LEJEUNEA SUBELOBATA AND LEJEUNEA DRUMMONDII
(JUNGERMANNIOPSIDA) IN AUSTRALASIA

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Abstract. Lejeunea subelobata Carrington & Pearson has been regarded as a synonym of L. drummondii Taylor, but the two species differ in patterns of variation in lobule morphology, shapes of the gynoecial bracteole, female bract underleaf and vegetative underleaves; in stem anatomy, and ecology. Lejeunea subelobata is a rheophyte from south-east Australia, Tasmania, and New Zealand that grows primarily as a lithophyte on rock within and around waterways, in association with basicolous substrates particularly basalt, rhyolite and andesite. Lobules in L. subelobata are always explanate, the female bract underleaf is obovate, underleaves are rotund and remote, and the stem medulla has 19–26 cells with small concave trigones. Lejeunea drummondii is, in its current circumscription, an ecologically and morphologically malleable taxon confined to Australia. The relationship between L. drummondii and plants from New Zealand described as L. epiphylla Colenso nom. illeg. requires further investigation.

Key words: Australia, New Zealand, liverwort, Flora, Lejeuneaceae, synonymy

INTRODUCTION

In 1839 James Drummond received from Sir William Jackson Hooker a letter requesting seeds and plants and an offer to dispose of the collections on Drummond’s behalf (Sherwood 2010). Six consignments were sent to W. J. Hooker between 1839 and 1852, during which time Drummond resided in the Perth Region (Sherwood 2010). Hooker senior evidently passed Drummond’s early bryophyte collections to Joseph Dalton Hooker and Thomas Taylor, who at the time would have been collaborating on the cryptogams collected by J. D. Hooker on the Antarctic voyage of HMS Erebus and Terror between 1840 and 1843. In 1846 Lejeunea drummondii Taylor was named for Drummond on the basis of plants collected by him at ‘Swan River’ (Taylor 1846). As it is unclear whether Drummond’s locality refers to the settlement, the river, or the region, the precise origin of the type is difficult to elucidate, beyond the fact that it must have come from somewhere within what is today the wider Perth region in Western Australia.

Lejeunea drummondii has since been recorded in all states and territories of Australia. In its current usage it is the most widespread, abundant, and ecologically malleable species of Lejeunea Libert in Australia, occupying an array of forest microsites, from leaves, twigs, branches, trunks, roots, logs, and rocks on the forest floor to rocks within streams, and may even be found growing submerged under running water. Considerable morphological variation has been ascribed to L. drummondii, in keeping with this broad ecological tolerance.

On one of his last visits to New Zealand in 2003, Professor Rudolf M. Schuster identified in the field a rheophytic plant growing submerged on rocks in the Okahu Stream within Herekino State Forest, Northland, as an undescribed species for which he had a manuscript name (R. M. Schuster, pers. comm.). This entity is distinctive in its consistent production of explanate lobules and rheophytic habit. It has proved widespread in New Zealand, and the same as some plants from similar microhabitats in Tasmania, Victoria and New South Wales represented in Australian herbarium material, including the syntypes of Lejeunea
subelobata" Carrington and Pearson (Carrington & Pearson 1888).

A survey of Australian and New Zealand specimens indicated morphological differences between *L. drummondii* and *L. subelobata* that were correlated with habitat. Furthermore, these two species were included in a molecular phylogeny based on nrITS1 and *trnL-F*, within which they were separated by the basal-most node within the *Lejeunea*-generic complex (Renner et al. 2011). Though only single representatives of each species were included, high support values were resolved for intervening nodes, and phylogenetic signal was congruent between markers. This suggests subtle morphological differences are significant with regards their ability to circumscribe phylogenetically distinct lineages. However, in this phylogeny *L. subelobata* was wrongly called *L. tasmanica* Gottsche (Gottsche 1857) due to misinterpretation of type material by the author. Morphological, molecular, and ecological evidence support the recognition of two morphologically and phylogenetically isolated and ecologically different species. Therefore *L. subelobata* is here reinstated from synonymy under *L. drummondii*.

