2–5 rows of thick-walled cells extending up to 1 mm from point of insertion, armed with closely set, slender, unicellular, sometimes recurved spinose teeth, the spinose strip usually strongly red pigmented; cells at leaf base elongate-rectangular, 75–95 x 17–20 μm , trigones bulging, cell walls nodose thickened; median cells (18–)20–23(–27) μm , trigones concave to moderately bulging, 2–3 rows of marginal cells evenly thick walled; cuticle striolate to verrucose; oil bodies 5–8(–10) per cell, spherical to elliptical, granulose; specialized asexual reproduction produced in masses at apices of leaves, frequent, spherical or elliptical to rounded polygonal, 2(–4) celled, pale green to light tan.

Sexual condition dioicous; androecia not known; gynoecia terminal, occasional, female bracts in one pair, distinctly larger than sterile leaves, dorsal lobe to 1.7 mm, ventral lobe to 2.9 mm; small bractlets sometimes included; perianth deeply plicate to base, long emergent, mouth lobulate-ciliate, lobulae branched, slender, sharp tipped, 6–10(–20) cells long, 1–4 cells wide; sporophytes not known.

Etymology. The specific epithet refers to the prominent, spinose-toothed, reddish orange basal margin of the ventral lobes.

Ecology and distribution. Entirely restricted to organic substrates, commonly on bark of trees near their base or on decaying logs, occasionally on peaty humus, confined to coniferous forests near the coast of Alaska, British Columbia, Washington, Oregon, and California. The frequent occurrence on tree bases in the immediate coastal zone is in striking contrast to the other species of the genus, which are primarily terrestrial on cliffs, boulders or sandy soil. Although *M. rubrum* occurs with frequency on hummocks in wetlands in the northern parts of its range, these are distinctly organic substrates.

Additional specimens examined. See Appendix 1.



Figure 1. *Macrodiplophyllum rubrum*. A. Plants *in situ* on *Pseudotsuga* log. B. Hand specimen. Photos by D.H. Wagner.

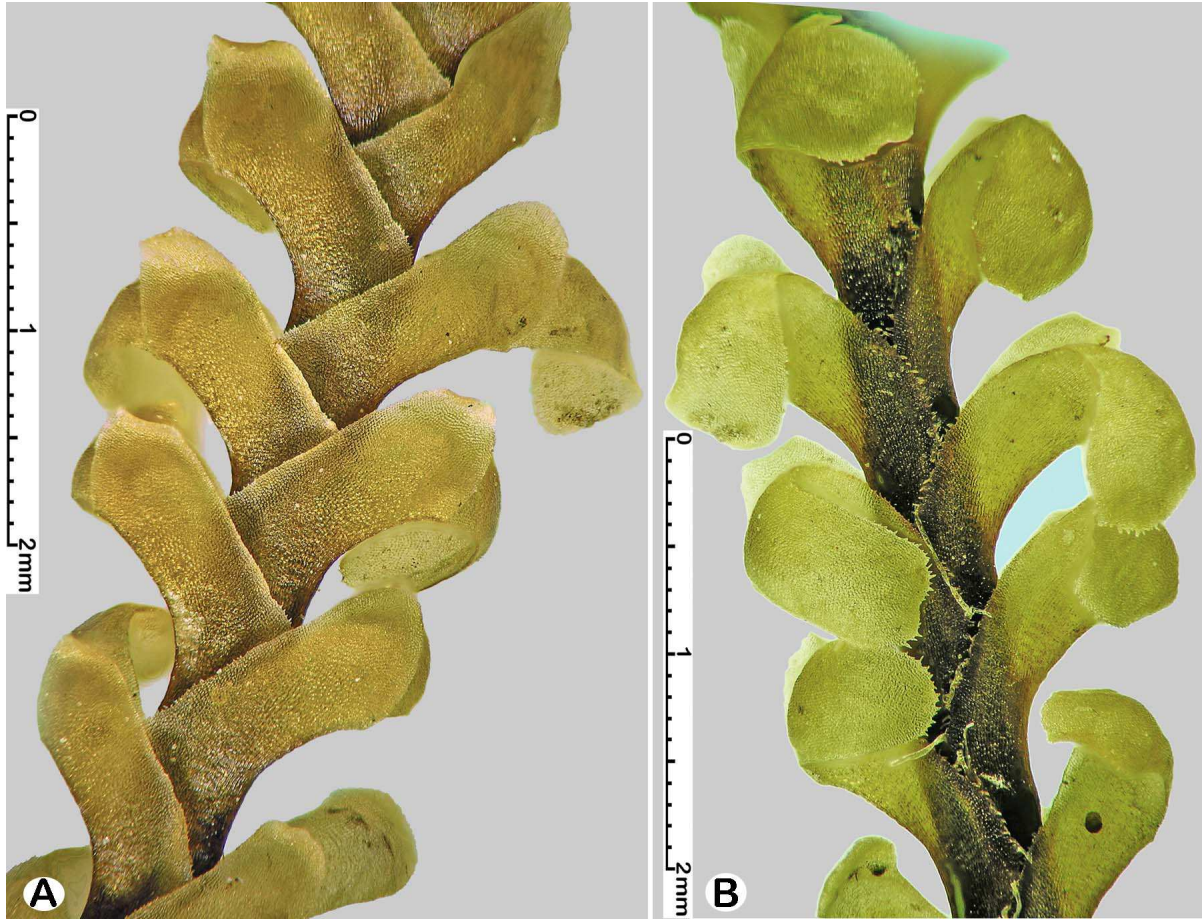


Figure 2. *Macrodiplphyllum rubrum*. A. Dorsal aspect. B. Ventral aspect. A&B. Schofield 86525 (UBC)

These images (Fig. 2) were made with a Nikon Coolpix E8800 mounted on a Nikon Eclipse E200 microscope. Reflected light was provided by two Expilion Cygolite bicycle headlamps. Stacked images were processed with Helicon Focus.

The nearly parallel keel and dorsal lobe margin are clearly demonstrated in Figure 2A. This is easily recognized in herbarium specimens with a dissecting microscope examination. Fresh specimens have their ventral lobes spreading nearly horizontally, not tightly curled around the lower side of the stem as in herbarium specimens.

This photographed specimen is dry; the colors are not typical of fresh specimens. In Figure 2B note the spinose teeth along the basal margin of the ventral lobes. These are strongly red pigmented in almost all collections seen but even when unpigmented the character is clearly recognizable, distinctive and diagnostic.

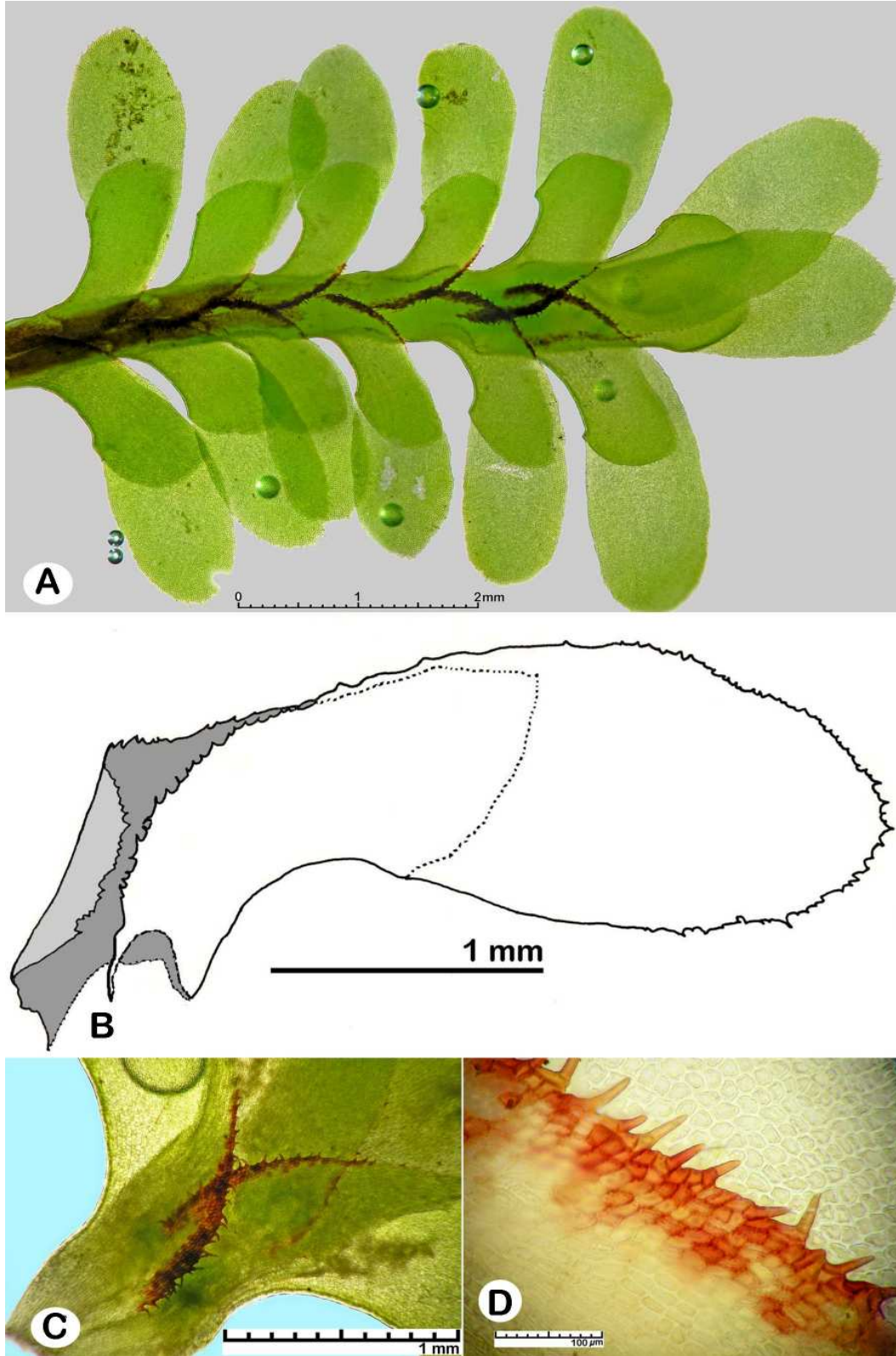


Figure 3. *Macrodiplophyllum rubrum*. A. Whole shoot, ventral aspect. B. Leaf, ventral aspect. C. Ventral lobe base detail. D. Spinose teeth on ventral lobe base. A,C,D from *D.H. Wagner m3006* (OSC). B from *L.Russell s.n.* (OSC).

