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Cover image: *Lepyrodon australis*, habit with capsule, moist. Drawn by Rebecca Wagstaff from *A.J. Fife 7276*, CHR 405885.

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Introduction

The Lepyrodontaceae are a monotypic family, with the sole genus *Lepyrodon* including seven or fewer species distributed in tropical and temperate South America and temperate Australasia, and with a single species extending northward into Mexico and the Caribbean. Two species of *Lepyrodon* are accepted for the New Zealand flora; both form dense and often large cushions on bark or rock. *Lepyrodon australis* is predominantly an epiphytic species distributed in drier parts of the two main islands. It has a N.Z. type and is marked by having distinctly plicate leaves and a single endostomal peristome. Outside of N.Z. it is known confidently from Tasmania, where it is documented by only a few collections. The differences between *L. australis* and the South American *L. hexastichus* (Mont.) Wijk & Marg. are not wholly convincing, but the former name is here applied to the N.Z. material. Limited material (but including the type) of the latter species has been seen, but no conclusion concerning their taxonomic relationship has been reached. If the two names prove to be synonymous after further study, *L. hexastichus* would have priority.

Our other species, *L. lagurus*, has an Argentinian type; it forms cushions both on rock and bark throughout the main islands. It is also occurs in Tasmania, wetter parts of mainland Australia, and southern South America. Although the distinction of Australasian material (as *L. pseudolagurus* B.H. Allen) has been proposed, this is rejected here.

Lepyrodontaceae

Taxonomy: The Lepyrodontaceae are considered here to be monotypic, with the sole genus, *Lepyrodon*, distributed in Australasia and tropical and temperate South America north to Mexico.

The family was treated as monotypic and placed in the order Isobryales in the general relationship of the Ptychomniaceae and the pantropical Prionodontaceae by Brotherus (1925). Goffinet et al. (2009) also considered the family to include a single genus; they placed it in the order Hypnales in the general relationship of Orthorrhynchiaceae and Neckeraceae.

A proposal to shift *Dichelodontium* into the Lepyrodontaceae by Allen (1999), based partly on peristome studies by Magill (1987), is not accepted here. Molecular studies by Bell et al. (2007) show *Dichelodontium* to be strongly nested within a clade with other members of the Ptychomniaceae, and therefore *Dichelodontium* is placed in that family here.

The family was treated for Australia by Klazenga (2012).

The generic description given below applies to the family.

Lepyrodon Hampe, *Ann. Sci. Nat., Bot. sér. 5,* 4: 367 (1865)

Type taxon: *Lepyrodon suborthostichus* (Müll.Hal.) Hampe

Plants forming cushions usually on bark or rock. **Stems** creeping and much branched, forming a densely intertwined mat and giving rise to numerous erect branches. **Microphyllous secondary** branches frequently present. **Leaves** lanceolate, oblong-lanceolate, or broadly oblong, often plicate, unbordered, serrulate above, not decurrent, usually abruptly tapered to a fine acumen or pilifer that is uniseriate apically; **mid laminal cells** vermicular, smooth, firm-walled, variably porose; **cells at insertion** shorter and wider; **alar cells** not or poorly differentiated. **Costa** single, often branched, weak and usually less than ½ the leaf length. **Axillary hairs** reportedly present.

Dioicous, sometimes with dwarfed ♂ plants. **Capsules** erect, symmetric, smooth and weakly constricted below the mouth when dry; **exothecial cells** irregular in outline, l:w mostly less than 2:1, firm-walled; **stomata** restricted to capsule base; **annulus** persistent, composed of a single row of cells. **Peristome** single or double; **exostome teeth** absent or rudimentary; **endostome** hyaline, with a low basal membrane and narrowly perforate segments, linear or irregular in outline, lacking nodules and appendiculae; **cilia** usually absent but rarely rudimentary. **Operculum** obliquely rostrate from a high conic base. **Calyptra** cucullate, smooth. **Spores** spherical, smooth or nearly so.

Taxonomy: A genus of c. seven species distributed almost exclusively in tropical and temperate South America and Australasia; a single species extends northward into Mexico and the Caribbean islands. The genus was monographed by Allen (1999), but not all of his taxonomic decisions are accepted here.

