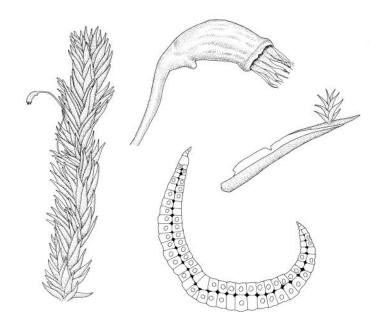


## **LEUCOBRYACEAE**



A.J. FIFE

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Cover image: *Leucobryum javense*, habit with capsule, dry capsule, dwarf  $\circlearrowleft$  plant on leaf, and cross section at mid leaf. Drawn by Rebecca Wagstaff from *J.E. Beever 31-28*, CHR 406176, *G. Brownlie 681*, CHR 427667, and *J.E. Beever 31-99*, CHR 406114.



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### Introduction

The Leucobryaceae are considered here to include only the type genus *Leucobryum*. Species of *Leucobryum* are erect mosses growing mostly on the forest floor, with erect or secund leaves and single, red, forked, and vertically striolate peristome teeth. Their peristome morphology is similar to that of many members of the Dicranaceae. The most distinctive feature of *Leucobryum* is a highly unusual leaf structure, that consists of a single layer of chlorophyllose cells (chlorocysts) enclosed on both surfaces by one or more layers of large, dead cells (hyalocysts). The leaves are interpreted as consisting nearly entirely of the costa, and the superficial dead cells are connected by conspicuous intercellular pores. Although *Leucobryum* is a large genus distributed widely in tropical and temperate regions, only one species, *L. javense*, occurs in New Zealand. It forms conspicuous, whitish (as the generic name implies) cushions in many types of N.Z. forests, particularly drier southern beech forest. New Zealand *L. javense* is considered to be conspecific with material that is widespread in Malesia and parts of southern Asia.

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### Leucobryaceae

**Taxonomy:** There is little consensus on the limits of the Leucobryaceae, and the boundaries separating this family from the Dicranaceae and the Calymperaceae are particularly fluid. Regionally, neither Sainsbury (1955) nor Scott & Stone (1976) recognised the Leucobryaceae, and both included *Leucobryum* within their broad interpretation of the Dicranaceae. Brotherus (1924) considered it to include eight predominantly tropical genera and placed it in the order Dicranales; he divided the eight genera among four subfamilies, and this reflects the problems in its definition. Apart from *Leucobryum*, all the genera placed by him in the family have erect, often cylindric (but sometimes cupulate) capsules, and only *Leucobryum* has striate peristome tooth markings.

The Leucobryaceae has received extremely diverse circumscriptions since Brotherus's influential treatment. Enroth (1990) described the Brotherean family concept as representing "an unnatural and artificial assemblage ... which share some superficial similarities." Enroth presented a very different view of the family, which included several additional tropical genera. Confusingly, he noted that the family name is used "in a purely descriptive sense, implying no taxonomic significance". In the same year Eddy (1990) treated the family as monogeneric, and separated some of the genera included in the family by Enroth into their own family, the Schistomitriaceae.

Goffinet et al. (2009) and Goffinet & Buck (2020, viewed 22 Sept 2020), accepted 12 genera in the family, including the very large *Campylopus*, and retained it in the Dicranales. The assemblage of genera they placed in the family differs greatly, and with little explanation, from that presented by either Brotherus or Enroth. The largest genus included by them, *Campylopus*, lacks both the well-defined inter-cellular pores and the single layer of chlorocysts sandwiched within multiple layers of hyalocysts that are such a prominent feature of *Leucobryum*. *Campylopus* does not sit comfortably in the Leucobryaceae, and it is treated here as a member of the Dicranaceae.

A sustainable definition of the Leucobryaceae has been sought by bryologists for many decades and is outside the ambit of this Flora. The Leucobryaceae is treated here as distinct from the Dicranaceae, but to exclude the other genera placed in it by both Enroth (1990) and Goffinet & Buck (2020). The Leucobryaceae are considered here to be monotypic. Accordingly, the generic description that follows applies to the family.