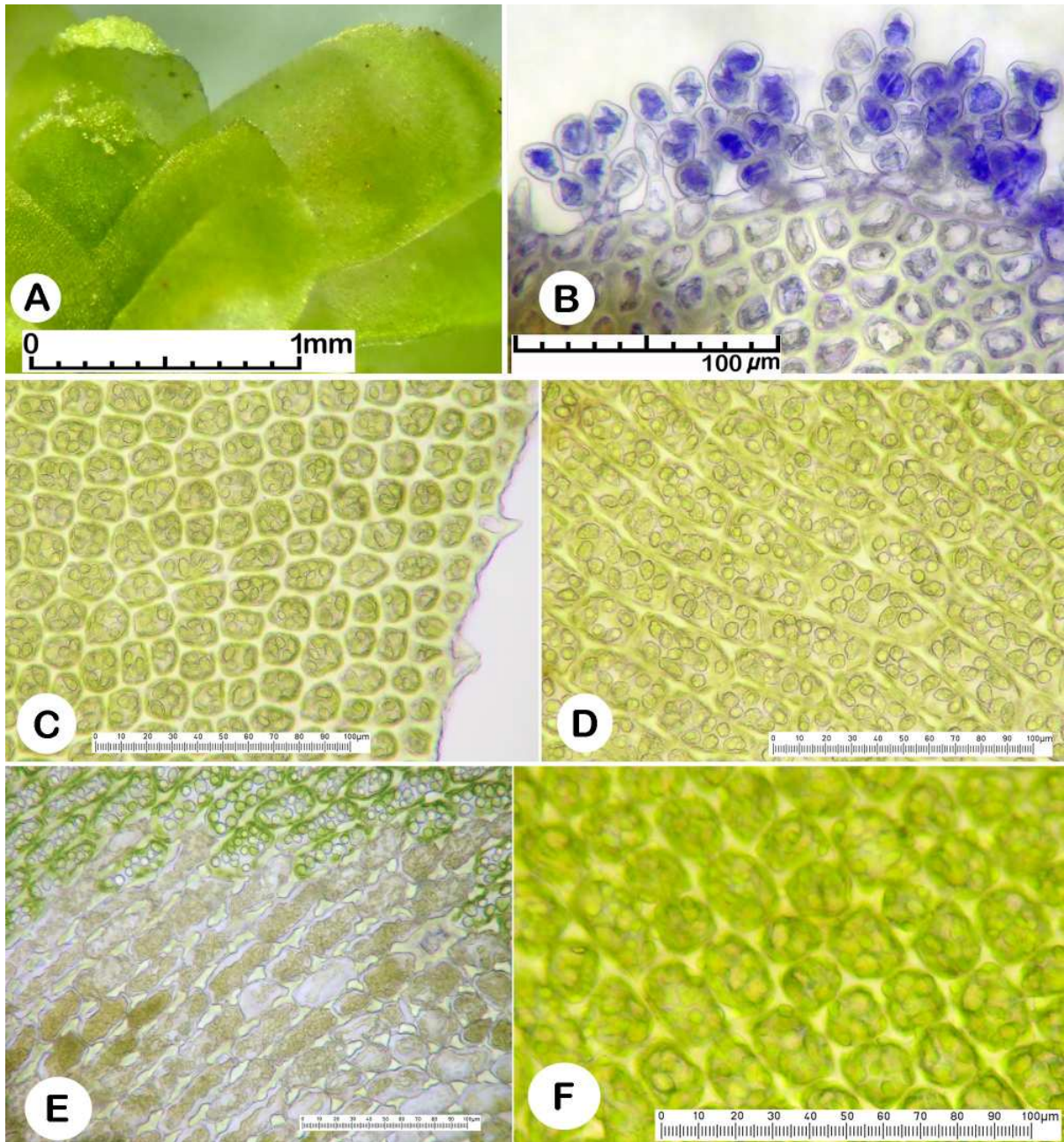


Figure 4. *Macrodiplophyllum rubrum*. A. Fresh shoot apex with gemmae on leaf margins. B. Stained gemmae along leaf margin. C. Marginal to interior leaf cells of fresh specimen, with oil bodies clearly visible. D. Proximal cells near base of ventral lobe, showing oil bodies. E. Basal leaf cells, with cell wall thickenings in dead cells clearly shown. F. Median leaf cells, focus on leaf surface to show verrucose-papillose surface. A, F: *Wagner m3014* (Holotype, OSC). B: *Wagner 9051* (OSC). C, D, E: *Wagner m3006* (OSC).

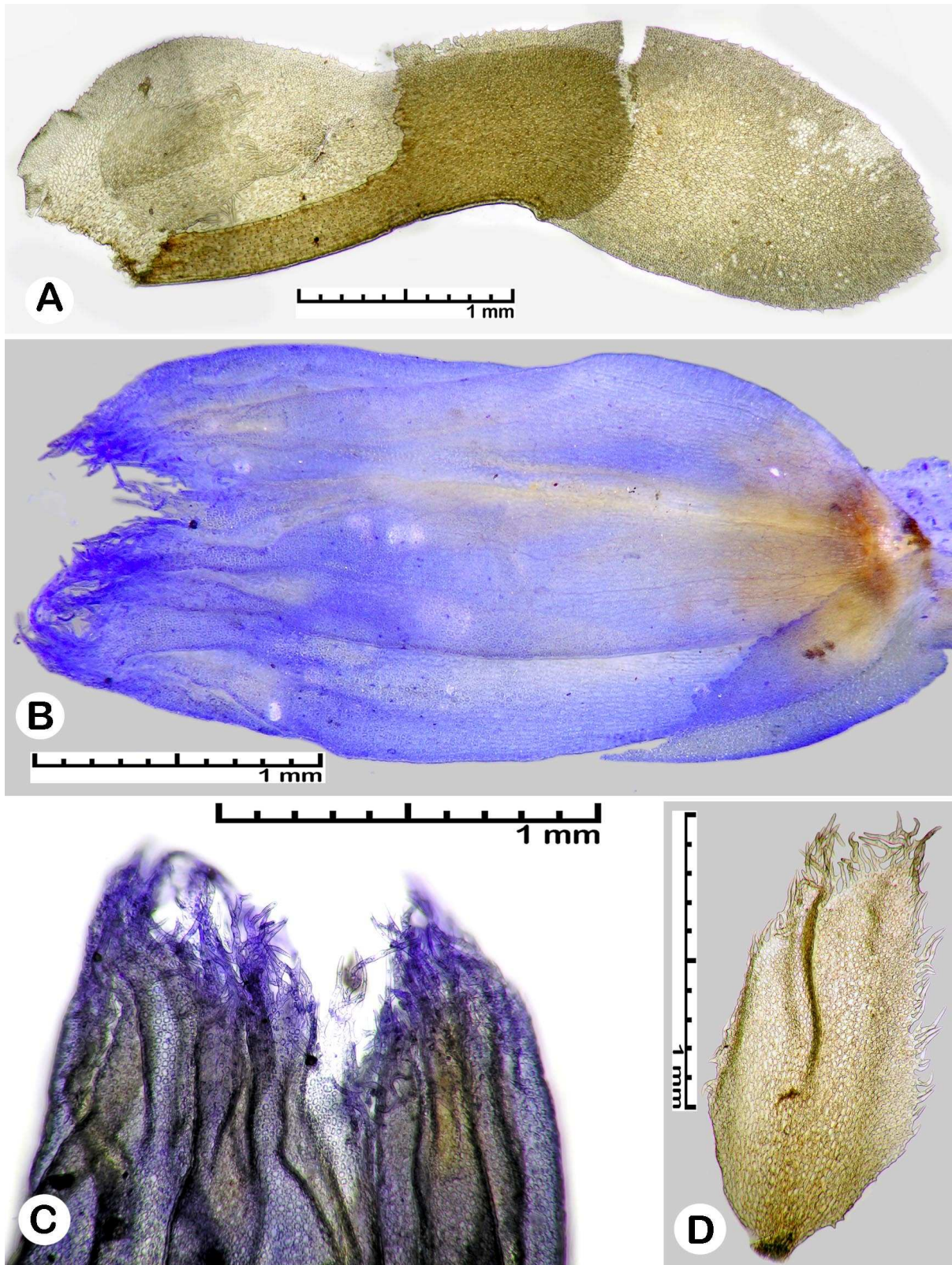


Figure 5. *Macrodiplrophyllum rubrum*. A. Female bract, ventral aspect; ventral lobe base removed to reveal bractlet. B. Perianth, stained. C. Branched lobulae at perianth mouth. D. Bractlet. A--D Wagner m1120 (OSC).

MACRODIPLOPHYLLUM FLACCIDUM D.H. Wagner, **sp. nov.** (Figures 6-9).

Plantae 20–60 x 2–4 mm, ex lutescenti-viridi pallide olivaceo-virides, interdum prope apicem rubro-tinctae; caules sparsim ramosi; folia complicato-biloba, contigua vel pro parte maxima imbricata, longitudine lobi dorsalis 0.45–0.7 longitudinis lobi ventralis, lobo dorsali vel ventrali longitudine proportione latitudinis 0.5–0.7. Lobus dorsalis leniter decurrens usque portionem 0.1–0.2 latitudinis caulis, linea media a base usque apicem aequicurva, sub angulo 30–80° ex axe caulis abiens, oblique obovatus vel arcuatus, planus vel subconvexus, apice obtusus vel rotundus, margine basali paene caulem transiente ad latus oppositum attingente. Lobus ventralis usque portionem 0.1–0.2 latitudinis caulis decurrens, oblique obovatus vel spathulatus, leniter falcatus, subconvexus, siccitate contortus, ad marginem subtiliter dentatus, ad basem lobi dentibus paucis praeditus, dentibus uniformiter effectis in triente distali nisi in parte erosa per propagationem gemmarum, apice lobi ventralis interdum dentibus multicellularibus praedito, cellulis trigonis maximam partem valde tumidis, cuticula praeprimis laevi, carina a base aequicurvante, saepe atrofusca vel atra, 0.3–0.5 lobi ventralis attingente. Corpora oleosa per cellulam 2–3(–4), reniformi-fusiformia, textura amorphica, pallide brunnea, paene lumen cellulare implente Dioica, androecia frequentia, bracteis uti foliis vegetativis sed ad basem gibberis; gynoecia frequentia, terminalia, perianthiis frequentibus, ore lacerato lobulis gracilibus sparsim ramosis usque longitudinem 8 cellularum. Sporophyta ignota..

TYPE: CANADA. British Columbia. Haida Gwaii (Queen Charlotte Islands): Graham Island, along Rennell Sound Forest Service Road, between Rennell Sound and the Queen Charlotte Main Line Junction, W of Phantom Creek, 53° 21' 21" N, 132° 19' 17" W, elev. 244–247 m, 15 Jul 2010, *S. Joya* and *J. & W. Harpel 945* (holotype: UBC; isotypes: CAS, E, F, H, MO, NY, OSC, VBG1).

Plants 20–60 x 2–4 mm, ascending to erect, yellowish green to pale olive green, sometimes tinged red near apex, glossy when dry, stems 335–370 x 235–260 µm, outer cortical cells thick walled in 2–4 layers, olive green at apex, dark brown to black below, sparsely branched, leaves contiguous to imbricate, contorted when dry; dorsal to ventral lobe length ratio 0.5–0.7; dorsal lobe subtransversely inserted, insertion line weakly arched, weakly decurrent for 0.1–0.2 of stem width, midline smoothly curved from base to apex, angled 30–80° from stem axis, obliquely obovate to arcuate, flat to slightly convex, apex obtuse to rounded, basal margin reaching across stem not quite to opposite side, 1.2–1.6 x 0.5–0.8 mm; ventral lobe transversely inserted, insertion line slightly arched, decurrent for 0.1–0.2 of stem width, midline angled 60–90° from stem axis, obliquely obovate to spatulate, weakly falcate, slightly convex; 1.4–1.9 x 0.4–0.9 mm; keel curving evenly from base, often dark brown to black, 0.3–0.5 of ventral lobe; margins finely dentate with few teeth at lobe bases but teeth regularly produced on distal third except where eroded by gemma production, apex of ventral lobe with occasional multicellular teeth; cells at leaf base elongate-rectangular, 36–40 x 18–20 µm, trigones strongly bulging, walls nodose; median cells isodiametric to short rectangular, (15–)20–26(–27) µm, trigones bulging, evenly thick walled cells in 2–3 cell rows at margin; cuticle smooth; oil bodies 2–3(–4) per cell, reniform-fusiform, amorphous texture, pale brown, nearly filling cell lumen, specialized asexual reproduction not known.

