

A reassessment of the New Zealand endemic *Plagiochila deltoidea* (Plagiochilaceae, Marchantiophyta), a liverwort with sporophyte waxes

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Abstract

Plagiochila deltoidea Lindenb. contains three supported phylogenetic lineages that are divergent to a degree consistent with separation among other *Plagiochila* species. However, morphological characters exhibit considerable amplitude of variation within, and overlap among, the three lineages. The extensive morphological overlap on the one hand and the phylogenetic divergences and different morphological tendencies on the other complicate subdivision of *Plagiochila deltoidea* into taxa, of any rank, that reflect the phylogenetic diversity within the species as currently circumscribed. *Plagiochila deltoidea* is here reinterpreted as a variable species with two varieties to accommodate different facets of lineage-correlated morphological variation. *Plagiochila deltoidea* var. *densa* J.J.Engel and G.L.Merr. is recognised for the lineage comprising individuals whose medial leaf cells tend to be narrower than in other lineages, and whose basal vitta is broader relative to the leaf insertion. This variety, like *P. deltoidea* var. *deltoidea*, is widespread throughout New Zealand south from the Coromandel Range. *Plagiochila deltoidea* var. *deltoidea* is generally larger than *P. deltoidea* var. *densa* in terms of shoot stature, leaf size, and in the number of leaf teeth. A new species *P. geminata* M.A.M.Renner is separated from *P. deltoidea* to accommodate smaller plants with fewer teeth on the leaf margins, and more numerous short-triangular teeth on the perianth, from Northland, Auckland, and the Chatham Islands. *Plagiochila geminata* is reliably distinguished by its smaller size and widely spaced leaves, in addition to characters of the female bracts and perianth mouth. Distinguishing these taxa is challenging when informative characters, including perianths, are missing or when specimens are poor and fragmentary. The recognition of *P. geminata* renders *P. deltoidea* paraphyletic, which likely reflects the fact that, even as re-circumscribed here, the varieties of *P. deltoidea* represent two cryptic species. The outer surfaces of the capsule valves of *P. deltoidea* var. *deltoidea* are water repellent and covered by platelet-like projections from a thin film that cracks and lifts irregularly, giving the capsule surface a ragged appearance. This film, the projections, and the water-repellent properties of the outer capsule surface are all removed by chloroform, consistent with their comprising waxes, in the broad sense of that term.

Introduction

Besides the collection of *Monoclea forsteri* Hook. on Cook's second voyage, the first deliberate bryophyte collections from New Zealand were made by Archibald Menzies,

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surgeon on the H.M.S. *Discovery* which anchored at Dusky Bay, New Zealand, from 2 to 22 November 1791 (Engel and Glenny 2008). Many new species were described from Menzies' collections, including in part *Plagiochila deltoidea* Lindenb.

Plagiochila deltoidea was based on collections from Dusky Bay (New Zealand), Tasmania (collected by Fraser), and Barbados (Lindenberg 1843). To appreciate the challenges that have been associated with the application of the name, and the current circumscription of the species, it is useful to review published treatments of *P. deltoidea*, starting with the original description. In the protologue, Lindenberg compared *P. deltoidea* with *P. corrugata* (Nees) Mont. & Nees, *P. renitens* (Nees) Lindenb., and *P. retrospectans* Lindenb., and gave distinguishing features for each. He noted that the specimen from Van Diemen's Land (Tasmania) in herb. Hooker had leaves with minutely denticulate teeth and commented that another plant from Van Diemen's Land collected by Labillardière and held under the name *P. ramosissima* (Hook.) Lindenb. in herb. Montagne had a smaller stature, leaves less evidently secund, and leaf form approaching *P. ramosissima* and *P. abietina* (Nees) Nees & Mont., but differing in the widely spaced branches. At the outset, the describing author's concept of *P. deltoidea* encompassed at least two unrelated Australasian species.