**Materials and Methods**

The morphological descriptions and comparisons are based on observations of *Lejeunea* populations observed in New South Wales, Tasmania, Victoria, Western Australia (Australia) and New Zealand, and those held in the herbaria AK, BM, CANB, CHR, FH, G, HO, MEL and NSW (Holmgren et al. 1990), using a stereomicroscope and compound microscope. Material was initially identified with reference to Grolle (1982). Digital images of gametophyte structures were captured with a Leica DFC420 camera on a Leica DM2500 compound microscope. Descriptions are based on two specimens considered representative of observed variation for *L. subelobata*, and from a single western Australian specimen for *L. drummondii*. Allometric dimensions were measured using ImageJ (Abramoff et al. 2004) calibrated with a slide micrometer, with ranges based on twenty measurements taken haphazardly from each specimen. For rare structures such as perianths and female bracts, ranges are based on the largest and smallest examples observed, and measured using an eyepiece micrometer. Illustrations of plant parts were produced with the aid of an Olympus CH-2 compound microscope with camera lucida attachment.

**Taxonomic Treatment**

*Lejeunea drummondii* Taylor  
Fig. 1

London Journal of Botany 5: 400. 1846. – *Eulejeunea drummondii* (Taylor) Rodway, Tasmanian Bryophytes 2 (Hepatics): 89. 1916. – **Type**: AUSTRALIA, ‘Swan River, Mr. James Drummond’. Holotype: FH! Iso- 

types: G-19616! W (Lindenb. Hep. 6440).

*Lejeunea gunniana* Mitt. in Hooker, Flora Tasmaniae 3: 235. 1859. – *Cheirolejeunea gunniana* (Mitt.) Steph. Species Hepaticarum 5: 675. 1914. – **Type**: AUSTRALIA ‘Tasmania, Gunn’ Syntype: BM! ‘Brown’s River, Oldfield’. Syntype: BM!

*Lejeunea luchmannii* Steph., Hedwigia 28: 261. 1889. – *Strepsilejeunea luchmannii* (Steph.) Steph., Species Hepaticarum 5: 292. 1913. – **Type**: AUSTRALIA ‘Gippsland, Moe River, ... leg. Luchmann’ HOLOTYPE: G! Iso- 

types: BM!

*Lejeunea tasmanica* Gottsche, Linnaea 28: 558. 1857. – *Eulejeunea tasmanica* (Gottsche) Rodway, Tasmanian Bryophytes 2 (Hepatics): 89. 1916. – *Eulejeunea tasmanica* (Gottsche) Steph., Species Hepaticarum 6: 653. 1924. – **Type**: AUSTRALIA Tasmania ‘Terra Van Diemen’, leg. Stuart. Lectotype (Grolle 1982): G-19624!

=* Eulejeunea tumida* f. parvilobula Rodway, Tasmanian Bryophytes 2: 89. 1916. – **Type**: AUSTRALIA, Tasmania, Mt Field, Rodway (not located).

**Description.** Forming near pure mats on sedimentary boulders in and around watercourses. Shoots yellow-green to mid-green when fresh, brown in herbaria, medium-sized for genus, shoots to 40 mm long and 0.8–1.3 mm wide, branching frequent, shoot system monomorphic or sub- 