Sexual condition dioicous; androecia frequent, like vegetative leaves but strongly gibbous at base, with 3–5 antheridia in each bract; gynoecia terminal, frequent, female bracts similar to but larger than sterile leaves; perianth deeply plicate in distal half, long emergent, mouth lacerate with slender, sparsely branched lobulae up to 8 cells long; sporophytes not known.

Etymology. The specific epithet refers to the appearance of herbarium specimens, the dead leaves appearing limp and flaccid like dried lettuce.

Ecology and distribution. This species grows exclusively on inorganic substrates, typically on cliffs and streamside rocks at low elevations, often associated with waterfalls, occasionally on

mineral soil around rocks. It is known from British Columbia, Washington, Oregon and California. It is notably absent from tree trunks or fallen logs.

Additional specimens examined. See Appendix 2.

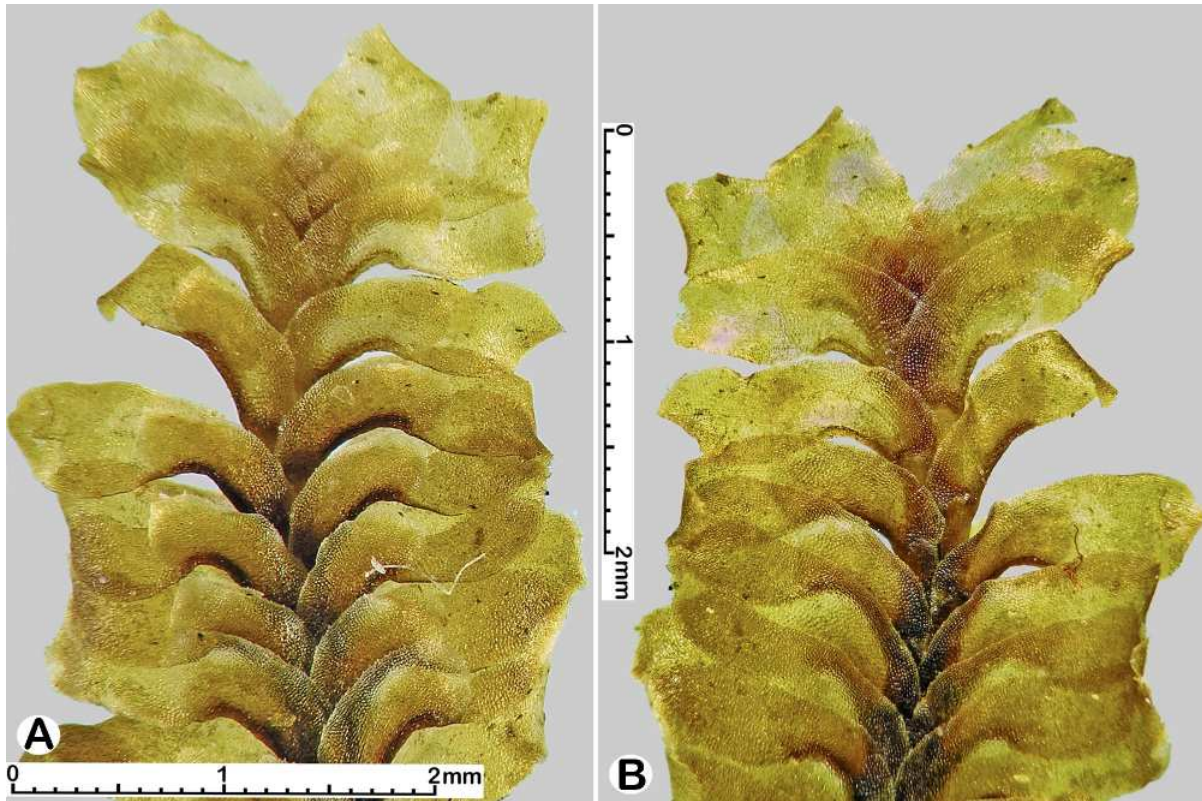


Figure 6. *Macrodiplrophyllum flaccidum*. A. Dry shoot, dorsal aspect. B. Dry shoot, ventral aspect. Both images at same magnification. A & B: Schofield 84237 (UBC).

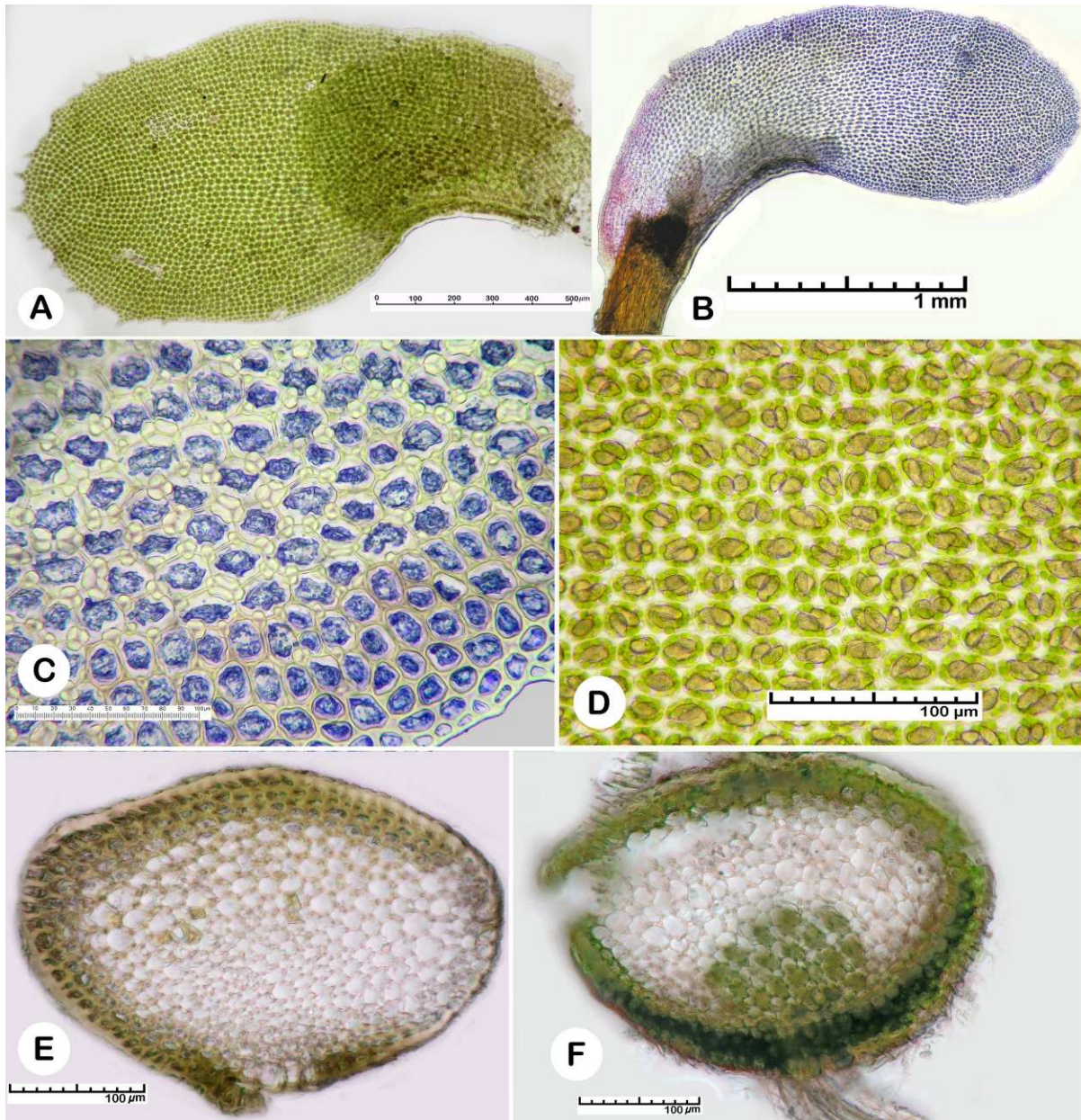


Figure 7. *Macrodiplophyllum flaccidum*. A. Fresh leaf, dorsal aspect. B. Stained leaf, ventral aspect. C. Marginal basal cells, stained, female bract. D. Median cells with oil bodies. E. Stem section. F. Stem section. A, D, E, F: Wagner m2795 (OSC). B, C: Schofield 67624 (UBC).

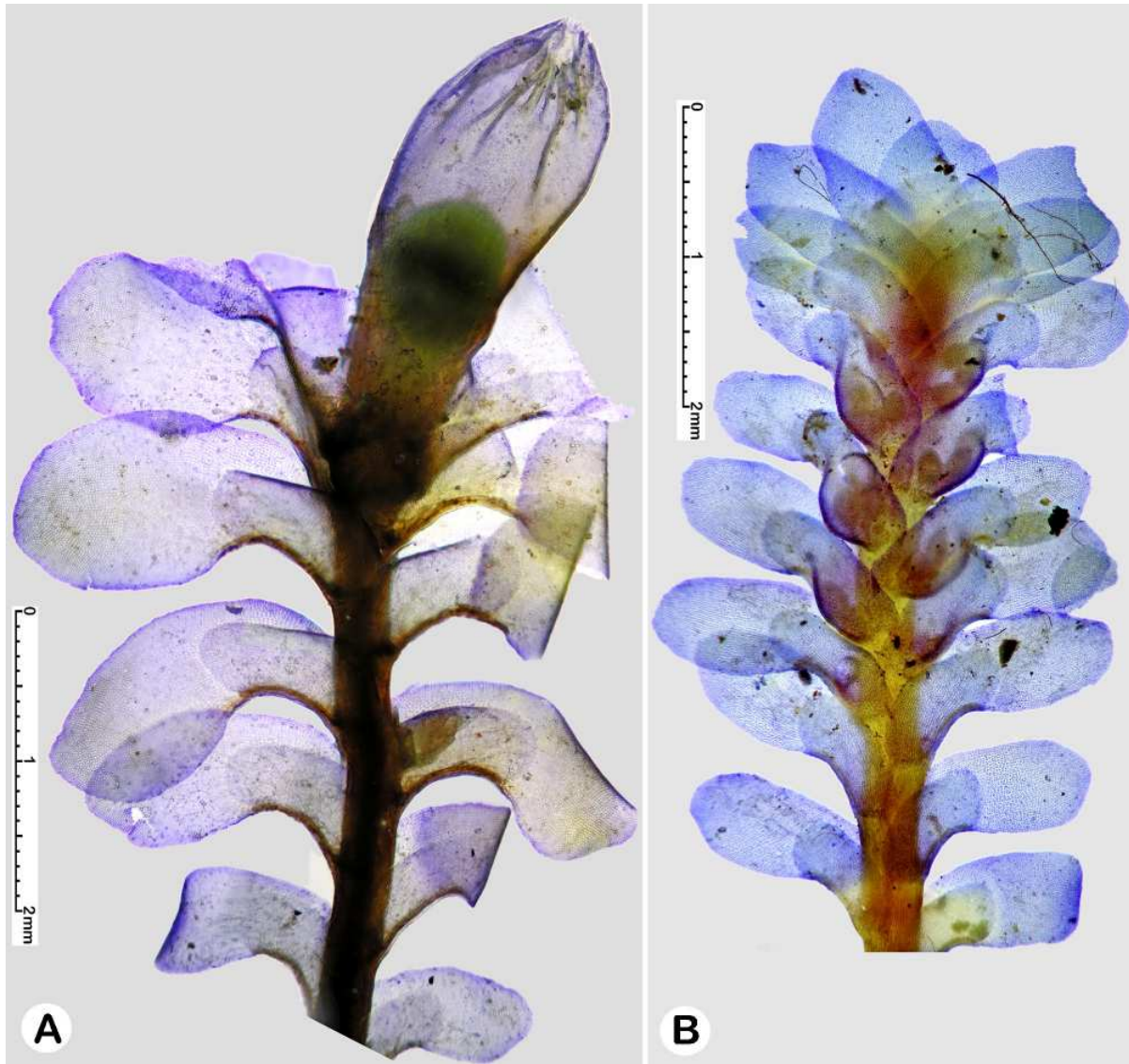


Figure 8. *Macrodiplphyllum flaccidum*. A. Female shoot with perianth, dorsal aspect, stained, distal two thirds of female bracts removed to expose perianth base. B. Male shoot, dorsal aspect, with antheridia visible in male bracts, stained. Both images at same magnification. A & B: Schofield 21535 (UBC).