In the *Synopsis Hepaticarum* Gottsche *et al.* (1845) cited only material from two localities, the Labillardière collection from Van Diemen's Land "in Hb. M. et N.; Hb. Lg." and plants from Dusky Bay, New Zealand in "Hb. Lg". By implication the element from Barbados was excluded, as was Fraser's collection from Van Diemen's Land. The Labillardière specimen was mentioned only incidentally in the protologue of *P. deltoidea*, it was not listed with the specimens examined under the *Habit* section, and Gottsche *et al.* (1845) rightly considered that it did not constitute a type element. Still, the Gottsche *et al.* (1845) concept of *P. deltoidea* also encompassed two unrelated Australasian species.

Plagiochila deltoidea was not listed by Hooker and Taylor (1844), probably because they had neither seen specimens nor Lindenberg's publication. Mitten (1860) listed *P. deltoidea* in Hooker's *Flora of Tasmania*, citing the collection by Labillardière from Van Diemen's Land as the type element, in contrast to Gottsche *et al.* (1845). Bastow (1887) followed Mitten, again citing the very fine large plant collected by Labillardière. Stephani (1906) reported *P. deltoidea* for Tasmania, and eastern Australia, again citing the collection by Labillardière, and others by Weymouth and von Müller. He stated that *P. deltoidea* was probably not in New Zealand, where it had been confused with a plant Stephani described as *P. howeana* Steph. Stephani did not identify specific gatherings in the protologue of *P. howeana* but stated, somewhat dismissively, 'New Zealand, ubique communis'.

Pearson (1923) took the opposite view to Stephani. He argued that Stephani's *P. howeana* and the type of *P. deltoidea* were one and the same, and restricted *P. deltoidea* to New Zealand, by implication defining the name with reference to the Dusky Bay specimen(s) presumably gathered by Menzies and cited by Lindenberg. Pearson (1923) proposed a new species, *P. neohoweana* Pearson, for Tasmanian plants previously confused with *P. deltoidea*, using the name so that an epithet honouring his colleague, Marshall Howe, would be preserved.

Inoue and Schuster (1971) confirmed Pearson's view that the Tasmanian and New Zealand plants previously attributed to *P. deltoidea* were distinct and had been confused. However, they pointed out that in proposing *P. neohoweana*, Pearson had overlooked *P. strombifolia* Taylor ex Lehm., and they formalized this synonymy. Whether they followed Pearson in restricting *P. deltoidea* to New Zealand is unclear, as no specimens examined from Tasmania were cited, nor was any positive reference made to the species' restriction to New Zealand, or its absence from Tasmania. Inoue and Schuster (1971) cited a specimen from Dusky Bay in STR as 'Type' of *P. deltoidea*, and designated a collection by T.W.N. Beckett from the Kelly Range determined by Stephani and held in NY as the lectotype of *P. howeana*.