Etymology: According to Meagher (2011), the generic name is derived from the Greek roots *lepyros* (stripped off) + *odon* (tooth), alluding to the membranous outer peristome and perhaps also to the delicate inner peristome teeth.

1 **Well-developed leaves** 2–2.5 mm long, markedly plicate, not rugose or rugose only at extreme apices when dry, moderately concave; **mid laminal cells** mostly 4–5 µm wide; **peristome** single, lacking an exostome ..... *L. australis*

1' **Well-developed leaves** to 4.0 mm long, not plicate, rugose throughout when dry, strongly concave; **mid laminal cells** mostly 6–9 µm wide; **peristome** double, usually with a weakly developed exostome in N.Z. material .... *L. lagurus*

Lepyrodon australis Hampe ex Broth., *Nat. Pflanzenfam. [Engler & Prantl] 1(3),* 773 (1906)

Lectotype: N.Z., Nelson Mountains, 1860, *Dr Sinclair*, NY 00985294 (Image seen online at JSTOR Global Plants, accessed 11 Dec. 2017.) Probable isotype: N.Z., s. loc., s. coll., BM-Hampe!

= *Leucodon implexus* Hook.f., *Handb. New Zealand Fl.* 457 (1867) nom. illeg.

Plants soft, yellow-green, glossy, forming extensive cushions to 0.5 m or more in diameter, usually epiphytic. **Stems** pale green, in cross section with 2–3 layers of thick-walled cortical cells and an ill-

defined central strand, densely beset and bound together by rust-coloured, smooth rhizoids. **Branches** erect, not or sparsely branched, to c. 15 mm long; **microphyllous branches** with small (c. 0.5–1.0 mm), non-plicate, ecostate leaves frequently present and abundant. **Leaves** not or weakly 6-ranked (when moist), closely spaced, erect-spreading, symmetric, strongly plicate to base of acumen, slightly rugose only at apices, broadly lanceolate and rather abruptly tapered to a slender acumen that is c. 0.1 the total leaf length, plane at margins, moderately concave, not decurrent, serrulate in upper half or more, 2.0–2.5 × 0.6–0.7 mm; **acumen** 0.2–0.6 mm; **mid laminal cells** faintly porose, 39–60 × 4–5 µm, somewhat longer (to c. 75 µm) in lower portion of leaf, but not otherwise differentiated; **alar** and **extreme basal cells** shorter and wider, but not forming a well-defined group. **Costa** single, often bifurcate, c. ⅓ the leaf length.

Apparently dioicous. **Perichaetia** on lower portions of vegetative branches, c. 1 mm long, but elongated to c. 2–3 mm following fertilisation, with leaves broadly lanceolate, tubular, ecostate, spreading at apices. **Perigonia** not seen. **Setae** 9–14 mm, straight, c. 150 µm diam. not or twisted very weakly to the left, red-brown; **capsules** oblong or short cylindric from a short, rugose neck, 2–3 mm, pale red-brown; **exothecial cells** weakly thickened in corners; **operculum** 1.2–1.7 mm. **Peristome** single; **exostome teeth** absent; **endostome** with basal membrane extending c. 100 µm past the capsule mouth, segments c. 315–415 µm long, keeled, irregular in outline and often anastomosing in upper half, finely papillose-lirate throughout and **cilia** absent or rarely present and rudimentary. **Calyptra** 4.0–5.0 mm. **Spores** 13–18(–24) µm, pale brown.

Illustrations: Plate 1. Sainsbury 1955, pl. 55, 1; Allen 1999, figs 2–3; Malcolm & Malcolm 2003, p. 41.

Distribution: NI: S Auckland, Gisborne (Rākauroa Scenic Reserve, numerous sites near Lake Waikaremoana), Hawke's Bay (Tūrangakumu, Puketīriri, Makahu River), Wellington; SI: Nelson, Marlborough, Canterbury, Westland (Ōtira Gorge, Kelly Range), Otago, Southland. The lack of collections from St is curious and may be in part due to the absence of southern beech trees on that island.