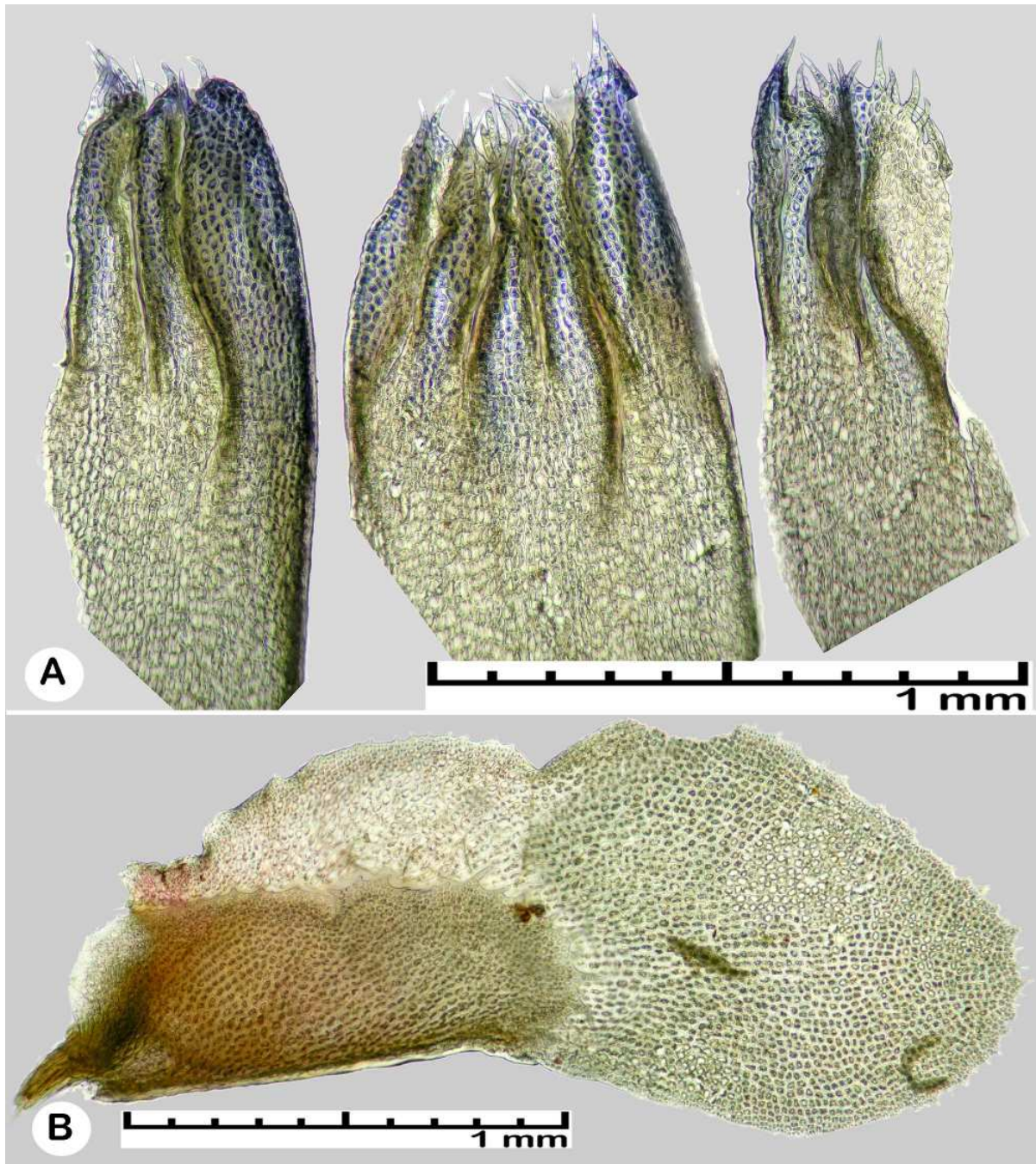


Figure 9. *Macrodiplrophyllum flaccidum*. A. Dissected perianth, lightly stained. B. Female bract. A & B: Schofield 67624 (UBC).

Key to species of *Macrodiplophyllum*

1. Dorsal lobe base reaching across stem and tightly curled around stem opposite the keel; ventral lobe base with a well defined strip of thick-walled marginal cells armed with slender, unicellular, spinose teeth; spinose strip often strongly red pigmented; on either organic or inorganic substrates.
2. Cuticle striolate to verrucose; leaves contiguous, evenly spaced so the keel is usually exposed at stem to leaf junction; midline of distal half of ventral lobes diverging 42—54° from stem; spinose strip at base of ventral lobe usually bright red; invariably on bark, wood or humus
 **Macrodiplophyllum rubrum** D.H. Wagner
2. Cuticle strongly papillose with several globose papillae over each median cell; leaves closely imbricate with few keels exposed; midline of distal half of ventral lobes diverging around 90° from stem; spinose strip at base of ventral lobes not pigmented; on rock or arctic peaty soil
 **Macrodiplophyllum microdontum** (Mitt.) Perss.
1. Dorsal lobe base reaching 0.5 to 0.9 across stem but not wrapped around opposite side; ventral lobe base entire or with scattered marginal teeth, low or up to 4 cells long, not spinose; margins unpigmented or at most light pink; mostly on inorganic substrates but including peaty arctic soil.
3. Dorsal lobes 0.7—0.9 as long as ventral lobes; margins uniformly entire
 **Macrodiplophyllum imbricatum** (M.A. Howe) Perss.
3. Dorsal lobes less than 0.7 as long as ventral lobes; margins sparsely to moderately dentate, at least at apex of lobes.
4. Distal half of ventral lobe angled less than 75° from stem; lobes with few teeth; leaf shape changed little upon drying **Macrodiplophyllum plicatum** (Lindb.) Perss.
4. Distal half of ventral lobe angled close to 90° from stem; both lobes usually dentate, teeth usually prominent at lobe apices; leaf shape collapsing upon drying
 **Macrodiplophyllum flaccidum** D.H. Wagner

Discussion

Macrodiplophyllum is distinguished by its robust character, rounded, long linguulate leaf lobes, elongated basal cells, arcuate and decurrent ventral lobe, and plicate perianth, usually to the base, with a constricted mouth. It is a natural group characterized by an array of ancestral traits rather than strict phylogenetic lineage. Phylogenetic analysis shows that *Macrodiplophyllum* is derived from the more generalized genus *Diplophyllum* and is basal to two more specialized genera, *Douinia* and *Scapania*. Alternate classifications would place the known species of *Macrodiplophyllum* in *Diplophyllum* (Hong 1980; Steere 1978), all in *Scapania* (Potemkin 2002), or divide its species between *Scapania* and an enlarged *Douinia* (Konstantinova et al. 2013). Until the two new species are subjected to molecular analysis their position in phylogenetic trees cannot be used to evaluate alternate classifications in Scapaniaceae.

The similarity of these two new species to *Macrodiplophyllum plicatum* is reflected in the UBC herbarium, where none of the approximately 100 specimens of each were identified as either of the other two species of the genus, *M. imbricatum* (M.A. Howe) Perss. or *M. microdontum* (Mitt.) Perss. Their evolutionary closeness may not be reflected in molecular phylogeny of this group (Heinrichs et al. 2012).

Macrodiplophyllum flaccidum is the most similar of the two to *M. plicatum* in morphology and ecology. Both occur almost exclusively on inorganic substrates such as cliff faces, boulders, and sandy soil. One of the most distinctive character of *M. flaccidum*, dry and contorted leaves, is seen only in dried specimens. Therefore, it is more easily recognizable in the herbarium than in the field. The presence of a black keel and black stem is suggestive but not diagnostic. Whereas most species of this genus have at least some roughening of the cuticle, described as striolate or verruculose, the

cuticle of *M. flaccidum* is usually nearly quite smooth so the plants appear glossy or shiny when dry. Dry specimens of *M. plicatum* have a distinctly velvety or satiny appearance. Perianths with plications in the distal half only, as in *M. flaccidum*, are anomalous in *Macrodiplophyllum*, the other species having perianths plicate to the base.

Although superficially quite different in general appearance, *Macrodiplophyllum rubrum* shares some of its most distinctive characters with *M. microdontum*. *Macrodiplophyllum microdontum* is the taxonomically most remote member of traditional *Macrodiplophyllum*. Phylogenetic cladograms suggest it is closer to *Scapania* than the rest of *Macrodiplophyllum* (Heinrichs et al. 2012). The significance of their evolutionary closeness when additional molecular phylogeny is obtained might suggest optimal generic delimitation in the future. The most prominent diagnostic characteristic of this species, the bright red, spinose margin of the ventral lobes, is quite easily detected in the field with a hand lens.

The extensive lists of specimens examined demonstrate that these two new species are not likely to be of immediate conservation concern except at the margins of their range. Within their relatively narrow distribution, they are both of frequent occurrence. The cluster of populations of *Macrodiplophyllum rubrum* in Coos County, Oregon is striking. It may be a consequence of the local botanists being tuned to a search image but records elsewhere in Oregon and to the north in Washington State indicate limited abundance in most of Oregon coastal forests. The record of *M. rubrum* from California is supported by communications with William Doyle regarding a collection he made in Humboldt County (Doyle & Stotler 2006) originally named *Diplophyllum plicatum*.

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Appendix 1. Additional specimens examined, *Macrodiplophyllum rubrum*

CANADA. British Columbia.

North Coastal Islands. Pitt Island, Newcombe Harbor, base of *Chamaecyparis* tree, 53° 43' N, 130° 06' W, *Schofield* 86967, 12 Aug 1986 (UBC); Pitt Island, Holmes Lake, S shore, base of tree on bog slope, 53° 35' N, 130° 00' W, 21–23 Jun 1979 *Schofield, Vitt, & Horton* 72498 (UBC); Larsen Island N of Banks Island, Larsen Harbour, Hecate Strait, shaded outcrop face, 53° 35' N, 130° 35' W, 4 Jun 1970, *Schofield* 41803 (UBC); Pitt Island, Monckton Inlet, streamlet on N side of inlet, slope in open *Chamaecyparis* forest, 53° 19' N, 129° 40' W, 10 Aug 1986, *Schofield* 86758 (UBC); Moore Islands, Hecate Strait, shaded cliff in forest, 52° 40' N, 129° 25' W, 1 Jun 1970, *Schofield* 41552 (UBC); Powell Anchorage, Tuno Creek mouth, S. Don Peninsula, up base of *Chamaecyparis*, 52° 17' N, 128° 19' W, 7 Aug 1986, *Schofield* 8639 (UBC); King Island, Codville Lagoon, Sager Lake, bank in open forest, 52° 03' N, 127° 49' W, 4 Aug 1986, *Schofield* 86243 (UBC); King Island, near Codville Lagoon, slopes of Codville Hill, cliff in forest, 52° 03' N, 127° 52' W, 12 Apr 1970, *Schofield* 40884 (UBC); Lagoon Lake continuous with Fish Egg Inlet, on cliff in forest, 51° 40' N, 127° 46' W, 13 Apr 1970, *Schofield* 41056 (UBC); Keith Anchorage area, Kwakshua Channel, NW Calvert Island, base of tree in forest, 51° 40' N, 128° 08' W, 18–20 Jun 1965, *Schofield & Williams* 27039 (UBC); Robinson Island, Brandon Point, mouth of Blunden Harbour, shaded bank in forest, 50° 54' N, 127° 17' W, 14 Apr 1970, *Schofield* 41153 (UBC); Inlet on E side of Nigei Island, just NW of Browning Passage, N end, on shaded bank near lake, 50° 52' N, 127° 40' W, 10 Apr 1970, *Schofield* 40749 (UBC); Fraser Island, Port Alexander, SE side of Nigei Island, damp cliff crevice, 50° 51' N, 127° 38' W, 10 Apr 1970, *Schofield* 40703 (UBC).