dimorphic, with leading shoots larger in stature than branches. Stems with external and internal cortical cell walls unthickened, medullar cell walls unthickened, with seven or eight cortical cells and 14–21 smaller medullar cells in transverse section, dorsal leaf-free strip absent. Lobes rotund-ovate, 310–855 μm long and 275–645 μm wide, contiguous to imbricate, overlapping and obscuring the stem in dorsal view, erecto-patent when moist, same when dry, margins weakly crenulate due to bulging cells; lobe apex broadly rounded to weakly obtuse, all
Fig. 1. *Lejeunea drummondii* Taylor. A – ventral view of robust shoot, B – stem transverse section, the ‘ninth cortical cell’ belongs to a leaf, C – stem dorsal view, D – underleaf base, E – ventral view of weak shoot, F – perianth transverse section, G – fertile lateral branch, with gynoecium subtended by sterile subfloral innovation. Scale bar: A, E–G = 500 μm; B = 100 μm; C & D = 200 μm. All from NSW889060.
margins curved from keel to apex though slightly at first. Lobules mostly weakly developed, of 20 or more cells, lobules 128–162 μm long and 88–112 μm wide, with a prominent first lobule tooth with the lobule papilla attached at its proximal base; explanate lobules occasionally produced, of 8–10 cells and smaller than the reduced lobules, with the papilla affixed to the apex of the first lobule tooth; weakly developed lobules intergrade with normal lobules along shoots; normal lobules 192–240 μm long and 98–125 μm wide, one twentieth the lobe area, with lobule arch straight, 3 cells long; lobe-lobule junction lying postical to the base of the first lobule tooth, first tooth prominent, second tooth unicellular, keel arched with a broadly inflated carinal region. Underleaves contiguous to imbricate, elliptic-ovate, broadest at midpoint, 272–640 μm long and 304–658 μm wide, bifid to 0.5, sinus narrow or broad, V-shaped, 144–245 μm deep, lobes acute, margins weakly crenulated due to bulging cells; underleaf insertion arched across two or three ventral cortical cells, lateral basal cells of underleaf inflated. Lobe, lobule and underleaf cell surfaces smooth. Lobe cell walls with small triangular trigones and weak medial thickenings. Oil-bodies small, homogeneous, spherical to fusiform, more than thirty per cell arranged in a submarginal ring. Asexual reproduction absent. Autoicous, or mixed autoicous and paroicous. Antheridia either on short, determinate, achenic lateral branches or on subfloral innovations adjacent to gynoecia, bearing 2–5 pairs of bracts, underleaves at branch base only or at branch base and at basal bract pair, bracts isobilobous, epistatic, decreasing in stature along branch, housing 1–2 antheridia each. Gynoecia typically produced on lateral branches, occasionally mid-shoot, subtended by single Lejeuneoid subfloral innovation that either continues vegetative growth or produces androecium and terminates, rarely subtended by two subfloral innovations; female bracts subsymmetrical, one lobe slightly smaller, lobes 400–435 μm long, 290–315 μm wide, obovate, lobule rectangular, 210–260 μm long, margins reflexed, free portion 8–10 cell tiers high and 4 or 5 rows wide, bract underleaf fused with lobules on both sides, bract underleaves elliptic ovate, squat, 285–320 μm wide, 365–440 μm long, sinus 120–150 μm deep, narrow, lobes broad, apices acute. Perianths 350–420 μm diameter and up to 760 long, pentacarinate, carinae prominent; rostrum short; perianth stipe not developed on perianths containing immature sporophytes, perianths with emergent sporophytes not seen.

**Distribution and ecology.** As currently circumscribed, *L. drummondii* is the most widespread *Lejeunea* species in Australia, being recorded from Western Australia, Tasmania, Victoria, New South Wales and Queensland. On the basis of herbarium material, it is the most abundant *Lejeunea* in Tasmania, from where several dozen vouchers attributed to this species have been gathered. *Lejeunea drummondii* occupies a range of habitat types, from tall forest, including cool- and warm-temperate rainforest and subtropical and tropical rainforest, to woodlands, low-forest and heath. In all habitat types it is typically a trunk or branch epiphyte although it may grow as an epiphyll on ferns or as a lithophyte, as at Tulbrinup in Western Australia.

**Representative Specimen Examined:** AUSTRALIA. Western Australia: Toolbrinup, on the climbing track from SE, 10 Oct. 2004, M.A.M. Renner 2286 & E. O’Brien (NSW889060).

**Recognition.** *Lejeunea drummondii* is currently circumscribed to include medium to large, mid-green plants with large ovate to rotund underleaves, and penta-carinate perianths. *Lejeunea drummondii* has smooth leaf-lobe cell surfaces, unlike *L. cuspidistipula* (Steph.) Steph. ex Watts, *L. flavica* (Sw.) Nees, and *L. gracilipes* (Taylor) Spruce, (with which it is sometimes confused) which have cells bearing punctate or finely granular ornamentation.