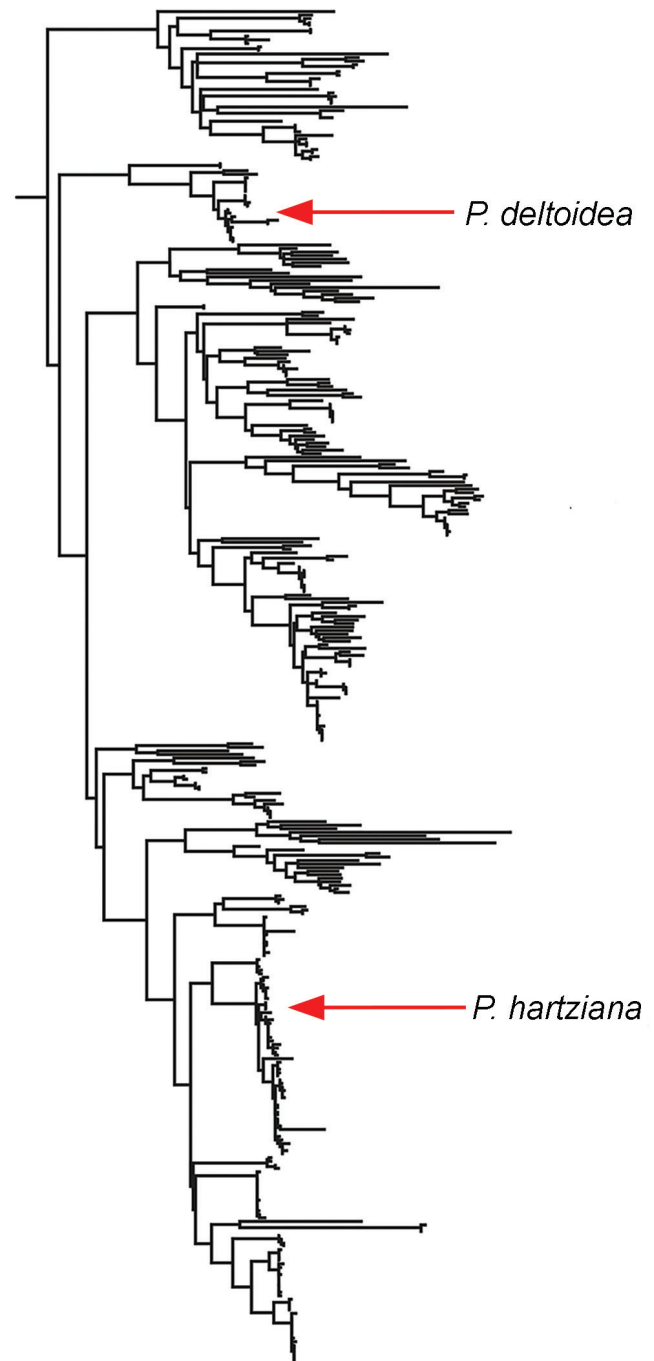


Figure 1. A phylogeny of the genus *Plagiochila* showing the *Plagiochila deltoidea* complex and *P. hartziana*, the latter placed in synonymy of *P. deltoidea* by So (2001). The phylogeny is the Majority Rule tree summarizing samples from the posterior probability distribution obtained by MrBayes from Renner *et al.* (2017).

For Australia, Inoue (1986) noted that *P. deltoidea* was reportedly rare on the Australian mainland, even though it had 'long been known' from Tasmania. Only one specimen was cited by Inoue (1986) from mainland Australia, collected at Gloucester Tops (Streimann 1547); this specimen has both *Frullania*-type vegetative branching and stolons originating by lateral-intercalary branching. These characters, together with leaf shape and dentition including the strong U-shaped stem insertion line and decurrent wing on the ventral stem insertion, make this plant *P. fasciculata*. McCarthy (2006) accepted *P. deltoidea* for all eastern states and territories based on determinations on specimens in Australian herbaria. *Plagiochila deltoidea* was excluded from Australia by Renner (2018) and Renner *et al.* (2024), all Australian reports being based on misidentifications of other species, including *P. fasciculata*, *P. retrospectans*, and *P. strombifolia*.

So (2001) previously had broadened the circumscription of *P. deltoidea* to include plants with terminal *Frullania*-type vegetative branching and toothed male bracts when she placed *Plagiochila hartziana* Pearson, with a Tasmanian type, into synonymy of *P. deltoidea*. Engel and Merrill (2010) made no mention of this synonymy when they proposed the male plants in the New Zealand material collected by Menzies and held in Vienna (W) as the lectotype of *P. deltoidea*. The identity of *P. deltoidea* in New Zealand had been well established and was 'no longer in question' at the time of Engel and Merrill's study (Engel and Merrill 2010: 505). Engel and Merrill (2013) reinstated *P. hartziana* as the earliest name available for the plant then known in New Zealand as *P. virido-nigra* (E.A.Hodgs.) Inoue. However, Engel and Merrill's (2010) lectotypification of *P. deltoidea* was redundant as a type had, for better or worse, been effectively designated by Inoue and Schuster (1971), based on a duplicate of the same Menzies gathering held in STR (Renner 2018, 2021).