Haida Gwaii (Queen Charlotte Islands). Graham Island, Cape Fife Trail from Tow Hill toward E coast, hummock in forest, 54° 05' N, 131° 45' W, *Schofield, Ellis & Schofield* 119760, 20 Jun 2002 (UBC). Graham Island, Cape Fife Trail, humus bank in forest, 54° 05' N, 131° 45' W, *Schofield, Ellis & Schofield* 120042, 26 Jun 2002 (UBC). Graham Island, Tow Hill, 54° 05' N, 131° 51' W, *Varaama* 64162Q-01, 7 Jun 1964 (UBC). Graham Island, near Tow Hill, bog, 54° 04' N, 131° 48' W, *Schofield & Krajina* 39392, 22 Jul 1969 (UBC). Graham Island, Trail to E coast from Tow Hill, on humus banks in forest, 54° 03' N, 131° 55' W, *Schofield* 29908, 22 Jun 1966 (UBC). Tow Hill, Graham Island, on boulder of forest slope, 54° 03' N, 131° 55' W, *Schofield & Vaarama* 23745, 7 Jun 1964 (UBC). Graham Island, just N of Port Clements, log in forest, 53° 40' N, 132° 10' W, *Schofield & Beil* 55940, 22 Jun 1974 (UBC). Graham Island, Masset Inlet, head of Dinan Bay, up tree base in forest, 53° 38' N, 132° 40' W, *Schofield, Ellis & Schofield* 119813, 21 Jun 2002 (UBC). Graham Island, Blackwater Creek, near junction with Mamin River, S of Juskatla, humus at base of tree in forest, 53° 37' N, 132° 20' W, *Schofield & Vaarama* 24551, 14 Jun 1964 (UBC). NE Graham Island, Massett Sound, near road, 2 mi S. of Massett, on banks and up tree bases in swampy spruce forest, 53° 55' N, 132° 08' W, *Schofield* 34794, 27 Jul 1967 (UBC). N Graham Island, Eden Lake, central E side, on base of cedar, 53° 50' N, 132° 45' W, *Schofield* 35194, 30 Jul 1967 (UBC). W

Graham Island, Virgalias Cove, Port Louis, shaded cliff, 53° 42' N, 132° 58' W, *Schofield* 34128, 25 Jun 1967 (UBC). Graham Island, McClinton Bay, SW Massett Inlet, epiphytic on apple tree, 53° 40' N, 132° 40' W, *Schofield* 35260, 30 Jul 1967 (UBC). Graham Island, V.J.K. Ecological Reserve, Athlow Bay, Port Chanal, Empire Anchorage-Goose Cove, 53° 35' N, 132° 55' W, *Godfrey & Godfrey* 3996, 7 Jun 1977 (UBC). W Graham Island, Goose Cove, Athlow Bay, on hummocks near tree base in forest, 53° 35' N, 132° 55' W, *Schofield* 30588, 2 Jul 1966 (UBC). W Graham Island, Goose Cove, Athlow Bay, near anchorage, shaded cliff shelf in canyon, 53° 35' N, 132° 55' W, *Schofield* 37192, 29 Jul 1968 (UBC). W Graham Island, Goose Cove, Athlow Bay, stump on forest slope, 53° 35' N, 132° 55' W, *Schofield* 64613, 610 Jun 1977 (UBC). Graham Island, 4 mi S of Tlell, on hummocks in swampy forest, 53° 30' N, 131° 55' W, *Schofield* 29787, 20 Jun 1966 (UBC). Graham Island, near Brent Creek, *Chamaecyparis* bog, 53° 20' N, 132° 15' W, *Schofield* 30110, 26 Jun 1966 (UBC). Graham Island, ca 5 mi N of Honna River mouth, on bank in forest, 53° 18' N, 132° 15' W, *Schofield* 30151, 26 Jun 1966 (UBC). SW Graham Island, Van Inlet, between head of inlet and lake, at base of spruce in floodplain, 53° 17' N, 132° 29' W, *Schofield & Sjors* 32092, 22 Jul 1966 (UBC). Moresby Island, sandspit area, near mouth of Hanns Creek, on log in forest, 53° 15' N, 131° 50' W, *Schofield & Krajina* 39625, 24 Jul 1969 (UBC). Graham Island, Queen Charlotte City, close to the sea, 53° 15' N, 132° 04' W, *Persson s.n.*, 1 Jul 1957 (UBC). Moresby Island, sandspit, on *Picea sitchensis*, 53° 14' N, 131° 49' W, *Krajina s.n.*, 25 Jul 1968 (UBC). Moresby Island, near Centre Bay, Skidgate Channel, open hummock in forest, 53° 12' N, 132° 30' W, *Schofield* 30751, 4 Jul 1966 (UBC). Moresby Island, Skidegate Channel, S side of West narrows, humus hummock in forest, 53° 10' N, 132° 25' W, *Schofield* 30699, 3 Jul 1966 (UBC). Moresby Island, canyon near S bay, Skidegate Channel, bases of trees, 53° 09' N, 132° 05' W, *Schofield & Sharp* 25917, 12 Sep 1964 (UBC). Moresby Island, brooklet near entrance to E narrows, Skidegate Channel, on rotten logs, 53° 09' N, 132° 32' W, *Schofield* 14012, 17 May 1961 (UBC). Moresby Island, Deena River, dampish bank in woodland, 53° 08' N, 132° 08' W, *Schofield* 15789, 28 Aug 1961 (UBC, WTU). Moresby Island, Deena River, ca 8 mi from mouth, on alder in floodplain, 53° 08' N, 132° 08' W, *Schofield* 30779a, 4 Jul 1966 (UBC). Chaatl Island, frequent under trees in forest, 53° 07' N, 132° 30' W, *Schofield & Boas* 18697, 9-12 Jul 1962 (UBC). Chaatl Island, up tree base, 53° 07' N, 132° 30' W, *Schofield & Boas* 18909, 9-12 Jul 1962 (UBC). NW Moresby Island, Mackenzie Cove, bank in woods, 53° 05' N, 132° 20' W, *Schofield* 31136, 9 Jul 1966 (UBC). Graham Island, Long Inlet, Lagins Creek, common on banks in floodplain forests, 53° 00' N, 132° 00' W, *Schofield* 29979, 24 Jun 1966 (UBC). Moresby Island, S entrance of Louise Narrows, up base of Sitka spruce in forest, 52° 57' N, 131° 54' W, *Schofield* 45335, 7 Jul 1971 (UBC). Moresby Island NW, N slope of 'Laing Point' Mountain, NE side of Peel Inlet, on hummocks in forest, 52° 59' N, 132° 05' W, *Schofield* 30267, 28 Jun 1966 (UBC). NW Moresby Island, Peel Inlet, on log, 52° 59' N, 132° 06' W, *Schofield* 15414, 23 Aug 1961 (UBC). Louise Island, Mathers Lake, S end, base of *Pyrus* tree of lake shore, 52° 58' N, 131° 50' W, *Schofield* 37332, 31 Jul 1968 (UBC). Princess Royal Island, Chapele Inlet, stream canyon near mouth, E side, slope in open forest, 52° 55' N, 129° 08' W, *Schofield* 86596, 9 Aug 1986 (UBC). Moresby Island, stream to lake on NE side of Newcombe Inlet, Tasu Sound, on bank by stream, 52° 50' N, 132° 05' W, *Schofield* 37359, 1 Aug 1968 (UBC). Moresby Island, Tasu Creek mouth, head of Newcombe Inlet, Tasu Sound, damp earth near stream, 52° 50' N, 132° 08' W, *Schofield* 37616, 4 Aug 1986 (UBC). Moresby Island, Kootenay Inlet, N side, near head, on humus at tree base, 52° 50' N, 132° 11' W, *Schofield & Krajina* 39524, 24 Jul 1969 (UBC). Moresby Island, Kootenay Inlet, S side near head of inlet, mouth of waterfall filled creek, 52° 50' N, 132° 11' W, *Schofield & Krajina* 39587, 23 Jul 1969 (UBC). Richardson Island, SE end, E coast of Moresby Island, humus of bank above sea cliff, 52° 44' N, 131° 44' W, *Schofield & Vaarama* 24191, 11 Jun 1964 (UBC). Moresby Island SE, Crescent Inlet, humus near tree base, 52° 44' N, 131° 48' W, *Schofield & Vaarama* 24401, 12 Jun 1964 (UBC). E Moresby Island, Bigsby Inlet, small harbor just S, base of cliff, 52° 37' N, 131° 43' W, *Schofield* 32521, 28 Jul 1966 (UBC). Moresby Island, Barry Inlet, S side, near mouth, 52° 35' N, 131° 50' W, *Schofield, Spence, Lemmon & Brown* 84452, 21 Aug 1985 (UBC). Burnaby Island, Section Cove, up base of Sitka spruce trunk, 52° 25' N, 131° 21'

W, *Schofield* 44720, 2 Jul 1971 (UBC). Kunghit Island, Monserrat Bay, S of Rainy Island, cliff face, 52° 05' N, 131° 03' W, *Schofield* 44775, 2 Jul 1971 (UBC).

South East Mainland. Haney Research Forest, near banks of Alouette River, overturned tree root in forest, 49° 13' N, 122° 36' W, *Schofield, Godfrey, Godfrey & Nuszdorfer* 68319, 6 Apr 1978 (UBC).