Australasian. Reported from Tasmania by Klazenga (2012) on the basis of two modern collections from the Lake St Clair region. Allen (1999) also cited a historical Mueller collection from "Nov. Holl.", suggesting that this species might occur in Vic.

Habitat: Growing on tree trunks and large branches, less commonly on rocks or soil, primarily in drier parts of the country. On the North I. documented from 110 m (Ahi Paku Station in eastern Wairarapa, Wellington L.D.) to 1300 m (Ōhakune Mountain Road, Wellington L.D.) and on the South I. from c. 30 m (Pelorus Bridge Scenic Reserve, Marlborough L.D.) to at least 1600 m (Mt Tapuaenuku, Marlborough L.D.), but probably extending to over 1700 m. On the South I. this species is best developed in southern beech forest east of the Main Divide and is nearly absent from regions of high rainfall. It is often abundant in drier sites and can produce pure colonies extending 4 m or more in greater diameter on *Fuscospora* spp. trunks and large branches. It also occurs on the genera *Beilschmiedia*, *Carpodetus*, *Griselinia*, *Hoheria*, *Olearia*, *Pennantia*, *Plagianthus*, and *Pseudopanax*, as well as the gymnosperms *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Prumnopitys ferrugineus*, and *Phyllocladus*.

Notes: *Leucodon implexus* Hook.f. [*Handb. N. Zeal. Fl.* 457, 1867] is illegitimate since at the time of its publication Hooker cited the legitimate *Leucodon hexastichus* Mont. in synonymy. As noted by Allen (1999), Brotherus (1901–1909) subsequently made direct reference to the illegitimate *Leucodon implexus* in the protologue of *Lepyrodon australis* Hampe *ex* Broth., apparently the first legitimate name for this taxon based on a N.Z. type.

Leucodon implexus Hook.f. *nom. illeg.* is founded on two syntypes from Nelson and Otago, collected by Sinclair and Hector & Buchanan, respectively. Allen (1999) designated the Sinclair collection, represented in NY, as the lectotype of both *Lepyrodon australis* and *Leucodon implexus*.

The continued use here of the name *Lepyrodon australis* rather than the South American *L. hexastichus* is a convenience and follows Allen (1999). The type of *L. hexastichus* (Mont.) Wijk & Marg. (Chili austral., *Gay*, BM-Besch.!) lacks intact capsules. The plants have many leaves with fragmented apices, but on some branches the slender and serrate acumens are intact. The upper portions of the shoots are decidedly six-rowed when wet. South American specimens in BM accord well with the range of variability of N.Z. material, but comparison to a wider range of material is warranted. In the only fruiting material available for study (*S. Yakubsen 10772*, Argentina, Isla el Centinela, Lago Nahuel Haupi, CHR 645984), peristome segments appear smoother than in N.Z. material. Material with six-ranked leaves occurs at Peel Forest (Canterbury L.D., *T.W.N. Beckett*, Jan. 1900, CHR 645983!, BM!). If the two names prove to be synonymous, the South American name has priority.

Recognition: The microphyllous secondary branches present are especially abundant on the central, older portions of *L. australis* colonies. With reduced (c. 0.5–1.0 mm), non-plicate, and narrowly ovate-lanceolate leaves, these shoots are often extremely numerous and, if collected in isolation of more typical portions of the plant, could well be misnamed, likely as a species of *Hypnum*. The contorted apical portions of the leaves, and the faintly porose nature of the laminal cells, however, are suggestive of their true identity. The microphyllus branches may produce deciduous buds (as in *B.H. Macmillan 73/522* from Lowry Peaks Range, Canterbury L.D., CHR 242150!), and both structures probably serve a dispersal function.

Etymology: The species epithet refers to the southern distribution of this species.

Lepyrodon lagurus (Hook.) Mitt., *J. Linn. Soc., Bot.* 12: 421 (1869)

≡ *Leucodon lagurus* Hook., *Musci Exot. 2,* 126 (1819)
Isotype: Argentina, Staten Id, *A. Menzies 22*, 1787, BM-Hooker! Holotype: Staten Id., *A. Menzies s.n.*, Herb. Hooker 2141, BM 000986935 (Image seen online at JSTOR Global Plants, accessed 11 Dec. 2017.)