### Leucobryum Hampe, Linnaea 13: 42 (1839)

**Type taxon:** Leucobryum vulgare Hampe = Leucobryum glaucum (Hedw.) Ångstr.

**Plants** medium-sized to robust, pale- or white-green, forming dense cushions or tufts. **Stems** erect, mostly forked, in cross-section lacking (usually) or with a central strand, rhizoids usually sparse. **Leaves** erect, spreading, or secund, narrowly to broadly lanceolate from a ± oblong or elliptic base, rarely auriculate, ± subtubulose above, mostly acute, entire or denticulate near apex, often scabrous abaxially near apex by protruding cell ends. **Lamina** restricted to leaf base, consisting of 1–c. 20 rows of dead cells (hyalocysts) on either side of the costa. **Alar cells** not differentiated (but leaves sometimes auriculate at base). **Costa** broad and occupying nearly all of the leaf, at mid leaf and above consisting of a single layer of subquadrate chlorophyllose cells (chlorocysts) enclosed both abaxially and adaxially by one or more layers of large dead cells (hyalocysts) that are connected by conspicuous pores, in the alar region often with multiple layers of hyalocysts. **Deciduous leaves** often present at stem tips.

**Pseudautoicous**. **Perichaetia** lateral or terminal. **Dwarf male plants** in the tomentum or on leaves of female plants. **Setae** single, elongate; **capsules** inclined, asymmetric, sulcate when dry, often strumose; **stomata** none; **annulus** mostly lacking; **operculum** long-rostrate. **Peristome teeth** 16, lanceolate, bifid ± halfway, vertically striolate below, papillose above. **Calyptra** cucullate. **Spores** spherical.

**Taxonomy:** Leucobryum is a large and taxonomically difficult genus widely distributed in tropical and temperate regions. Recent regional treatments (e.g., Enroth 1990 for part of Papua New Guinea; Eddy 1990 for Malesia; Yamaguchi 1993 for Asia; Peterson 1994 for Mexico; and Klazenga 2012 for Australia) have reduced substantial numbers of described names to synonymy. The past description of large numbers of regional variants as species and lack of consensus concerning taxonomic limits make an estimate of the size of the genus impractical.

The layers of large, non-chlorophyllose cells interconnected by pores in this genus are in many ways suggestive of the structure of *Sphagnum* leaves. The pores of *Leucobryum* are not "ringed" as they are in many species of *Sphagnum*, nor do they open to the surface of the cell. The pores of *Leucobryum* are easily seen in both surface view and in costal cross-section with a compound

microscope. In *Leucobryum* the photosynthetic cells (chlorocysts) are restricted, in the upper leaf, to a single layer that is covered both abaxially and adaxially by one or more layers of dead cells (hyalocysts). In *Sphagnum*, by contrast, the leaf is only a single layer thick and the living and dead cells form a net-like reticulation. The pores in *Leucobryum* probably facilitate water absorption and storage.

**Etymology:** According to Meagher (2011), the generic name derives from "*leukos* (white) and *bryon* (moss), clearly alluding to the typically almost white colour (usually very pale green to bluish green), although Hampe did not say so in the protologue".

**Excluded Taxa:** Leucobryum speirostichum Müll.Hal. nom. nud. [Genera Musc. Frond. 80, 1900] was cited as a synonym of *L. candidum* var. pentastichum (Dozy & Molk.) Dixon by Dixon (1923, p. 97). The basionym of the latter is based on a Javanese collection by *Junghuhn* and in turn was considered a heterotypic synonym of *L. javense* by Enroth (1990). Six specimens in the Beckett herbarium, determined by Müller and by Brotherus, do not differ significantly from other Australasian *L. javense*, and this name is therefore not considered further here.