As circumscribed by Engel and Glenny (2008) and Engel and Merrill (2013), *Plagiochila deltoidea* was distinct among Australasian species in its entire male bract lobes, usually solitary male branches, complete absence of terminal branching, and triangular teeth on the leaf margins and perianth. To accommodate some of the variation in leaf cell size and cell areolation manifest in *P. deltoidea*, Engel and Merrill (2013) proposed *P. deltoidea* var. *densa* for those plants with consistently smaller leaf lobe cells, and a more pronounced basal vitta. *Plagiochila deltoidea* belongs to *Plagiochila* sect. *Austrocaules*, a lineage unusual in its stolons arising by ventral-intercalary branching only (Renner *et al.* 2017a), and is the only member of this section in New Zealand (Renner 2018).

Molecular phylogenetic study resolved *P. deltoidea* as it had been circumscribed by So (2001), in two separate lineages (Renner *et al.* 2017b) corresponding to *P. hartziana* and *P. deltoidea* (Fig. 1). The *P. deltoidea* lineage exhibited significant internal phylogenetic structure (Fig. 2), comprising three supported monophyla. General Mean Yule Coalescent (GMYC) and Automatic Barcode Gap Detection (ABGD) analyses consistently equated two of these monophyla with separate phylogenetic lineages, while the third was split into three or four separate groups on the basis of sequence divergence and branch lengths (Fig. 3). The significant phylogenetic structure resolved within *P. deltoidea* suggested this species, even as circumscribed in the narrower sense of Engel and Merrill (2010) was a complex. In this study the morphology of individuals belonging to the three lineages comprising *P. deltoidea* is reassessed and the circumscription and distribution of *P. deltoidea* is reconsidered against morphological and molecular data.

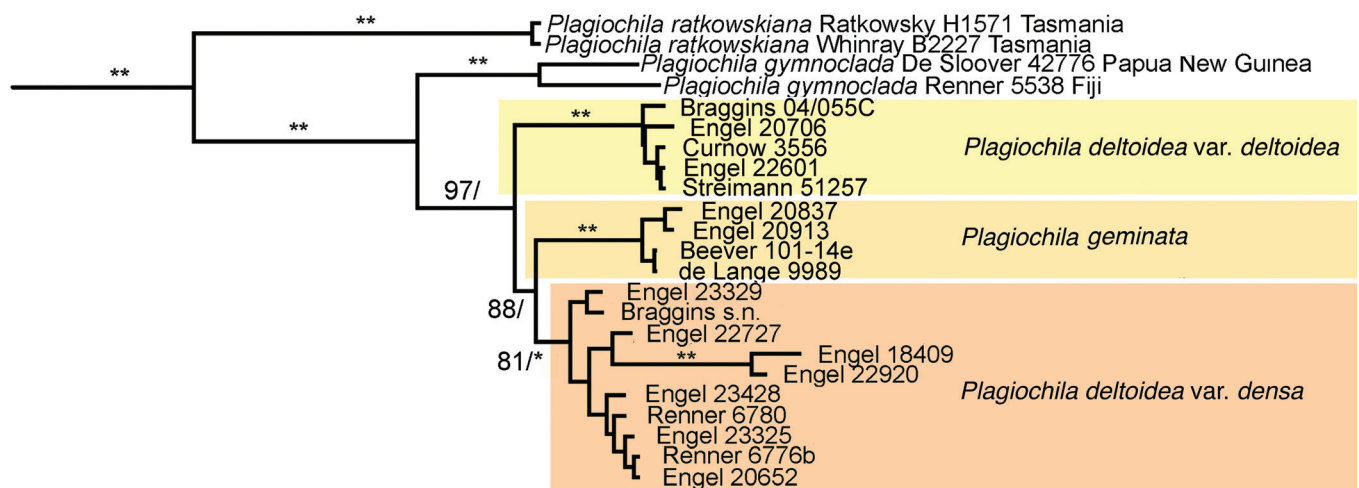


Figure 2. Relationships between sampled individuals belonging to the *P. deltoidea* complex. Terminal names reflect taxa recognized by this study. Support values are likelihood bootstraps calculated with RAxML and posterior probabilities, respectively. * indicates 100% bootstrap or 1.0 posterior probability. See Renner *et al.* (2017) for species delimitation methods.