= *Lepyrodon pseudolagurus* B.H.Allen, *Bryobrothera* 5: 40 (1999)
Holotype: N.Z., Nelson, Flora Saddle–Mt Arthur Hut track, 25 km SSW of Motueka, 950 m, *H. Streimann 51054*, MO 3991688 (Image seen online at JSTOR Global Plants, accessed 11 Dec. 2017.)

Plants soft, yellow- or brown-green, not glossy, forming extensive cushions to 0.5 m or more in diameter, terrestrial or epiphytic. **Stems** creeping and much branched, forming a loosely intertwined mat and giving rise to numerous erect branches, red-brown, in cross section with 2–3 layers of thick-walled cortical cells and a weak central strand, densely beset and bound together by rust-coloured, smooth rhizoids. **Branches** ± erect, sparsely branched, to c. 20 mm (rarely to 50 mm or more); **microphyllous branches** with small (c. 0.5–1.0 mm), non-plicate, ecostate leaves occasionally present, usually sparse and fragile, sometimes abundant. **Leaves** not ranked, imbricate, erect-spreading, symmetric, not plicate, rugose in upper half (often with convex areas at back of dry leaf), broadly oblong or oblong-lanceolate, abruptly tapered to a slender acumen up to ⅓ the total leaf length, strongly concave, serrulate in upper half or more, (2.0–)3.0–3.5(–4.0) × 0.9–1.4 mm (without acumen; reduced in size on lower portion of branch); **acumen** c. 0.5–1.0 mm; **mid laminal cells** firm-walled, vermicular, porose, mostly 54–90 × 6–9 µm, somewhat longer in lower portion of leaf, but not otherwise differentiated; **cells at insertion** shorter and wider; **alar cells** not differentiated. **Costa** variable, stout or thin, often bifurcate or spurred, extending ¼ to ½ the length of the lamina. **Axillary hairs** difficult to observe, apparently 3–4 cells long in N.Z. material.

Apparently dioicous. **Perichaetia** scattered on lower branches, c. 1 mm long, but elongating to c. 3 mm following fertilisation, with leaves broadly ovate-acuminate, tubular, ecostate and spreading at apices. **Male plants** not observed. **Setae** 13–23 mm, straight, not twisted, red-brown; **capsules** variable in length, oblong-cylindric from a short, rugose neck, (1.5–)1.8–2.8 mm, pale red-brown; **exothecial cells** not thickened in corners; **annulus** persistent, composed of a single row of inflated cells; **stomata** superficial; **operculum** as per genus, 1.0–1.5 mm. **Exostome teeth** rudimentary or sometimes absent; **endostome** with basal membrane extending 75–130 µm past the capsule mouth; segments linear, 300–520 µm long, keeled, narrowly perforate nearly throughout, not anastomosing, finely papillose-lirate throughout (but often becoming ± smooth in older material). **Calyptra** 4–5 mm, split to c. ½ its length. **Spores** 12–17 µm, smooth, pale brown.

Illustrations: Plate 1. Brotherus 1925, fig. 515, A–G; Beever et al. 1992, fig. 57; Allen 1999, figs 8–9. Seppelt has provided an informative and elegant illustration of this species in Australian Mosses Online (as *L. pseudolagurus*).

Distribution: NI: S Auckland (Maungaorangi), Gisborne (near Matawai, Lake Waikaremoana), Wellington; SI: Nelson, Marlborough, Canterbury, Westland (Camp Creek, Victoria Range, Ōtira River), Otago, Southland. Vitt (1974) reported this species from C.

Austral. Tasmania*, mainland Australia*, Argentina*, Chile*. The significance of Scott & Stone's (1976) report from "Antarctica" is unclear.