*Leucobryum interruptum* Müll.Hal. [Genera Musc. Frond. 81, 1900] is a *nom. nud.* It was placed in the synonymy of *L. candidum* by Dixon (1923, p. 97). Fragmentary "type" material is present in the Beckett herbarium at CHR (622475!).

*Leucobryum spinidorsum* Müll.Hal. [Hedwigia 36: 331, 1897] is based on Tasmanian and N.Z. syntypes, the latter collected by *C. Fristedt* at "Whangarou" [probably Whangaroa]. Dixon (1923, p. 97) put this name in the synonymy of *L. candidum*. I have not seen type material.

# Leucobryum javense (Brid.) Mitt., J. Proc. Linn. Soc., Bot. Suppl. 1–2: 25 (1859)

- ≡ Sphagnum javense Brid., Bot. Zeitung (Regensburg) 1: 200 (1802)

  Type: Java, Commerson. Not seen. (Type material in B cited by Enroth 1990, p. 72.)
- = Dicranum candidum Brid. ex P.Beauv., Prodr. Fam. Aethéog. 53 (1805)
- Leucobryum candidum (Brid. ex P.Beauv.) Hook.f. & Wilson in Wilson, Bot. Antarct. Voy. II (Fl. Nov.-Zel.) Part II, 64 (1854)

Type: Australia, Timor, or New Guinea, *Dampier*. Not seen. (Type material cited by Downing & Marner 1998)

- = Leucobryum pentastichum Dozy & Molk., Pl. Jungh. [Miquel], 319 (1854)
- = Leucobryum candidum var. pentastichum (Dozy & Molk.) Dixon, Bull. New Zealand Inst. 3: 97 (1923)
  Type: Java, Junghuhn. Not seen. (Isotype cited by Enroth 1990, p. 76.)
- = Leucobryum laticaule Müll.Hal., Hedwigia 36: 331 (1897)
- Leucobryum candidum var. majus A.Jaeger ex Dixon, Bull. New Zealand Inst. 3: 97 (1923) nom. nov. pro Leucobryum laticaule Müll.Hal. 1897
   Syntype: N.Z., prope Greymouth, 1885, R. Helms 47, CHR 622474!

Misapplications: Leucobryum brachyphyllum sensu Beckett (1896)

Plants extremely variable in stature and habit, white-green, pale brown-green to nearly white above and often pale brown-green below when fresh, very pale and iridescent when dry, forming small to very large dense cushions or occurring as individual stems among other bryophytes, mostly terrestrial. Stems from c.10-80 mm, often branched by forking, brown, ± brittle, in cross-section lacking a central strand, with 2-3 layers of thick-walled cortical cells; rhizoids very sparse. Leaves crowded, oblongovate and ± abruptly tapered to an acute apex to narrowly oblong-lanceolate, secund or erectspreading, often in 5 strongly or weakly defined spiral ranks, strongly concave below, subtubulose above, entire, often appearing transversely corrugate, scabrous (cristate) abaxially at apex (sometimes to ½ of leaf) due to projecting hyalocysts, (2.8–)4.5–7.0(–11) × 1.0–1.4(–1.8) mm (under cover slip), often with smooth rhizoids arising at apices; lamina narrow and inconspicuous, in the leaf base mostly 5 or fewer cells wide. Costa nearly filling the leaf, at mid leaf consisting of a single layer of subquadrate chlorocysts surrounded by layers of hyalocysts; cross-section at widest part of the leaf base and in the upper median region with hyalocysts in one abaxial and one adaxial layer and with the abaxial hyalocysts smaller; cross-section in the alar region with hyalocysts mostly in 2-4 abaxial layers and 2-3(-4) adaxial layers, but with only one abaxial and one adaxial hyalocyst layer in the middle of the cross-section (the "isthmus" or "median furrow"), with one conspicuous round to elliptic pore (mostly 10-14 µm in greater diam.) per hyalocyst; in surface view the chlorocysts at the widest part of the leaf base rectangular and 1–2:1; alar cells neither differentiated nor auriculate.