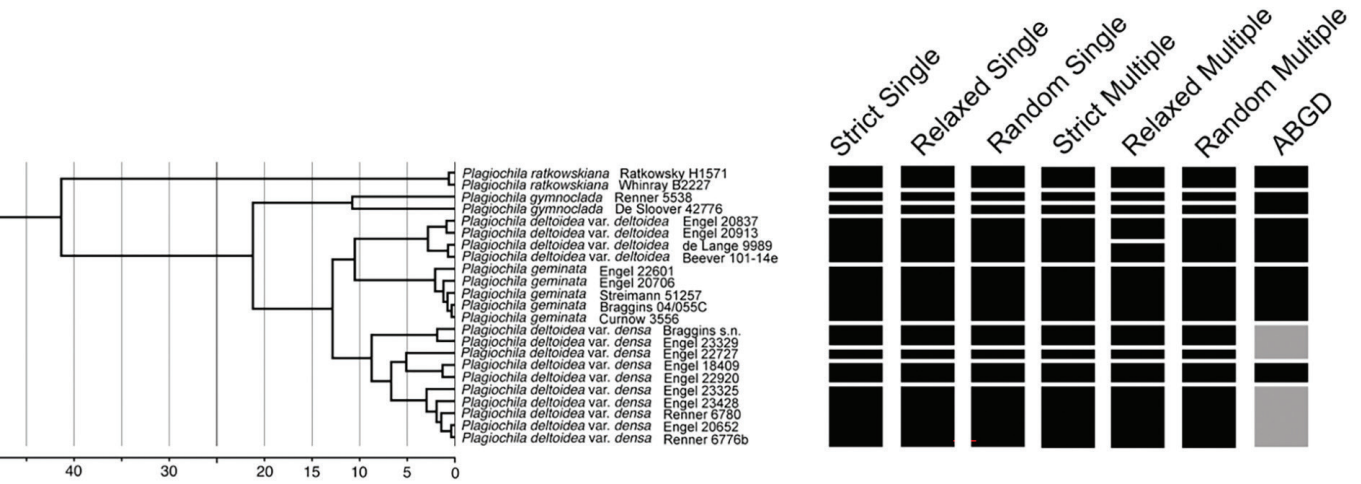


Figure 3. Summary of GMYC and ABGD results and assessment of morphology for specimens belonging to the *Plagiochila deltoidea* complex, from Renner *et al.* (2017), for details of methods see that paper.

Materials and Methods

Taxon sampling and molecular phylogeny reconstruction

Molecular sequence data from 22 specimens belonging to *P. deltoidea* sens. lat., as circumscribed by So (2001) and Engel and Merrill (2010), were sampled to capture morphological and geographic variation. Specimens were sourced from the herbaria AK, CANB, F, and from dedicated fieldwork in New

Zealand. DNA extraction, polymerase chain reaction (PCR), sequencing methods, alignment and composition of the full molecular dataset follow Patzak *et al.* (2016) and Renner *et al.* (2017b). Phylogeny reconstruction based on Maximum likelihood and Bayesian inference methods using RAXML (Stamatakis 2014) and MrBayes (Ronquist and Huelsenbeck 2003) followed Renner *et al.* (2017b). Molecular sequence data were deposited in GenBank, and accession numbers pertaining to the sequences analysed here are listed in Table 1.

Table 1. Voucher specimens and GenBank accession numbers for DNA sequence data analysed as part of this study.