*Lejeunea drummondii* and *L. subelobata* have been regarded as morphologically different forms of a single species. The most obvious differences between *L. drummondii* and *L. subelobata* are in underleaf and lobule morphology. The underleaves of *L. drummondii* are elliptic-ovate, and contiguous on small-stature shoots through to imbricate on robust shoots. The spacing and width of the underleaves means the lobules of *L. drummondii* are
almost always obscured in ventral view (Fig. 1). In *L. subelobata* the underleaves are more or less ro-
tund, and are usually remote (Fig. 2). The spacing 
and width of the underleaves means the lobules of
*L. subelobata* are visible in ventral view. In terms
of variation in lobule morphology, both *L. drum-
mondii* and *L. subelobata* produce explanate lob-
ules however, populations of *L. subelobata* rarely if
ever produce normal lobules, while *L. drummondii*
transitions between explanate and normal lobules
as a regular function of shoot stature, such that
a spectrum of lobules from explanate to normal
can be found on single shoots and robust shoots
always bear some normal lobules (Figs 1–3). Per-
haps most significantly, *Lejeunea drummondii* dif-
fers from *L. subelobata* in the shape of its female
bracteole and gynoecial bracts. In *L. drummondii*
the female bracteole is broadly elliptic and over-
laps the female bracts and bract underleaf, the bract
underleaf is also broadly elliptic. In *L. subelobata*
the female bracteole is transversely broadly ovate,
and hardly overlaps the female bracts and bract
underleaf, which is rectangular-ovate. The stem
anatomy of *L. drummondii* and *L. subelobata* also
exhibits significant differences. In *L. drummondii*
there are seven or rarely eight cortical cell rows,
and 14–21 medulla cell rows, whose walls are
unthickened. In *L. subelobata* there are seven to
ten cortical cell rows, and 19–26 medulla cell rows
whose walls bear small concave trigones at their
junctions.

REMARKS. *Lejeunea drummondii* seems to be
the only southern-temperate Australasian *Lejeunea*
species to exhibit paroicy, with some of the andr-
ocia produced on the single determinate subfloral
innovation subtending the gynoecium (Fig. 2). The
regular production of gynoecia on short lateral
branches is also distinctive, but not unique. Al-
though *L. drummondii* can also produce andro-
cia and gynoecia on separate branches, all other
regional species familiar to me are exclusively
autoicous, with gynoecia and androecia always on
separate branches, the androecia being scattered
throughout the shoot system. Robust shoots in the
Type of
the other specimen examined was autoicous only,
and androecia were not produced as densely as in
the type specimen. Otherwise, the morphology of
both specimens was similar and the differences
from *L. subelobata* consistent.

The relationship between *L. drummondii* in
Australia, and plants from New Zealand described
as *L. epiphylla* Colenso nom. illeg. non Mitt. 1884
(Colenso 1889) requires further investigation, as
does the relationship between the type and other
mainland Australian plants, and the myriad of Tas-
manian forms attributed to this species.

*Lejeunea subelobata* Carrington & Pearson

Proceedings of the Linnean Society of New South Wales
series 2, 2: 1039. 1888.

≡ *Lejeunea elobata* Pearson in Watts, Proceedings of
the Linnean Society of New South Wales 27: 493. 1903
‘1902’ orthographic variant of *L. subelobata*.

≡ Eulejeunea subelobata (Carrington & Pearson) Steph.,
Hedwigia 28: 170. 1889. – Type: New South Wales: near
Sydney, Balls Head Bay, June 1888, leg. Whitelegge
no. 47. LECTOTYPE (designated by Grolle 1982): BM
(2 packets);! ISOLECTOTYPES: ex herb hort. Kew BM
(1 packet)!, G-19832!, JE, MANCH; PARALECTOTYPE:
AUSTRALIA. Georges River, Botany Bay, on wet
rocks, Jan 1885, T. Whitelegge, No. 42, BM!

DESCRIPTION. Forming pure or near pure radiating
mats on igneous (andesitic, rhyolitic, and doleritic)
boulders in stream beds, occasionally submerged
but typically growing at and immediately above
the normal winter base-flow level; also mixed with
other bryophytes on rotting logs and soil banks
adjacent to or within the water course. Shoots
mid-green to black-green when fresh, brown in
herbaria, medium sized for genus, shoots to 40 mm
long and 0.8–1.2 mm wide, branching infrequent,
shoot system monomorphic. Stems with external
and internal cortical cell walls evenly thickened,
medullar cell walls unthickened except for weak
concave trigones of primary wall around cell wall
junctions, usually seven but up to nine cortical cell
rows and 19–26 smaller medullar cell rows; dorsal
leaf-free strip absent. Lobes rotund-ovate, 317–
719 μm long and 275–670 μm wide, contiguous