Pseudautoicous. Perichaetia lateral or on short lateral branches, aggregated in clusters, enclosing a single archegonium, the outer leaves very small, the inner leaves c. ½ the length of vegetative leaves and strongly sheathing. Dwarf males c. 2–3 mm tall, epiphytic on leaves of female plants or embedded in tomentum, with erect-spreading bracts, often enclosing only 1–2 antheridia. Setae single, variable in length, 8–22 mm, straight or slightly flexuose, weakly twisted to the left, red-brown; capsules inclined to cernuous, asymmetric, obovoid-cylindric, sulcate, strongly strumose, with a short but distinct neck, c. 1.5 mm; exothecial cells elongate and firm-walled; stomata none; annulus present, of a single row of thin-walled and persistent cells; operculum obliquely rostrate, ± equal to the capsule. Peristome teeth red, lanceolate, inserted at mouth, unequally bifid c. halfway to base, with a distinct divisural line on the outer surface, lamellate on inner surface, strongly vertically striolate below, spinose-baculate above. Calyptra c. 3 mm. Spores c. 12–15 μm, nearly smooth.

Illustrations: Plate 1. Sainsbury 1955, pl. 16 (as *L. candidum*); Scott & Stone 1976, pl. 26 (as *L. candidum*); Enroth 1990, figs. 4–7; Beever et al. 1992, fig. 22 (as *L. candidum*); Malcolm & Malcolm 2003, p. 41 (as *L. candidum*); Meagher & Fuhrer 2003, p. 27 (as *L.candidum*).

**Distribution:** K; NI: N Auckland including offshore islands (HC, LB, GB, RT), S Auckland, Gisborne, Hawke's Bay, Taranaki, Wellington (including KA); SI: Nelson, Marlborough, Canterbury, Westland, Otago, Southland; St; Ch.

Palaeotropical? Tasmania\*, mainland Australia\*. Also widespread in Asia, Malesia, and western Polynesia (*fide* Enroth 1990, p. 78).

**Habitat:** Terrestrial, forming large, dense cushions (to at least 0.5 m diameter). Usually best developed on tree bases and over exposed roots. Occurring in a wide range of forest types, but best developed in drier southern beech forest. Also occurring on humic banks, rotten logs and stumps, and sometimes on rock faces. Sometimes epiphytic (especially on *Cyathea* spp., but also on species of southern beech, *Dacrydium cupressinum*, *Podocarpus* sp., *Dicksonia squarrosa*, and *Populus* sp.). *Leucobryum javense* has a very broad ecological amplitude and it can occur in exotic plantations. Although typically forming hemispherical cushions, it can occur as individual strands among other bryophytes. On the North I. ranging from near sea level to c.1200 m (Mt Hauhungatahi, Wellington L.D.) and on the South I. from near sea level to at least 1120 m (Paparoa Range, Nelson L.D.).

**Notes:** Frequently associated species include *Campylopus introflexus*, *Dicranoloma* spp., *Eurhynchium asperipes*, *Pyrrhobryum bifarium*, *Rhaphidorrhynchium amoenum*, and *Wijkia extenuata*, and the hepatics *Bazzania adnexa*, *B. involuta*, *Heteroscyphus coalitus*, and *Schistochila* spp. (especially *S. nobilis*). Smaller species of Lepidoziaceae often trail among the lower leaves of *Leucobryum*. When it occurs over rock it is often associated with *Lepyrodon lagurus*. Compact and very dense cushions frequently have strongly 'corrugate' leaves and are associated with drier habitats. Plants laxer and more elongate in growth are usually associated with more mesic or moist microhabitats, and extreme forms are sometimes pendent from ledges or exposed tree roots.