Voucher	nrITS	rps4	rbcL
New Zealand, Curnow 3556 (CANB9408642)	KY051398	KY051151	KY050903
New Zealand, Engel 20706 (F1141750)	KY051405	KY051160	KY050912
New Zealand, Engel 22601 (F1141724)	KY051401	KY051156	KY050908
New Zealand, Streimann 51257 (CANB9306707)	KY051397	KY051150	KY050902
New Zealand, Braggins 04/055C (AK290978)	KY051395	KY051148	KY050900
New Zealand, Engel 18409 (F1141063)	-	KY051153	KY050905
New Zealand, Engel 20652 (F1141748)	KY051403	KY051158	KY050910
New Zealand, Engel 22727 (F1141080)	KY051400	KY051155	KY050907
New Zealand, Engel 22920 (F1140885)	-	KY051152	KY050904
New Zealand, Engel 23325 (F1141064)	KY051399	KY051154	KY050906
New Zealand, Engel 23428 (F1141729)	KY051402	KY051157	KY050909
New Zealand, Renner 6776b (NSW899342)	KY051410	KY051165	KY050917
New Zealand, Renner 6780 (NSW899341)	KY051409	KY051164	KY050916
New Zealand, Braggins s.n. (AK287128)	KY051394	KY051147	KY050899
New Zealand, Beever 101-14e (AK298125)	KY051396	KY051149	KY050901
New Zealand, de Lange 9989 (AK327793)	KY051417	KY051172	KY050922
New Zealand, Engel 20837 (F1141749)	KY051404	KY051159	KY050911
New Zealand, Engel 20913 (F1141788)	KY051406	KY051161	KY050913
Australia, Tasmania, Curnow 2660 (CANB8808028)	KY051423	KY051178	KY050928
Australia, Tasmania, Ratkowsky H1553 (CANB8408762)	KY051420	KY051175	KY050925
Australia, Tasmania, Curnow 2606 (CANB8807975)	KY051422	KY051177	KY050927

Statistical Parsimony

Statistical parsimony calculates the number of unambiguous changes connecting pairs of aligned sequences, and then connects haplotypes into networks (Templeton *et al.* 1992). Statistical parsimony analysis was performed on alignments of each marker separately using TCS 1.21 (Clement *et al.* 2000), with connection limit set to 95%.

Morphological assessment

Dissections of leaves, female bracts, and perianths were performed by hand with tweezers on material rehydrated in water. Perianth longitudinal and transverse sections were prepared by hand with double-edged razor blades. All dissections and sections were slide-mounted in glycerine jelly (Zander 1997) for examination and storage.

Measurements of median cell length and width were taken from the leaf interior halfway between the end of the basal vitta and the leaf apex. Length was measured along the longest axis at the midpoint of the end walls if the cell end was formed by a single wall, and from the vertex formed by two walls if the end was formed by two walls. Width was defined as the maximal distance between the two sidewalls, measured perpendicular to length. Images of cells were captured with a Leica DM2500 compound microscope with a DFC295 digital camera, and measurements made with Fiji v2.0.0 (Schindelin *et al.* 2012). Counts of leaf teeth and measurements of leaf width and length were made from dissected, slide-mounted leaves, while counts of perianth labium teeth were made directly from dried herbarium specimens examined under magnification on a dissecting microscope. Taxon, as identified by molecular and morphological data, formed the basis for comparisons of quantitative data.

Outlines from a haphazard selection of the flattened leaves prepared for examination from each voucher specimen were made using a drawing tube and digitised for landmark digitisation with tpsDIG2 (available from <http://life.bio.sunysb.edu/morph/> verified 22 Feb 2017). All successfully flattened leaves from among those prepared were included. The outlines captured the leaf outline between the dorsal and ventral ends of the leaf insertion lines, and the actual insertion line. A landmark was placed at each end of the stem insertion, and another 25 sliding semi-landmarks were placed equidistant along the leaf margin. For superimposition these landmarks were allowed to slide between their neighbours. Landmark sets were aligned and superposed using Generalised Procrustes Analysis in the geomorph package of R (Adams and Otárola-Castillo 2013). Visual summaries of the major axes of variation in multidimensional shape space were obtained with plotTangentSpace which plots Procrustes aligned specimens along their principal axes.

To assess the relationship between size and patterns of co-variation between size and shape within each lineage (Gould 1966, Mossiman 1970), Procrustes ANOVA, which quantifies the shape variation attributable to size in a linear model derived from a multivariate regression of shape onto centroid size (Loy *et al.* 1996; Monteiro 1999) and estimates the significance of this quantification against a null model, was used. Goodall's *F* tends to perform well even with relatively small sample sizes (Klingenberg 2016), as in this study. The null model was generated by permuted resampling, using a residual randomization

permutation procedure of 999 replicates (Collyer *et al.* 2015). Taxon membership inferred from molecular and morphological evidence, and leaf size were used as independent variables, and the two-dimensional matrix of Procrustes aligned coordinates was the response matrix.