Vancouver Island. Brooks Peninsula, on W side of lagoon near base camp, bogs, 50° 10' N, 127° 45' W, *Schofield* 76997, 19 Aug 1981 (UBC). Brooks Peninsula, on W side of lagoon near base camp, bogs, 50° 10' N, 127° 45' W, *Schofield* 77007, 19 Aug 1981 (UBC). Brooks Peninsula, toward base of 'Mt. Doom', bog slopes, 50° 10' N, 127° 45' W, *Schofield* 77178, 22 Aug 1981 (UBC). Tahsish Inlet, shaded forest cliff, humus on rock, 50° 08' N, 127° 05' W, *Halbert, Price & Doak* 7207, 6 Jun 1971 (UBC). Brooks Peninsula, barren gravel ridge above Cape Cook, base of tree trunk, 50° 07' N, 127° 54' W, *Schofield* 68515, 7 Jun 1978 (UBC). Ucluelet-Tofino Hwy, ca 19 mi E of junction, river margin, 49° 11' N, 125° 23' W, *Schofield* 38878, 7 May 1969 (UBC). Lost Shoe Creek nearby, Tofino Area, on cedar trunk in boggy forest, 49° 00' N, 125° 38' W, *Schofield* 26497, 2 May 1965 (UBC). Zeballos Inlet, Barr Creek N of Hecate Channel, trunk of *Malus diversiloba*, 49° 55' N, 126° 47' W, *R.L. Halbert, Price & Doak* 7380, 9 Jun 1971 (UBC). Zeballos Inlet, Barr Creek N of Hecate Channel, damp shaded cliff, on rock, 49° 55' N, 126° 47' W, *Halbert, Price & Doak* 7442, 9 Jun 1971 (UBC). Nootka Sound, near mouth of Tahsish Inlet, N of Strange Island, base of tree in forest, 49° 44' N, 126° 37' W, *Schofield & Halbert* 40243, 1 Oct 1969 (UBC). Nootka Island, Crawfish Lake, just W of lake, Moist mature Hemlock forest, 49° 41' N, 126° 50' W, *Halbert, Price & Doak* 4824, 12 Jun 1970 (UBC). Nootka Sound, Muchalat Inlet, S side King Passage, opposite Gore Island, damp slope near waterfall, 49° 38' N, 126° 23' W, *Schofield* 40303, 2 Oct 1969 (UBC). Bligh Island, Clerke Peninsula, Resolution Cove, S side, Nootka Sound, base of tree in forest, 49° 36' N, 126° 32' W, *Schofield & Halbert* 40345, 2 Oct 1969 (UBC). Tofino Inlet area, coastal *Thuja* forest, level, windthrow, humic gleysol, 49° 06' N, 125° 41' W, *D. Gagnon, F.M. Palmer* 80-50-6, 6 Aug 1980 (UBC). Trail from Rubas Hill down to beach, in dense Hemlock-Cedar-Spruce forest, on decaying wood, 49° 05' N, 125° 05' W, *Otto* 1781, 20 Jun 1967 (UBC). Effingham Inlet, just NE of Webster Island, shaded vertical cliff face, 49° 05' N, 125° 09' W, *Halbert, Price & Doak* 7024, 30 Oct 1970 (UBC). Effingham Inlet, just NE of Webster Island, shaded humus face, 49° 05' N, 125° 09' W, *Schofield* 43470, 30 Oct 1970 (UBC). Tofino Road, ca. 12 mi N of Ucluelet, on bark of tree, 49° 05' N, 125° 48' W, *Schofield* 13466, 23 Apr 1961 (UBC). Kennedy Lake, near E end of lake, bog near road, on tree trunk, 49° 04' N, 125° 34' W, *Schofield* 43747, 20 Mar 1971 (UBC). Tofino, ca. 10 km S, cedar trunks in forest, 49° 04' N, 125° 46' W, *Schofield & Schofield* 77756, 17 Jun 1982 (UBC). Long Beach area, near Wickannish Inn, 49° 03' N, 125° 40' W, *Wade s.n.*, Jun 1964 (UBC). Pacific Rim National Park, behind Long Beach, Sitka spruce forest, 49° 03' N, 125° 43' W, *Godfrey & Godfrey* 2674, 24 Jun 1975 (UBC). Pacific Rim National Park, behind Long Beach, Sitka spruce forest, 49° 03' N, 125° 43' W, *Godfrey & Godfrey* 2677, 24 Jun 1975 (UBC). Pacific Rim National Park headquarters, on road to E, behind picnic site, *Pinus contorta* - *Sphagnum* bog, peaty rotting stump over pool, wet, open to part shade, 49° 03' N, 125° 43' W, *Godfrey & Godfrey* 2717, 25 Jun 1975 (UBC). Effingham Inlet, lower slopes of Mt. Amedroz, 49° 02' N, 125° 09' W, *Schofield, L. Donovan & T. McIntosh* 75878, 2 Nov 1980 (UBC). Ucluelet Area, Quisitis Point, 'Spooky Woods', up base of tree in forest, 48° 59' N, 125° 39' W, *Schofield* 26583, 4 May 1965 (UBC). N of Ucluelet, W central coastal wet *Thuja* forest, nearly level, poor drainage, humic gleysol, 48° 58' N, 125° 33' W, *Gagnon, Spiers & Palmer* 81-87-4, 12 Aug 1981 (UBC). Barclay Sound, Mayne Bay, S side, near Lyall Point, log on upper beach, 48° 57' N, 125° 18' W, *Schofield* 43418, 29 Oct 1970 (UBC). Barclay Sound, West Brabant Island, shaded log, 48° 57' N, 125° 19' W, *Schofield* 43358, 29 Oct 1970 (UBC). Ucluelet area, W central coastal dry *Thuja* forest, on thick folisol over bedrock, 48° 56' N, 125° 28' W, *Gagnon, Spiers & Palmer* 81-88-3, 13 Aug 1981 (UBC). Barclay Sound, Willis Island, NW end, rotten log of upper beach, 48° 55' N, 125° 20' W, *Schofield* 43410, 29 Oct 1970

(UBC). Barclay Sound, SW bay of Turtle Island, shaded forest cliff, vertical humus, 48° 54' N, 125° 19' W, *Halbert, Price & Doak 6944*, 29 Oct 1970 (UBC). Barclay Sound, SW Bay of Turtle Island, shaded decaying log, 48° 54' N, 125° 19' W, *Halbert, Price & Doak 6949*, 29 Oct 1970 (UBC). E of Bamfield, coastal *Thuja* forest, level, poor drainage, 48° 50' N, 125° 04' W, *Gagnon & Palmer 80-57-7*, 14 Aug 1980 (UBC). E of Bamfield, Mile 58 near pond, up tree base, 48° 50' N, 125° 08' W, *Schofield 55372*, 30 Mar 1974 (UBC). Bamfield, Grappler Inlet, near old reservoir lake of Marine station, 48° 49' N, 125° 08' W, *Schofield, Donovan & McIntosh 75813*, 1 Nov 1980 (UBC). 'Rain Forest Trail', decaying stump, moist, partial shade, infrequent to abundant, 48° 42' N, 124° 58' W, *Godfrey & Godfrey 2777*, 26 Jun 1975 (UBC). 'Rain Forest Trail', western hemlock trunk; moist, partial shade, infrequent to abundant, 48° 42' N, 124° 58' W, *Godfrey & Godfrey 2778*, 26 Jun 1975 (UBC). Port Renfrew, high up on tree, 48° 34' N, 124° 25', *Gibbs s.n.*, 26 June 1901 (WTU).

USA

Alaska. Prince of Wales Island. Saltery cove, in flowing water, on rocks, 55° 24' N, 132° 19' W, *Frye 331*, 4 Jun 1913 (WTU). Prince of Wales Island, Exchange Cove, on stick in forest, 56° 12' N, 133° 5' W, *Frye 274*, 2 Jun 1913 (WTU). Prince of Wales Island, Ratz Harbor, on base of tree in very wet place, 55° 53' N, 132° 35' W, *Frye 293*, 3 Jun 1913 (WTU).

Oregon. Coos Co.: Cherry Creek Research Natural Area, N Fork Cherry Creek 20 miles SE of Coos Bay, (former) Big Tree Recreation Site, along road 27-11-27.0, on trunk of *Tsuga*, 43° 13' 10" N, 123° 56' 5" W, elevation 195 m, *Wagner 9051*, 4 Nov 1997 (OSC). Shotgun Creek, near junction of Road 26-9-21.0 and Road 26-9-17.0, riparian forest, 30 feet uphill from stream, bark of *Thuja plicata*, 43° 17' 36" N, 123° 45' 41" W, *Morgan 00-06*, 18 Apr 2000 (OSC). Shotgun Creek, about 0.5 mile above road BLM 26-9-21, *Pseudotsuga/Tsuga* forest, partial shade, *Thuja plicata* stump, 43° 17' 47" N, 123° 46' 46" W, *Sperling 00-JS-11, 00-JS-12, 00-JS-13*, 24 Apr 2000 (OSC). Unnamed stream off Burnt Mountain Tie Road, 26-10-35.0, *Pseudotsuga/Tsuga* forest, partial shade, *Pseudotsuga* short snag, 43° 17' 16" N, 123° 50' 33" W, *Sperling 00-JS-09*, 23 Feb 2000 (OSC). West Fork Smith River tributary, 12 miles above junction with Smith River, *Pseudotsuga/Tsuga/Thuja* forest, partial shade, rotten *Thuja plicata* log, 43° 53' 44" N, 123° 43' 32" W, *Donato ORI25/BRYO/DD015, ORI25/BRYO/DD016*, 9 Mar 2003 (OSC). Slide Creek, Myrtlewood Resource Area, *Pseudotsuga/Tsuga* forest, partial shade, rotten *Thuja plicata* log, 43° 0' 14" N, 123° 55' 16" W, *Donato ORI28/BRYO/DD013*, 4 Mar 2003 (OSC). West Fork Smith River tributary, 12 miles above junction with Smith River, *Pseudotsuga/Tsuga/Thuja* forest, full sun, on trunk of *Thuja plicata*, 43° 53' 52" N, 123° 43' 13" W, *Barrett ORI25/BRYO/BB-013*, 9 Mar 2003 (OSC). Tioga vicinity, unnamed tributary to Tioga Creek, 20 miles ESE of Coos Bay, 50 year old *Pseudotsuga menziesii* stand, *Thuja plicata* stump, 43° 15' 48" N, 123° 50' 51" W, *Sperling B2-JS-110*, 22 Oct 2002 (OSC). Burnt Mountain Road 27-10-1.1, fully shaded dry slope, bark of *Thuja plicata*, 43° 14' 47" N, 123° 49' 45" W, *Sperling B2-JS-113*, 24 Oct 2002 (OSC). Former Big Tree Recreation site adjacent to Cherry Creek Research Natural Area, riparian forest, bark of *Tsuga heterophylla*, 43° 13' 10" N, 123° 56' 5" W, *Rittenhouse 2125, 2126, 2127*, 16 Dec 1997 (OSC). Former Big Tree Recreation site adjacent to Cherry Creek Research Natural Area, riparian forest, bark of *Thuja plicata*, 43° 13' 10" N, 123° 56' 5" W, *Rittenhouse 2128, 2128A*, 16 Dec 1997 (OSC). Hatcher Creek Area near Tioga, ca 20 miles ESE of Coos Bay, *Pseudotsuga/Tsuga/Thuja* forest, partial shade, *Thuja plicata* stump base, 43° 17' 43" N, 123° 49' 27" W, *Sperling 00-JS-03*, 7 Feb 2000 (OSC). Doerner Fir Trail, ca. 20 miles SE of Coos Bay, *Pseudotsuga/Tsuga* forest, full shade, bark of *Tsuga heterophylla*, 43° 10' 52" N, 123° 48' 24" W, *Pipp AP98-29*, 16 Dec 1998 (OSC). Camas Creek drainage, tributary to South Fork Coquille River, ca. 30 miles SE of Coos Bay. *Pseudotsuga/Tsuga* forest, partial shade, bark of rotting *Pseudotsuga* log, 43° 5' 25" N, 123° 46' 14" W, *Sperling CVS105-4*, 23 Oct 2002 (OSC). Douglas Co.: Panther Creek Bureau of Land Management regeneration site, fully shaded, riparian, bark of *Thuja plicata*, 43° 15' 0" N, 123° 36' 52" W, *Sperling 99-02JS*, 5 May 1999 (OSC). North Fork Coquille River Area of Critical Environmental Concern, N