The genus *Leucobryum* in N.Z. has long been a source of great taxonomic and nomenclatural confusion. Since Wilson's (1854) moss treatment in *Flora Novae-Zelandiae*, the name most commonly applied to N.Z. material has been *L. candidum* (Brid. *ex* P.Beauv.) Hook.f. & Wilson. The basionym of this name, *Dicranum candidum* Brid. *ex* P.Beauv., was first validly published by Palisot de Beauvois in 1805 [Prodrome des cinquième et sixième familles de l'Aethéogamie, p. 53]. Downing & Marner (1998) discussed the type of *Dicranum candidum* at length and concluded that it was most likely collected by W. Dampier in 1699 in either Timor or New Guinea, rather than in Australia as stated by both Palisot de Beauvois and Enroth (1990).

In N.Z. the name *L. candidum* var. *majus* A.Jaeger has been often applied to larger and laxer plants, and *L. candidum* var. *pentastichum* (Dozy & Molk.) Dixon (or its basionym) has been applied to plants with leaves inserted in five more-or-less distinct ranks. The name *L. aduncum*, a species described from Java, has sometimes been applied to particularly compact and corrugate-leaved N.Z. plants, particularly those in which the three-layered "isthmus" at the leaf base is broader than usual.

The most helpful discussion of variation in N.Z. *Leucobryum* was provided by Dixon (1923), with Sainsbury (1955) essentially adopting Dixon's taxonomy and nomenclature.

After studying a range of N.Z. material Dixon (1923, p. 95) stated that he had "very little hesitation ... in reducing them [the *Leucobryum* taxa recognised from N.Z. by previous authors] all to the single type, *L. candidum* (Brid.) Hampe, with perhaps two fairly well-marked varieties. In all the fertile plants I have seen the fruit present no variation whatever, the length of the seta alone showing some variability, and this not correlated with any other characters, not even with the general degree of robustness of the plants. The vegetative characters are far more variable, but the internal leaf-structure is remarkably uniform throughout ..." Although Dixon (1923, p. 95–98) is correct that some N.Z. forms are striking when viewed in isolation, I believe that such extreme forms are primarily

environmental in nature, and that their formal taxonomic naming (at either the varietal or species level) is unwarranted.

Dixon (1923, p. 96) also presented a discussion of the leaf structure in N.Z. material. He stated that "while the leaf section in the middle and upper parts of the leaf shows a single ventral and a single dorsal layer of hyaline cells (hyalocysts), with the chlorocysts median, the basal section shows several layers (2–3) of hyalocysts on both the ventral and dorsal sides of the chlorocysts, corresponding to a considerable thickening of the leaf. This thickening, however, does not extend across the whole width of the nerve, as along the median line the hyalocysts are in two layers only, one ventral and one dorsal layer, so as to form a neck, so to speak, or isthmus, which may be of varying length". He noted that when the "isthmus" is broad, the structure approaches that of what has been termed *L. aduncum* Dozy & Molk, in Asia and Malesia.

With practice the multiple layers of hyalocysts at the leaf base can be visualised in surface view under the microscope or by quick sectioning under the stereoscope. The staining of leaves with toluidine blue or a similar dye may facilitate the observation of cellular structures, but in general staining is not necessary.

In a revision for the Huon Peninsula, Papua New Guinea, Enroth (1990) proposed that *L. candidum* (Brid. ex P.Beauv.) Hook.f. & Wilson be synonymised with the Javanese *L. javense* (Brid.) Mitt. He examined type material of *L. javense* (*leg.* Commerson) and discussed at length the difficulty in locating type material of *Dicranum candidum*. He nevertheless placed *L. candidum* in synonymy, arguing that he had examined "rather an extensive number of specimens (in H-BR, H-SOL, and H) which are assigned to *L. candidum*, and to the names given as its synonyms ... from New Zealand, Tasmania, etc. Accordingly, I feel myself thoroughly familiar with these 'species' and their inclusion in the protean and wide-ranging *L. javense* seems to me inevitable."