Whether the number of teeth on leaf and perianth mouth differed among taxa was assessed using the Kruskal Wallis test and Dunn's test as performed in the stats v. 4.4.1 and dunn.test v. 1.4.3 packages of R 4.4.1. (R Core Team 2023).

Waxes

During investigation of specimens and work to prepare capsules for examination of patterns of cell wall thickenings in capsule valves, it became evident that the outer surface of capsule valves of a specimen of *Plagiochila deltoidea* var. *deltoidea*, AK290978, were glaucous and strongly water repellent. Close investigation by light microscopy of the outer surface revealed a thin film, with cracks and membranous platelet-like extensions on the outer capsule surface. To determine whether waxes were present in this surface film and extensions, two valves from one capsule were dissected and washed in chloroform for two minutes. The washed and unwashed valves were then compared under magnification with a Leica compound microscope.

Results

Haplotype Networks

Networks for the three different loci all returned three clusters amongst sampled individuals from the *Plagiochila deltoidea* complex, corresponding to the three supported monophyla recovered in the phylogenetic analyses. Throughout the results and discussion that follows the monophyla are referred to using the names later proposed for them, for consistency and clarity.

For *rps4* all individuals were resolved within a single network in three clusters separated by 5 to 7 steps, each corresponding with a supported monophylum. For *nrITS* all individuals were resolved within a single network in three clusters separated by 6 to 13 steps; each cluster corresponded with a supported monophylum. For *rbcL* all individuals were resolved within a single, complex, network. Individuals of *P. deltoidea* var. *deltoidea* were separated from the others by 8 steps. Two individuals of *P. deltoidea* var. *densa* (Engel 18409 and Engel 22920) were separated from all other *P. deltoidea* var. *densa* specimens by 8 steps. Individuals of *P. geminata* and *P. deltoidea* var. *deltoidea* were separated by a minimum of three steps.

Morphology

Qualitative character differences between the three lineages were absent with the exception that in *P. deltoidea* var. *deltoidea* the leaf insertion was reflexed and extended back down the ventral side of the stem, where it bore a low wing. Quantitative characters including leaf size, spacing and orientation exhibited differences among the three molecular groups, as outlined in the taxonomic treatment below. The number of leaf and perianth teeth, and medial and basal cell dimensions showed species-specific parameters of variation (Fig. 4). The number of teeth on leaf margins overlapped between the three lineages, but intra-specific range and mean differed. *Plagiochila geminata*

had the fewest teeth, ranging from 5 to 24 with a mean of 12.9; *P. deltoidea* var. *densa* ranged from 7 to 25 teeth, with a mean of 15.1; and *P. deltoidea* var. *deltoidea* ranged from 9 to 31 with a mean 22.1, and these differences in mean were significant ($\chi^2=99.14$, $df=2$ $P<0.0001$), as were all pairwise comparisons (not shown). The number of teeth on perianth labia also overlapped between the three lineages, but intra-specific ranges and means again differed. *Plagiochila deltoidea* var. *deltoidea* had the fewest teeth, ranging from 10 to 17 with an average of 12.9; *P. geminata* ranged from 14 to 24 with a mean of 18.5; and *P. deltoidea* var. *densa* ranged from 11 to 27 with a mean of 17.2, and again these means were significantly different ($\chi^2=25.66$, $df=2$ $P<0.0001$), with pairwise comparisons significantly different among *P. deltoidea* var. *deltoidea* and the other two taxa, but not significantly different among *P. deltoidea* var. *densa* and *P. geminata*.