Habitat: Occupying a wide range of substrates but most frequently on either sheltered or fully exposed rock (e.g., limestone, gneiss, greywacke, and granite). Also epiphytic (on *Fuscospora cliffortioides* and/or *F. solandri*, *Lophozonia menziesii*, *Griselinia littoralis*), on humic soil in rock crevices, and occasionally on rotten wood. Occurring in both forested and alpine (boulder fields, herbfields, and tussock grassland) situations. On the North I documented from scattered localities

from Maungaorangi (an outlier of the Kaimanawa Range) southward, with most localities in Wellington L.D. Occurrences range in elevation from 680 m (near Matawai, Gisborne L.D.) to 1300 m (Ōhutu Ridge, Wellington L.D.). On the South I, occurring between near sea level (Tahakopa Bay Scenic Reserve, Otago L.D.) and 2000 m (Mt Tapuaenuku, Marlborough L.D.), but relatively uncommon below c. 600 m. Although found in all land districts on the South I., it is known from few localities in Westland L.D. It is, however, documented from many localities in wetter parts of Southland L.D., including Fiordland National Park. It is not documented from either Stewart or Auckland Is but has been recorded without detail from Campbell I.

Notes: Allen's (1999) proposal to segregate N.Z. material of *L. lagurus* (as *P. pseudolagurus* B.H. Allen, Bryobrothera 5: 40) from the South American species is not accepted here, although Klazenga (2012) followed this proposal in his treatment for Australia. Allen found many gametophytic characters to be "so variable they cannot be used to separate the two", but he considered material from South America to be a "somewhat smaller plant with a more weakly developed stem central strand" than Australasian material. He also found the axillary hairs to be 3–4 celled in South American material and 4–6 celled in Australasian material and cited differences in the degree of immersion of the stomata and in the presence/absence of a rudimentary exostome. The last feature was a distinction that he chose to emphasise in his key to species. All the features he used to segregate Australasian material are either ill defined, difficult to observe, or both. The majority of collections from both regions available for examination lack sporophytes, and even in some fruiting material observations on the nature of an exostome are difficult. Most South American material indeed seems to lack an exostome (as predicted by Allen), but other collections (e.g., CHR 456548; *M.R. Crosby 13057* from Prov. Malleo in southern Chile) clearly possess a rudimentary exostome and some N.Z. material also lacks an exostome (CHR 461964, *B.H. Macmillan 89/17* from Lake Peel, Nelson L.D.). Thus no clear distinction can be drawn using the nature of the exostome, nor can it be correlated with geographic distribution. The nature of the stomata is likewise difficult to observe in many fruiting specimens, albeit with some clearly not conforming to Allen's predictions. For example, *A.J. Fife 7471* (CHR 106562 from Hope Range, Nelson L.D.) has clearly superficial stomata, rather than the immersed stomata predicted by Allen.

Other differences cited by Allen (1999) appear to overlap or are equally non-convincing. Axillary hairs are here extremely difficult to observe; the few observed (seen only after staining) in N.Z. material (CHR 461964) appear to be 3–4 cells long and thus conform to Allen's description for *L. lagurus* rather than for the segregate species.

Male plants have not been seen. A single collection in CHR (*R. Mundy 382* from Mt Ruapehu, CHR 645985) was annotated by B.H. Allen to contain males, but close examination failed to locate perigonia. Allen's suggestion that ♂ plants are not dwarfed in this species is not accepted here. On the weight of available evidence, the continued application of the name *L. lagurus* to N.Z. material is desirable.

Recognition: When dry, the rugose leaves, while strongly convex overall in abaxial view, often have a concave area in the upper third of the leaf. The leaves are markedly smaller on lower portions of the branches, and highly reduced on lower portions of main stems.

Etymology: The epithet *lagurus* refers to the similarity of a well-developed branch to the foot of a hare.

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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*)
B	Bounty Islands
C	Campbell Island
c.	about (*circa*)
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 (*in herbario*)
in litt.	in a letter (*in litteris*)
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
subsect.	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

Symbols

Symbol	**Meaning**
µm	micrometre
♂	male
♀	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

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

Technical terms conform to Malcolm & Malcolm (2006), except for those in the glossary below.