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Fig. 2. *Lejeunea subelobata* Carrington & Pearson. A – cladogram, B – lobules, C – underleaves, D – androecia. *Lejeunea drummondii* Taylor. E – cladogram, F – underleaves, G – lobules. Scale bar: A & E = 10 mm; B & G = 100 µm; C, D & F = 500 µm. A–D from NSW872054; E–G from NSW889060.
Fig. 3. *Lejeunea subelobata* Carrington & Pearson. A – ventral view of typical shoot, B – stem transverse sections, C – stem dorsal view, D – perianth transverse section, E – underleaf, F – perianth transverse section, G – fertile lateral branch, H – female bract gyre, *in situ*, I – female bract gyre, flattened. Scale bar: A & F–I = 500 µm; B = 100 µm; C–E = 200 µm. All from NSW872054.
to imbricate, overlapping and obscuring the stem in dorsal view, weakly erecto-patent when moist, same when dry; lobe apex broadly rounded, all margins curved, from keel to apex though slightly at first, margins minutely crenulated due to bulging cells. Lobules mostly or exclusively explanate, 10–24 cells, 43–99 μm long and 56–91 μm wide, with a prominent first lobule tooth to which the lobule papilla is attached at its apex; plants growing on logs produce normal lobules more frequently than those on rock; normal lobules one twentieth the lobe area, with lobule arch straight, 3 cells long; lobe-lobule junction lying postical to the base of the first lobule tooth, first tooth prominent, second tooth unicellular, keel shallowly arched with a broadly but weakly inflated carinal region; normal and explanate lobules may co-occur and inter-grade along a single shoot. Underleaves rotund, broadest at midpoint, 160–357 μm long and 148–356 μm wide, bifid to 0.4, sinus narrow or V-shaped, 54–147 μm deep, lobes obtuse to acute; underleaf insertion transverse across two or three ventral cortical cells, lateral basal cells of underleaf inflated. Lobe, lobule and underleaf cell surfaces smooth. Lobe cell walls with small triangular trigones and weak medial thickenings. Oil-bodies small, homogeneous, spherical to fusiform, more than thirty per cell arranged in a submarginal ring. Asexual reproduction absent. Autoicous. Antheridia on short, determinate, achlorophyllous lateral branches bearing 1–3 pairs of bracts, underleaves either absent or at branch base only, or at branch base and at basal bract pair only; bracts isolobous, epistatic, decreasing in stature along branch, housing 1–2 antheridia each. Gynoecia typically produced mid-shoot, occasionally shortly after branching points, subtended by single Lejeuneoid subfloral innovation that continues vegetative growth; female bracteole squat, broadly transversely ovate, female bracts subsymmetrical, one lobe slightly smaller, lobes 560–595 μm long, 270–340 μm wide, obovate, lobule reduced to spur at lobe base, bract underleaf elliptic-oblong, 235–280 μm wide, 400–445 μm long, sinus to 150 μm deep, wide, lobes obtuse, fused with lobules on both sides. Perianths 350–420 μm diameter and up to 460–490 μm long, up to 900 μm with stipe, pentacarinate, carinae prominent; rostrum short; perianth stipe of enlarged colourless cells at perianth base present in mature perianths with emergent sporophytes.

**DISTRIBUTION AND ECOLOGY.** *Lejeunea subelobata* is currently known from Australia, and New Zealand. In Australia, *L. subelobata* occurs east of the Great Dividing Range in Victoria and in Tasmania, in association with cool temperate rainforest growing over igneous bedrock. In New Zealand, *L. subelobata* occurs in lowland habitats throughout the northern and eastern North Island, and on the eastern side of the South Island, particularly Banks Peninsula, again in areas associated with igneous rocks. Throughout its range, *L. subelobata* grows on volcanic boulders and bedrock within and alongside watercourses. The basicolous habit of *L. subelobata* is well illustrated in the middle reaches of catchments draining the north-eastern flanks of the Waitakere Ranges, Auckland New Zealand. In the middle reaches the bedrock changes from the volcanically derived Manukau breccia to the sedimentary Waitemata sandstone and mudstone (Brothers 1953). Where boulders derived from both bedrocks are present within streams, *L. subelobata* grows only on the andesite boulders derived from within the Manukau breccia, and as these are progressively replaced by Waitemata sandstone and mudstone so the abundance of *L. subelobata* declines. In sections of stream with boulders derived exclusively from the Waitemata formation, *L. subelobata* is absent. *Lejeunea subelobata* may also grow as an epiphyll on fern leaves (such as *Hymenophyllum demissum* (G. Forst.) Sw. overhanging waterways, particularly where these are in contact with established patches, or on decaying wood within and adjacent waterways, and occasionally as an epiphyte on trees growing alongside waterways. *Lejeunea subelobata* is associated with a range of lithophytic and rheophytic species, including the bryophytes *Fallaciella gracilis* (Hook.f. & Wils.) Crum, *F. robusta* Fife, *Lopholejeunea* sp., *Radula strangulata* Hook.f. & Taylor, *Metzgeria* spp. *Camptochaete arbuscula* (Sm.) Reichdt., *Cratoneuropsis relaxa* (Hook.f. & Wils.) Broth., *Pyrrhobryum para-
Lejeunea subelobata Carrington & Pearson in habitat on basalt boulder in the bed of the Waipoua River, Western Northland Ecological district, North Island, New Zealand. Not vouchered.
Lejeunea subelobata is one of the few southern temperate Australasian species of Lejeunea that produce explanate lobules almost exclusively. Individuals rarely if ever produce normal fully developed lobules. Only two other regional entities share this characteristic. Some morphs of L. drummondii have a similar tendency toward exclusive production of explanate lobules, particularly cor ticolous plants from Tasmania, as represented in the type of L. tasmanica. Lejeunea subelobata was wrongly called L. tasmanica in the phylogeny of Renner et al. (2011) due to a misinterpretation of L. tasmanica’s type. The recognition of L. drummondii, of which L. tasmanica is a synonym, is discussed above. Another species that produces primarily explanate lobules is a poorly known, smaller, lithophytic plant that grows on limestone within lowland forest settings in the central and western North Island of New Zealand. The identity and relationships of these calcicolous plants requires further investigation.