side of Coos Mountain, 15 miles ESE of Coos Bay. *Pseudotsuga/Tsuga/Thuja* forest, riparian, partially shaded, on trunk of *Thuja plicata*, 43° 17' 51" N, 123° 53' 30" W, *Brown OR125/BRYO/KB002*, 5 Mar 2003 (OSC). North Fork Coquille River Area of Critical Environmental Concern, N side of Coos Mountain, 15 miles ESE of Coos Bay, *Pseudotsuga/Tsuga/Thuja* forest, riparian, partially shaded, On trunk of *Thuja plicata*, 43° 17' 46" N, 123° 53' 27" W, *Stidham OR125/BRYO/MS018*, 5 Mar 2003 (OSC). Camp Creek watershed, ca. 30 miles NE of Coos Bay, *Pseudotsuga/Tsuga/Thuja* forest, partial shade, near a seep, on rotten log, 43° 32' 28" N, 123° 42' 11" W, *Donato OR124/BRYO/DD014*, 8 Mar 2003 (OSC). Lane Co.: Gwynn Creek Trail, 700 m above trailhead, in valley bottom. *Picea/Pseudotsuga/Tsuga* forest, full shade, *Pseudotsuga* down log, 44° 16' 12" N, 124° 5' 45" W, *Sperling, Rodenkirk, Roediger & Friedman B2JS109*, 16 Oct 2002 (OSC). Lincoln Co.: Cape Perpetua, Cape Creek Trail at bridge ca 100 m W of Giant Spruce. *Picea/Pseudotsuga/Tsuga* forest, full shade, bark of rotting *Pseudotsuga* log, 44° 16' 52" N, 124° 5' 11" W, *Rodenkirk, Sperling, Roediger, and Friedman 02TJRB1*, 16 Oct 2002 (OSC). Cape Perpetua, Cape Creek Trail at bridge ca 100 m W of Giant Spruce, *Picea/Pseudotsuga/Tsuga* forest, full shade, bark of rotting *Pseudotsuga* log, 44° 16' 52" N, 124° 5' 11" W, *Wagner m3006*, 24 Feb 2016 (OSC). Cape Perpetua, Cape Creek Trail below visitor center, *Picea/Pseudotsuga/Tsuga* forest, full shade, on upper trunk of *Alnus rubra*, 44° 17' N, 124° 7' W, *Wagner 1743*, 15-22 Jan 1978 (OSC). Cape Perpetua Scenic Area, Cape Creek Trail, on fallen log, 44° 17' N, 124° 7' W, *Wagner 2396*, 26 Jan 1980 (ORE, WTU). Cape Perpetua, Cape Creek Trail below visitor center. *Picea/Pseudotsuga/Tsuga* forest, full shade, on upper trunk of *Alnus rubra*, 44° 17' N, 124° 7' W, *Wagner 1743*, 15-22 Jan 1978 (OSC).

Washington. Clallam Co.: Trail from Ozette Lake to Cape Alava, between lake and Ahlstrom's prairie, on trunk of *Picea sitchensis*, ca. 48° 10' N, 124° 30' N, *Schofield & Spence 77615*, 7 Jun 1982 (UBC). Olympic National Park, James Pond, on very moist, rotten log, 47° 55' 10" N, 124° 36' W, *Norris 98895*, 2 Jun 2000 (WTU). Grays Harbor Co.: Quinalt Lake, on trunk of *Taxus brevifolia*, *Brown & Muenscher 7*, 10 July 1950 (WTU). Quinalt lake, Falls Creek campground, nature trail 1, old tree trunk, ca. 47° 30' N, 123° 50' W, *Schofield & Harpel 105194*, 28 May 1996 (UBC). Gattom campground, margin of lake Quinalt, up base of tree, ca. 47° 30' N, 123° 50' W, *Schofield & Harpel 105231a*, 29 May 1996 (UBC). West Fork Humptulips River Watershed, Petes Creek Trail, on shaded *Abies* trunk, UTM Z10 444348 E, 5257460 N [47° 28' 6" N, 123° 44' 19" W], *Hutten 6193*, 25 July 2002 (WTU). Jefferson Co.: Goodman Creek Watershed, 6.5 miles south of Forks, state forest red cedar bog, on decaying *Tsuga heterophylla*, 47° 51' 20" N, 124° 24' 25" W, *Wagner m1120*, 29 Mar 2003 (OSC). Goodman Creek Watershed, 6.5 miles south of Forks; state forest red cedar bog site, wetland dominated by *Thuja plicata*, seepy hillside, on base of *Thuja*, 47° 51' 20" N, 124° 24' 25" W, *Wagner m1125*, 29 Mar 2003 (OSC). Snohomish Co.: Wisconsin creek, up base of tree in forest, *Schofield 21888*, 4 Jul 1963 (UBC). S Fork Stillaguamish River, 22 Creek near Verlot, 22 Lake trailhead, elevation 336 m, 48° 4' 38" N, 121° 44' 45" W, *Russell s.n.*, 27 March 1979 (ORE, WTU).

Appendix 2. Additional specimens examined, *Macrodiplrophyllum flaccidum*

CANADA. British Columbia.

North Coast. Bear River, ca. 5 mi E of Hwy 37 crossing over river at Stuart, 30 mi W of Cranberry junction road, wet cliff, 55° 57' N, 129° 58' W, *Schofield 65102*, 6-10 Jun 1977 (UBC). Kaien Island, Prince Rupert, Hays Mountain, wet cliff, 54° 17' N, 130° 18' W, *Schofield & Boas 21535*, 14 Jul 1963 (UBC). Kaien Island, Prince Rupert, Hays Mountain, wet cliff shelf, 54° 17' N, 130° 18' W, *Schofield & Boas 21562*, 14 Jul 1963 (UBC). Kaien Island, Prince Rupert, Hays Mountain, damp cliff shelf, 54° 17' N, 130° 18' W, *Schofield & Sharp 25852*, 11 Sep 1964 (UBC). Kaien Island, Prince Rupert area, Hays Mountain, near summit, damp shaded cliff, 54° 15' N, 130° 20'

W, *Schofield* 72950, 27 Jun 1979 (UBC). Kloiya Bay, ca 10 mi E of Prince Rupert, on cliff shelf, 54° 14' N, 130° 11' W, *Schofield* 13858, 14 May 1961 (UBC).

Haida Gwaii (Queen Charlotte Islands). N Graham Island, near center, Jalun Lake, central bank in forest near lake, 53° 58' N, 132° 50' W, *Schofield* 35152, 30 Jul 1967 (UBC). Frederick Island, NE side, damp cliff face, 53° 55' N, 133° 10' W, *Schofield* 34239, 26 Jun 1967 (UBC). Graham Island W, Boats River, near mouth, Port Louis, silty bank of river, 53° 42' N, 132° 58' W, *Schofield* 34054, 25 Jun 1967 (UBC). Graham Island, Mercer Lake, E end, near Athlow Bay damp cliff, 53° 35' N, 132° 55' W, *Schofield & Krajina* 39698, 26 Jul 1969 (UBC). Graham Island, V.J.K. Ecological Reserve, Athlow Bay, Port Chanal, Empire Anorage-Goose Cove, 53° 35' N, 132° 55' W, *Godfrey & Godfrey* 4155, 8 Jun 1977 (UBC). SE side W Graham Island, Goose Cove, Athlow Bay, in Creek Canyon near sea stacks, humid shaded cliff face, 53° 35' N, 132° 55' W, *Schofield* 33989, 25 Jun 1967 (UBC). W. Graham Island, Goose Cove, Athlow Bay, damp cliff in canyon, 53° 35' N, 132° 55' W, *Schofield* 64638, 6-10 Jun 1977 (UBC). W. Graham Island, Goose Cove, Athlow Bay, shaded wet canyon wall, 53° 35' N, 132° 55' W, *Schofield & Spence* 83653, 8-9 Aug 1985 (UBC). SW Graham Island, Van Inlet, SW end, near mouth, damp shaded cliff face, 53° 15' N, 132° 34' W, *Schofield* 33717, 22 Jun 1967 (UBC). SW Moresby Island, Dawson Inlet, streamlet on NW side, damp streamlet margin, 53° 13' N, 132° 29' W, *Schofield* 33483, 20 Jul 1967 (UBC). NE Moresby Island, Alliford Bay, dampish cliff face, 53° 12' N, 131° 58' W, *Schofield* 15745, 28 Aug 1961 (UBC). SW Graham Island, Tana Bay, E side near head, shaded cliff, 53° 11' N, 132° 21' W, *Schofield* 33514, 21 Jun 1967 (UBC). S Graham Island, Trounce Creek, Trounce Inlet, cliff face, 53° 10' N, 132° 19' W, *Schofield* 15590, 26 Aug 1961 (UBC). Moresby Island, Skidegate Channel, Seaside cliffs of E narrows, wet cliff, 53° 09' N, 132° 19' W, *Schofield* 14059, 17 May 1961 (UBC). Moresby Island, canyon near S bay, Skidegate Channel, wet cliff, 53° 09' N, 132° 05' W, *Schofield & Sharp* 25930, 13 Sep 1964 (UBC). Moresby Island, N face Mt. Moresby, cliff shelf, 53° 08' N, 132° 05' W, *Schofield* 25281, 25286, 31 Jul 1964 (UBC). Moresby Island, N face Mt. Moresby, damp shaded cliff face, 53° 08' N, 132° 05' W, *Schofield* 34467, 1 Jul 1967 (UBC). Chaatl Island, shaded damp cliff near stream, 53° 07' N, 132° 30' W, *Schofield & Boas* 18775, 9-12 Jul 1962 (UBC). NW Moresby Island, Kitgoro inlet, shaded humid cliff shelf, 53° 05' N, 132° 30' W, *Schofield* 30992, 9 Jul 1966 (UBC). Moresby Island, Cirque Lake, SW side of Mount Moresby, damp cliff near falls, 53° 05' N, 132° 00' W, *Schofield & Spence* 84237, 18 Aug 1985 (UBC). Moresby Island, mountain between peak of Mount Moresby and W end of Mosquito Lake, damp cliff ledge, 53° 01' N, 132° 07' W, *Schofield* 25403, 1 Aug 1964 (UBC). Moresby Island, mountain between peak of Mount Moresby and W end of Mosquito Lake, seepy mountainside outcrop, 53° 01' N, 132° 07' W, *Schofield* 32349, 24 Jul 1966 (UBC). Moresby Mountain, base of N slope, Moresby Island, wet cliff ledge, 53° 01' N, 132° 05' W, *Schofield & Sharp* 25905, 12 Sep 1964 (UBC). Graham Island, Long Inlet, Lagins Creek, humid shaded cliff, 53° 00' N, 132° 00' W, *Schofield* 29957, 24 Jun 1966 (UBC). NW Moresby Island coast, Hibben Island, NE side, damp rock face, 52° 59' N, 132° 20' W, *Schofield* 15246, 22 Aug 1961 (UBC). Moresby Island NW, N slope of 'Laing Point' Mountain, NE side of Peel Inlet, wet terraces by waterfall, 52° 59' N, 132° 05' W, *Schofield* 30273, 28 Jun 1966 (UBC). Moresby Island, mountain at head of W. branch of Braverman Creek, Peel Inlet area, subalpine cliff crevice, 52° 59' N, 132° 05' W, *Schofield* 30476, 30 Jun 1966 (UBC). W Moresby Island, 'Laing Point' Mountain Range, Peel Inlet, subalpine cliff, 52° 59' N, 132° 05' W, *Schofield* 34533, 2 Jul 1967 (UBC). Moresby Mountain, Takakia Lake, about 10 mi S of Moresby logging camp, cliff shelf, 52° 55' N, 132° 03' W, *Schofield* 25202, 29 Jul 1964 (UBC). NW Moresby Island, Kootenay Inlet, bog near mouth of northern arm, damp cliff, 52° 50' N, 132° 11' W, *Schofield* 31318, 10 Jul 1966 (UBC). Moresby Island, Kootenay Inlet, S side near head of inlet, mouth of waterfall filled creek, 52° 50' N, 132° 11' W, *Schofield & Krajina* 39582, 23 Jul 1969 (UBC). Moresby Island, Tasu Creek mouth, head of Newcombe Inlet, Tasu Sound, up wet base of cliff, 52° 50' N, 132° 08' W, *Schofield* 37623, 4 Aug 1968 (UBC). Moresby Island, Mine Mountain above Tasu Townsite, Tasu Sound, wet cliff, subalpine area, 52° 46' N, 132° 01' W, *Schofield* 37228, 31 Jul 1968 (UBC). Moresby Island, Mine Mountain above Tasu