Supplementary Glossary for Lepyrodontaceae

Term	Definition
lirate	describes surface ornamentation of a spore consisting of elongate ridges with slanted or rounded sides

Acknowledgements

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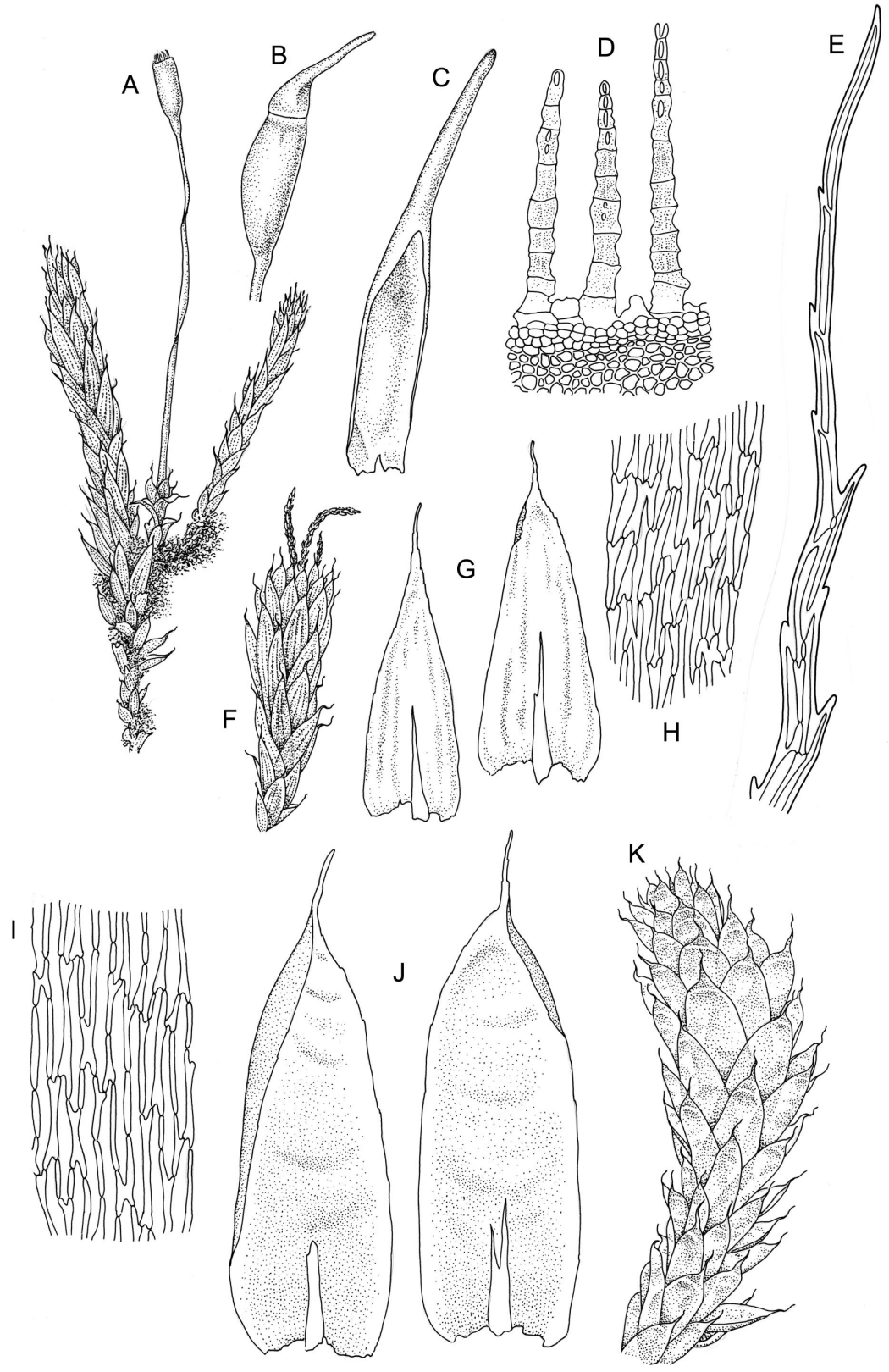