After the examination of a wide range of N.Z. and Australian *L. candidum* and a far lesser quantity of Malesian *L. javense*, I endorse Enroth's (1990) concept of a broadly distributed and morphologically plastic *L. javense*. He stated that "even among the many variable species in this genus, *L. javense* is truly a bryologist's nightmare. The only characters that remain constant in all specimens of *L. javense* from separate areas of its wide range are the cellular structure of the leaves and their abaxially scabrous tips. The orientation, shape, and size of the leaves and their apices exhibit exceeding plasticity." Only a single polymorphic species is accepted here for N.Z. The placement of *L. candidum* in the synonymy of *L. javense* was not accepted by Klazenga (2012).

The earliest N.Z. collection of *L. javense* seen is in the Turner herbarium at BM. Although labelled "New Zealand. *W.* [sic] *Menzies*. 1806", it was probably collected in 1791 at Dusky Sound. It is representative of the species and fruiting.

Strongly developed leaf corrugations are usually associated with plants with short stems, compact colonies, and short (c. 2 mm), ± elliptic leaves. Such plants appear to be associated with particularly dry habitats. The corrugations are due to the abaxial hyalocysts being arranged in overlapping transverse rows, and they are very conspicuous in some populations. Sainsbury (1955) described such leaves as rugose.

**Recognition:** The nearly white plants of *L. javense* are unlikely to be confused with any other moss in the N.Z. flora. When growing in unusual habitats, *Leucobryum javense* could possibly be confused with forms of *Sphagnum*, but the organisation of the photosynthetic (chlorocyst) cells in a single layer within the costa will readily distinguish the *Leucobryum*. The pores in the hyalocyst walls are intercellular rather than exposed to the surface of the leaf. Confusion could also possibly occur in the field with some of the paler species of *Dicranoloma* (such as *D. dicarpum*), but the costa that nearly fills the leaf width and the clear differentiation of hyalocysts and chlorocysts in *Leucobryum* easily distinguish it.

**Etymology:** The species epithet *javense* refers to the type locality on Java. The discussed epithet *candidum* means white.

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# **Conventions**

### **Abbreviations and Latin terms**

Abbreviations	Meaning
A	Auckland Islands
A.C.T.	Australian Capital Territory
aff.	allied to (affinis)
agg.	aggregate
Ant	Antipodes Islands
a.s.l.	above sea level
auct.	of authors (auctorum)
В	Bounty Islands
С	Campbell Island
C.	about ( <i>circa</i> )
cf.	compare with, possibly the species named (confer)
c.fr.	with fruit (cum fructibus)
Ch	Chatham Islands
comb. nov.	new combination (combinatio nova)
D'U	D'Urville Island
et al.	and others (et alia)
et seq.	and following pages (et sequentia)
ex	from
fasc.	fascicle
fide	according to
GB	Great Barrier Island
HC	Hen and Chicken Islands
Herb.	Herbarium
hom. illeg.	illegitimate homonym
I.	Island
ibid.	in the same place (ibidem)
incl.	including
in herb.	in herbarium ( <i>in herbario</i> )
in litt.	in a letter ( <i>in litteris</i> )
inter alia	among other things (inter alia)
Is	Islands
K	Kermadec Islands
KA	Kapiti Island
LB	Little Barrier Island
L.D.	Land District or Districts
leg.	collected by (legit)
loc. cit.	in the same place (loco citato)
l:w	length:width ratio
M	Macquarie Island
Mt	Mount
nec	nor
NI	North Island
no.	number
nom. cons.	conserved name (nomen conservandum)
nom. dub.	name of doubtful application (nomen dubium)
nom. illeg.	name contrary to the rules of nomenclature (nomen illegitimum)
nom. inval.	invalid name (nomen invalidum)
nom. nud.	name published without a description (nomen nudum)
non	not
N.P.	National Park
N.S.W.	New South Wales
N.T.	Northern Territory (Australia)
N.Z.	New Zealand
op. cit.	in the work cited (opere citato)
pers. comm.	personal communication
-	