Townsite, Tasu Sound, damp alpine outcrop, 52° 46' N, 132° 01' W, *Schofield* 37271, 31 Jul 1968 (UBC). Moresby Island, Mine Mountain above Tasu Townsite, Tasu Sound, damp cliff, 52° 46' N, 132° 01' W, *Schofield & Schofield* 73442, 10-11 Jul 1979 (UBC). Moresby Island, Mine Mountain above Tasu Townsite, Tasu Sound, 52° 46' N, 132° 01' W, *Schofield* 75021, 26 Jul 1980 (UBC). Moresby Island, mountain directly above Tasu Townsite, wet cliff, 52° 46' N, 132° 01' W, *Schofield* 34868, 28 Jul 1967 (UBC). Moresby Island, Fairfax Inlet, Tasu Sound, W side near head, 52° 45' N, 132° 00' W, *Schofield* 74924, 9 Jul 1980 (UBC). SE Moresby Island, Bigsby Inlet, cliff crevices, 52° 37' N, 131° 43' W, *Schofield & Vaarama* 24082, 10 Jun 1964 (UBC). Huxley Island, N end, damp shaded cliff, 52° 28' N, 131° 21' W, *Schofield* 44667, 1 Jul 1971 (UBC). SE Moresby Island, Jedway area, damp cliff, 52° 20' N, 131° 15' W, *Schofield* 34670, 26 Jul 1967 (UBC).

South Coast and Coast Range. Namu Lake, near mouth of Barke Channel, boulder of stream margin, 51° 51' N, 127° 51' W, *Schofield* 86169, 4 Aug 1986 (UBC). Wakeman Sound, Kingcome Inlet, damp cliff near waterfall, 51° 00' N, 126° 32' W, *Schofield* 41251, 15 Apr 1970 (UBC). Toba Inlet, N shore, E of Brahm Bay, damp canyon cliff, 50° 25' N, 124° 35' W, *Schofield* 38336, 25 Feb 1969 (UBC). Slopes of Mount Matier, trail following three lakes, E of Pemberton, damp cliff in subalpine forest, 50° 20' N, 122° 26' W, *Schofield* 56830A, 7 Aug 1975 (UBC). Raza Island, centre, W side, Raza Passage, seasonal streambed, rock wall in ravine of stream, wet, N facing, open, 50° 18' N, 125° 01' W, *Godfrey & Godfrey* 3828, 25 May 1977 (UBC). Raza Island, W side, Raza Passage, damp cliff, 50° 18' N, 125° 01' W, *Schofield* 64083, 25 May 1977 (UBC). Elaho Area, Sims Creek Valley, Peaches and Penor Waterfall, outcrop shelf by fall, 50° 15' N, 123° 35' W, *Schofield & Taylor* 118620, 17 Aug 2001 (UBC). Coin Creek, waterfall at natural bridge, in Ashlu Creek Valley, above Ashlu Creek, on S side, sand and humus over cliff face, wet-spray, open, abundant, 49° 57' N, 123° 26' W, *Godfrey and Godfrey* 3531, 3543, 3552, 17 Oct 1976 (UBC). Jervis Inlet, below waterfall at creek mouth into inlet, extreme upper end of Queens Reach, humus over slate canyon wall, wet, dripping, open, NW facing, abundant, 49° 45' N, 124° 10' W, *Godfrey & Schofield* 2002, 3 Sep 1974 (UBC). Squamish Highway (99), 5 mi N of Deek's Creek, waterfall E of highway, soil over boulder on stream bank by waterfall, wet-spray, open, 49° 30' N, 123° 15' W, *Godfrey & Godfrey* 2423, 14 Apr 1975 (UBC). Chehalis River, Harrison Mills Road, Mile 15.1, above mouth of Chehalis Lake, roadside cliffs, soil over outcrop, moist-wet, part shade, NE facing, 49° 23' N, 122° 01' W, *Godfrey, Godfrey & Schofield* 2576, 1 Jun 1975 (UBC). Golden Ears Provincial Park, 'lake lookout' trail and main trail to 'Burma Bridge', large waterfall, over rock on cliff face, wet in spray, N facing, 49° 22' N, 122° 30' W, *Godfrey & Godfrey* 3664, 16 Apr 1977 (UBC). N Vancouver, Capilano Canyon, below Cleveland Dam, humid cliff face, 49° 21' N, 123° 06' W, *Schofield & Jamieson* 41441, 2 May 1970 (UBC). N Vancouver, Lynn Canyon Park, exposed rock surface of boulder, steep, < 1 cm soil accumulation, 49° 20' N, 123° 01' W, *van Velzen & Leong s.n.*, 16 Jun 1980 (UBC). N Vancouver, Lynn Canyon, Twin Falls Bridge, downstream, rock in crevice along stream, little soil accumulation, irregular rock surface, 49° 20' N, 123° 01' W, *van Velzen & Leong s.n.*, 18 Jun 1980 (UBC). N Vancouver, Lynn Creek Canyon, cliff face, 49° 20' N, 123° 01' W, *Schofield & Boas* 18438, 1 Jul 1962 (UBC). N Vancouver, Lynn Creek Canyon, sandy soil among rocks above bank of Lynn Creek, 49° 20' N, 123° 01' W, *Godfrey & Godfrey* 209, 27 Sep 1973 (UBC). N Vancouver, Lynn Creek Canyon, damp cliff face, 49° 20' N, 123° 01' W, *Schofield, Godfrey & Godfrey* 67624, 16 Feb 1978 (UBC). Vancouver area, Indian Arm, head, wet cliff of canyon, 49° 20' N, 122° 55' W, *Schofield* 40550, 7 Jan 1970 (UBC).

Vancouver Island. O'Connor Lake area, ca 8 mi SW of Port McNeill, 1 mi W of O'Connor Lake, steep stream bed with frequent water falls, soil over rock on shaded cliff, 50° 32' N, 127° 17' W, *Halbert, Price, Doak* 5499, 21 Jul 1970 (UBC). Robson Bight, Tsitika River mouth, damp outcrop by stream, 50° 28' N, 125° 34' W, *Schofield* 85595, 28 Jul 1986 (UBC). Kashult Inlet, at Wood Cove, limestone cliffs and waterfall, dripping limestone wall by stream, 50° 09' N, 127° 18' W, *Halbert, Price, Doak* 7268, 7269, 7303, 8 Jun 1971 (UBC). Brooks Peninsula, Jakobson Creek, W of

Jacobson Point, cliff by creek, 50° 08' N, 127° 43' W, *Schofield* 82654, 13 Aug 1984 (UBC). Nootka Sound, near mouth of Tahsis Inlet, N of Strange Island, wet cliff of canyon, 49° 44' N, 126° 37' W, *Schofield* 40238, 1 Oct 1969 (UBC). Muchalat Inlet, near mouth Houston River & tributary, shaded moist river canyon, 49° 38' N, 126° 18' W, *Halbert, Price, Doak* 4716, 10 Jun 1970 (UBC). Nootka Sound, S side of Zuciarte Channel, E of Discovery Point, humus of slope in forest, 49° 35' N, 126° 32' W, *Schofield & Halbert* 40386, 2 Oct 1969 (UBC). Kennedy River, on river, 28 mi W of Sproat Lake, dampish cliff, 49° 14' N, 125° 23' W, *Schofield & Boas* 19062, 21 Jul 1962 (UBC). Tofino Ucluelet Hwy, waterfall 23 mi E of junction, humid cliff near waterfall, 49° 14' N, 125° 22' W, *Schofield* 38842, 7 May 1969 (UBC). Barclay Sound, near head of Effingham Inlet, damp cliff, 49° 04' N, 125° 09' W, *Schofield* 43541, 30 Oct 1970 (UBC). Stoney Creek, ca 5 mi W of Port Renfrew, shaded boulders and cliffs along stream through moist Cedar-Hemlock rainforest, shaded cliff base, humus over vertical rock face, 48° 33' N, 124° 32' W, *Halbert & Price* 2922, 1 Jul 1969 (UBC).

USA

Alaska. Wrangell Island, along road about 8.5 mi s. of Wrangell, open roadcut facing W, hemlock forest and shrubs above roadcut, wet rocks, 56° 20' 56" N, 132° 20' 19" W, *Worley* 7603, 4 Jun 1968 (UBC). Wrangell Island, slopes above sawmill, about 5 mi S of Wrangell, small fen opening in forest, 56° 23' 41" N, 132° 20' 7" W, *Worley & Hamilton* 7891, 7 Jun 1968 (UBC). Mitkof Island, Mitkof Highway, ca 7 mi S of Petersburg, stream gully, damp cliff near cascade, 56° 44' 16", 132° 56' 15", *Worley & Schofield* 8674, 23 Jun 1968 (UBC). Sitka County, Indian River Trail, valley bottom in Sitka spruce forest, on soil, *Wagner* m2797, 20 Aug 2012 (OSC). Douglas Island, N Douglas road, fish creek, salmon stream with occasional rock walls in spruce-hemlock forest with nearby muskeg, on rock by stream, 58° 20' N, 134° 34' W, *Worley & Boas* 11618, 11703, 28 Aug 1968 (UBC). Prince of Wales Island, Craig vicinity, trail to Sunny Hay Mountain, between muskeg and 2000' minor summit on ridge, wet rock crevices on N facing bluff, 55° 28' N, 133° 6' W, *Worley & Hamilton* 6973, 20 May 1968 (UBC). Revillagigedo Island, gorge of "second waterfall creek" by road N of Ketchikan, on shaded rocks, moist wall of gorge, 55° 30' N, 131° 45' W, *Worley & Hamilton* 6239, 6250, 12 May 1968 (UBC). Kenai Peninsula, Slim's Pass area, mountain above Wide Bay, humid shaded crevice of cliff, 57° 27' N, 156° 30' W, *Schofield & Talbot* 115109, 23 Jul 2000 (UBC). Whittier, shaded cliff grotto, 60°46'N, 148°39'W, *Schofield & Talbot* 117623, 5 Jun 2001 (UBC).

Oregon. Clatsop Co.: Saddle Mountain, N facing cliff, 45° 58' 8" N, 123° 41' 41" W, *Schofield & Lyford* 72296, 72253, 5 Jun 1979 (OSC, UBC). Saddle Mountain, slopes and peak, seepy n. facing cliff, 45° 58' 8" N, 123° 41' 41" W, *Schofield, Godfrey & Godfrey* 68037b, 68052, 22 Mar 1978 (UBC, OSC). Saddle Mountain State Park, slopes and peak of Saddle Mountain, damp N facing cliff, 45° 58' N, 123° 41' W, *Lyford* 2117, 5 Jun 1979 (OSC).

Washington. Snohomish Co.: Stillaguamish River, cliffs on bank, wet cliff base, *Schofield, Ireland & Boas* 18448, 4 Jul 1962 (UBC). Clallam Co.: Deer Lake trail, Soleduck Hot Springs area, cliff face, canyon of Soleduck Falls, 47° 57' 4" N, 123° 48' 12" W, *Schofield & Iwatsuki* 28301, 4 Oct 1965 (UBC).