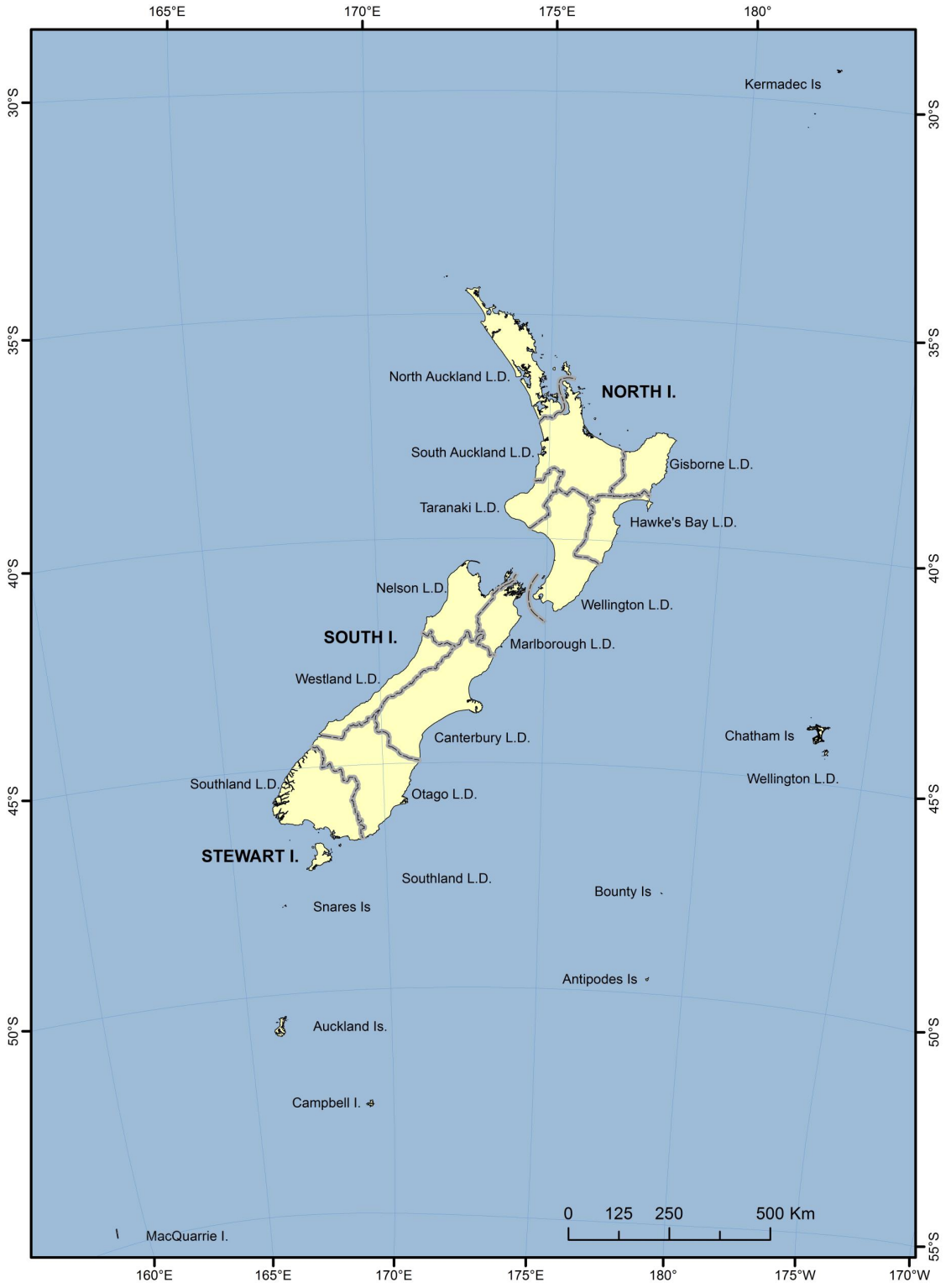
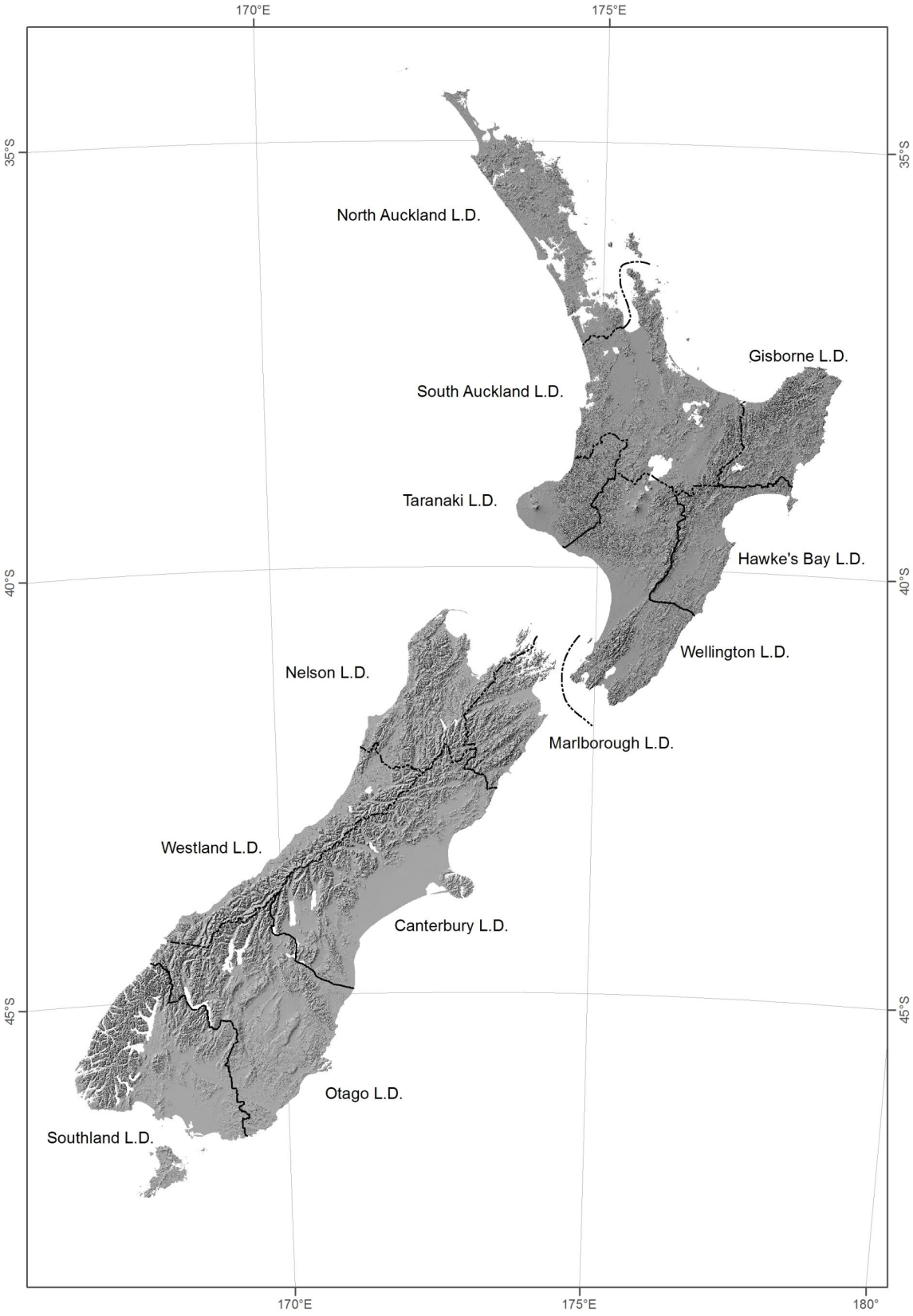


Plate 1: ***Lepyrodon*. A–H: *L. australis***. A, habit with capsule, moist. B, capsule. C, calyptra. D, peristome detail. E, leaf apex. F, portion of shoot, dry. G, leaves. H, mid laminal cells. **I–K: *L. lagurus***. I, mid laminal cells. J, leaves. K, portion of shoot, dry. *Lepyrodon australis* drawn from A.J. Fife 7276, CHR 405885. *L. lagurus* drawn from *G. Brownlie 823*, CHR 426150.



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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