PK Poor Knights Islands P.N.G. Papua New Guinea

pro parte in part
Qld Queensland

q.v. which see (*quod vide*)
RT Rangitoto Island
S.A. South Australia

s.coll. without collector (sine collectore)

s.d. without date (sine die)

sect. section

SEM scanning electron microscope/microsopy

sensu in the taxonomic sense of

SI South Island sic as written

s.l. in a broad taxonomic sense (sensu lato)

s.loc. without location (sine locus)

Sn Snares Islands

s.n. without a collection number (sine numero)

Sol Solander Island sp. species (singular) spp. species (plural)

s.s. in a narrow taxonomic sense (sensu stricto)

St Stewart Island

stat. nov. new status (status novus)

subg. subgenus subsection

subsp. subspecies (singular) subspp. subspecies (plural)

Tas. Tasmania

TK Three Kings Islands U.S.A. United States of America

var. variety vars varieties Vic. Victoria

viz. that is to say (videlicet)

vs versus

W.A. Western Australia

Symbol	Meaning
μm	micrometre
3	male
9	female
±	more or less, somewhat
×	times; dimensions connected by × refer to length times width
>	greater than
<	less than
≥	greater than or equal to
≤	less than or equal to
=	heterotypic synonym of the preceding name
≡	homotypic synonym of the preceding name
!	confirmed by the author
*	in distribution statements, indicates non-N.Z. localities from which material has
	been confirmed by the author

Technical terms conform to Malcolm, B.; Malcolm, N. 2006: *Mosses and other Bryophytes: an Illustrated Glossary*. Edition 2. Micro-Optics Press, Nelson.

Abbreviations for Herbaria follow the standard abbreviations listed in *Index Herbariorum*.