**DISCUSSION**

The reinstatement of Lejeunea subelobata brings to 24 the number of Lejeunea species accepted for Australia (based on McCarthy 2003), and to 16 the number of Lejeunea species reported for New Zealand (Glenny 1998; Renner et al. 2010; Renner & de Lange 2011).

The wide phylogenetic disparity between phenetically similar plants previously attributed to L. drummondii parallels the situation resolved recently within the L. tumida Mitt. aggregate (Renner et al. 2011). With L. subelobata included, L. drummondii exhibits polyphyly as extreme as that identified within L. tumida. Both L. drummondii and L. tumida emphasize the significance and relevance of subtle homologous morphological character differences to species circumscription. Unfortunately, homologies have sometimes been overlooked or interpreted as infra-specific variation in investigations of the Lejeuneaceae. Justification for differentiating infra- from inter-specific variation within this family is given by Reiner-Drehwald (2010). Cryptic morphological diversity within the Lejeuneaceae has been resolved by molecular data in other genera (Heinrichs et al. 2009), and Lejeunea drummondii and L. subelobata might be considered another example of morphologically cryptic species diversity, given the previous synonymy and phenetic similarity between taxa. However, as Johnson & Cairns-Heath (2010) pointed out, cryptic species complexes evaporate upon discovery of diagnostic characters for distinguishing each species. In the case of L. drummondii and L. subelobata, diagnostic characters exist in the shape of the female bracteole and stem anatomy. Indeed, an assessment of the significance of subtle, yet consistent, differences may best be made in concert with molecular data. For L. subelobata, molecular data, albeit a single accession, help substantiate subtle morphological and ecological differences from L. drummondii. Studies of Lejeuneaceae revisiting homology statements in lieu of molecular phylogenies have found

| Character                      | Lejeunea drummondii                              | Lejeunea subelobata                               |
|--------------------------------|--------------------------------------------------|--------------------------------------------------|
| Sexuality                      | Paroicous and autoicous                          | Exclusively autoicous                             |
| Androecia                      | 2–5 bract pairs                                  | 1–3 bract pairs                                  |
| Gynoecia production           | Lateral branches, regular.                       | Leading axes or branches, scattered.             |
| Female bract underleaf         | Elliptic                                         | Elliptic-oblang                                  |
| Female bracteole               | Elliptic                                         | Broadly transversely ovate                       |
| Lobe imbrication               | Imbricate                                        | Contiguous to imbricate                          |
| Normal lobules                 | Usually frequent                                 | Very rare                                        |
| Stem cell walls                | Unthickened                                      | Concave trigones                                 |
| Number of medulla cell rows    | 14–21                                            | 19–26                                            |
| Underleaves                    | Ovate, imbricate on robust shoots.               | Rotund, remote at most contiguous on robust shoots. |
diversity in homologous morphological character states mirroring underlying phylogenetic diversity, suggesting morphology can provide a sound basis for both proposing and testing hypotheses of relationship (Renner et al. 2010).

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