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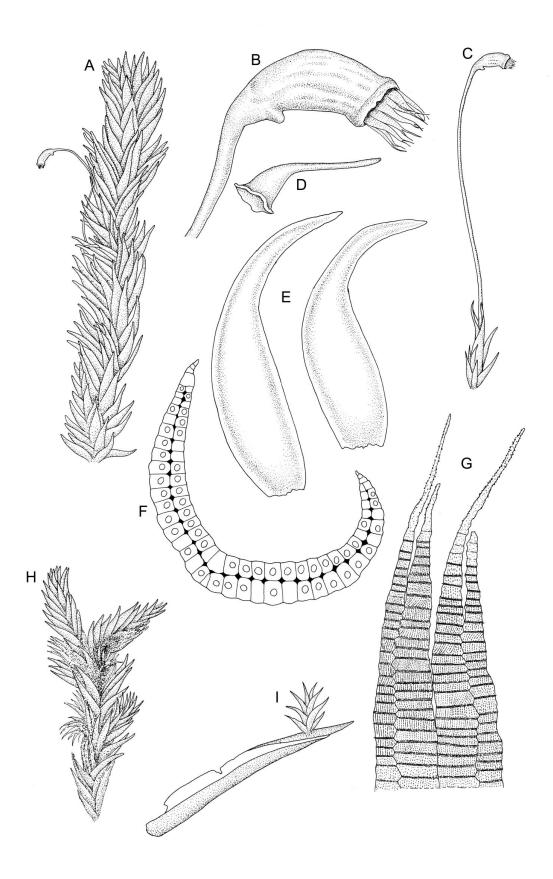
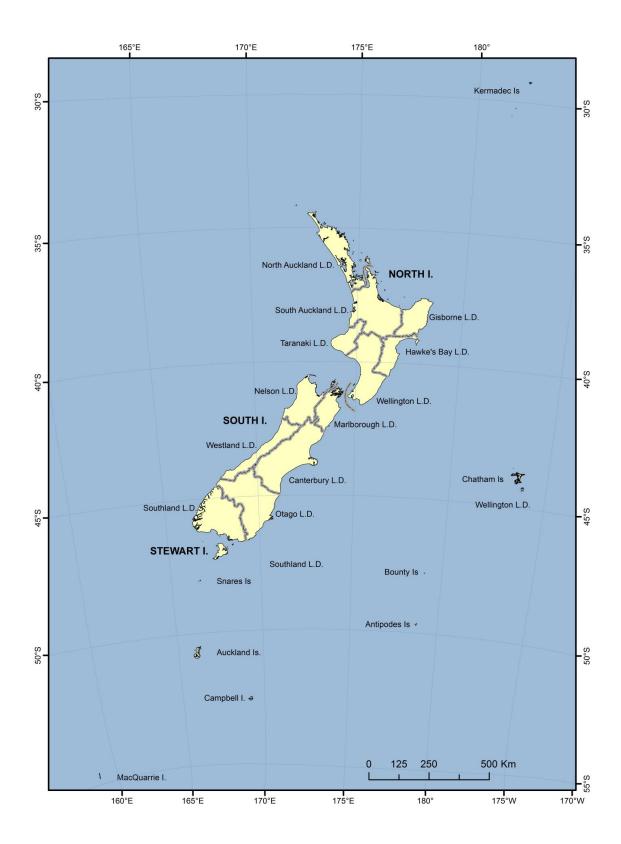
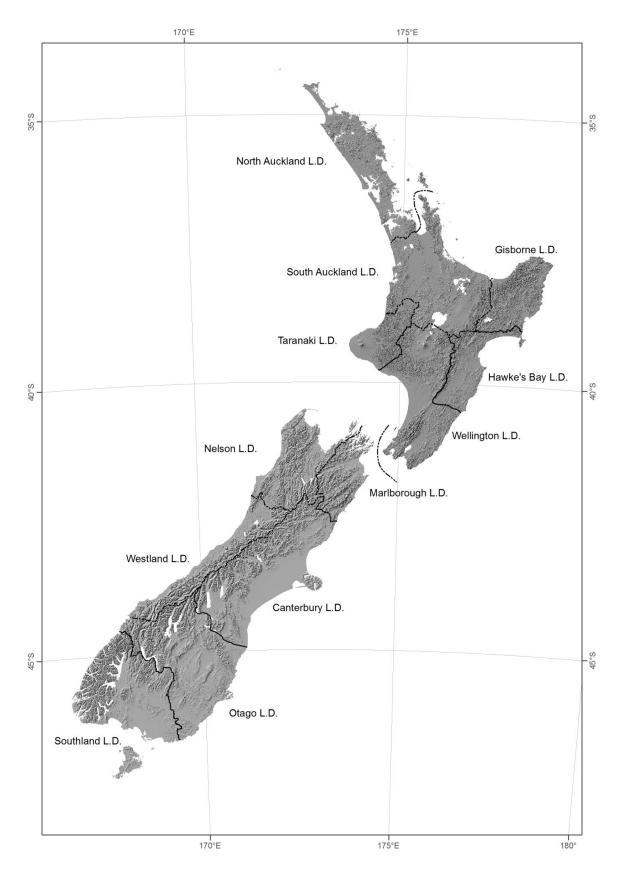


Plate 1: Leucobryum. A–I: L. javense. A, habit with capsule, dry. B, capsule, dry. C, perichaetium with capsule. D, operculum. E, leaves. F, cross section at mid leaf. G, two adjacent peristome teeth, outer surface. H, sterile shoot, moist. I, dwarf ♂ plant on leaf. Drawn from J.E. Beever 31-28, CHR 406176, G. Brownlie 681, CHR 427667, and J.E. Beever 31-99, CHR 406114.



Map 1: Map of New Zealand and offshore islands showing Land District boundaries



Map 2: Map of main islands of New Zealand showing Land District boundaries

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# **Image Information**

**Creator** R.C. Wagstaff A.D. Wilton Image Plate 1 Map 1 Map 2 A.D. Wilton

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