Medial cell width and length were normally distributed within each lineage. *Plagiochila deltoidea* var. *densa* had smaller medial cells, with widths ranging from 8.3 to 17.2 μm and lengths ranging from 8.3 to 23.9 μm . *Plagiochila deltoidea* var. *deltoidea* had cells 10.6 to 21.2 μm wide and 12.4 to 28.4 μm long. *Plagiochila geminata* had cells 9.8 to 16.3 μm wide and 11.7 to 18.2 μm long. However, there was no separation of lineages on the basis of cell dimensions, though *P. deltoidea* var. *densa* tended to cluster in the smaller end of both axes (Fig. 4). Basal cell width and length were also normally distributed in each lineage. *Plagiochila deltoidea* var. *densa* had narrower basal cells, with widths from 10.5 to 18.9 μm and lengths 22.2 to 86.2 μm . *Plagiochila deltoidea* var. *deltoidea* basal cells had widths ranging from 11.8 to 23.5 μm and lengths 25.3 to 66.6 μm long. *Plagiochila geminata* basal cells had widths ranging from 13.6 to 22.6 μm and lengths 27.1 to 73.0 μm long.

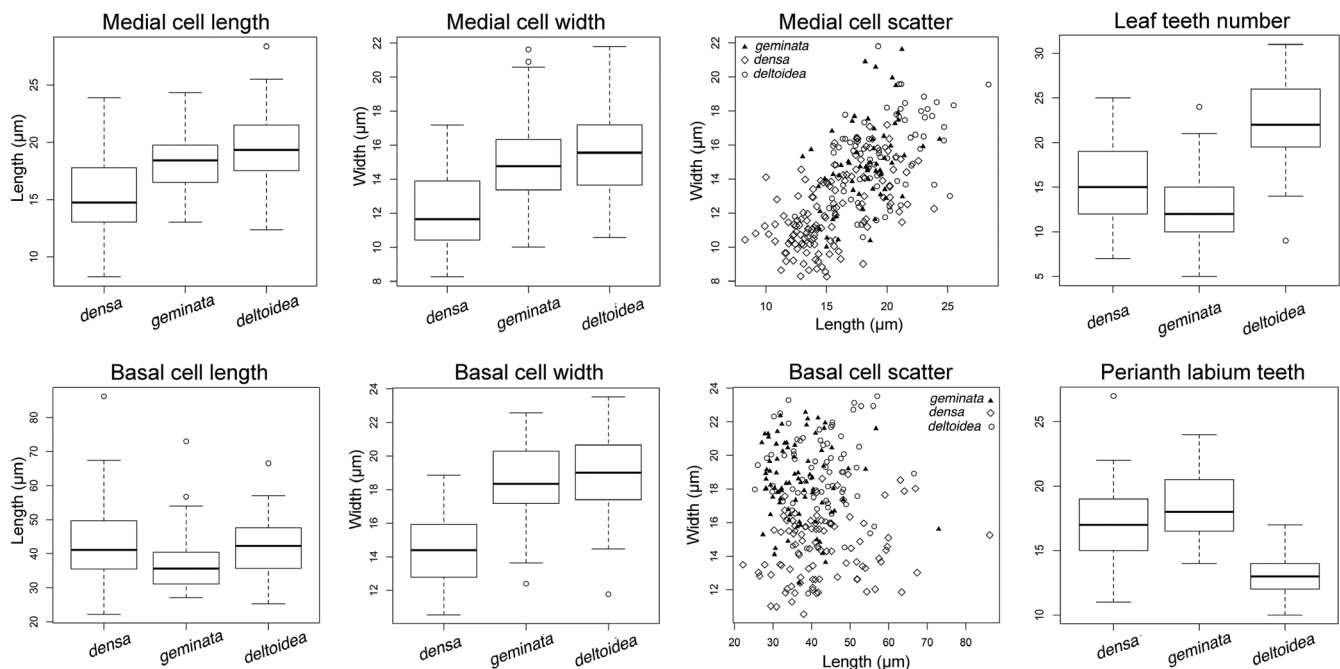


Figure 4. Boxplots for a selection of quantitative continuous and quantitative discrete traits exhibiting variation among sampled individuals; and scatterplots for cell dimensions from medial and basal leaf regions.

Geometric morphometric analysis of leaf shape

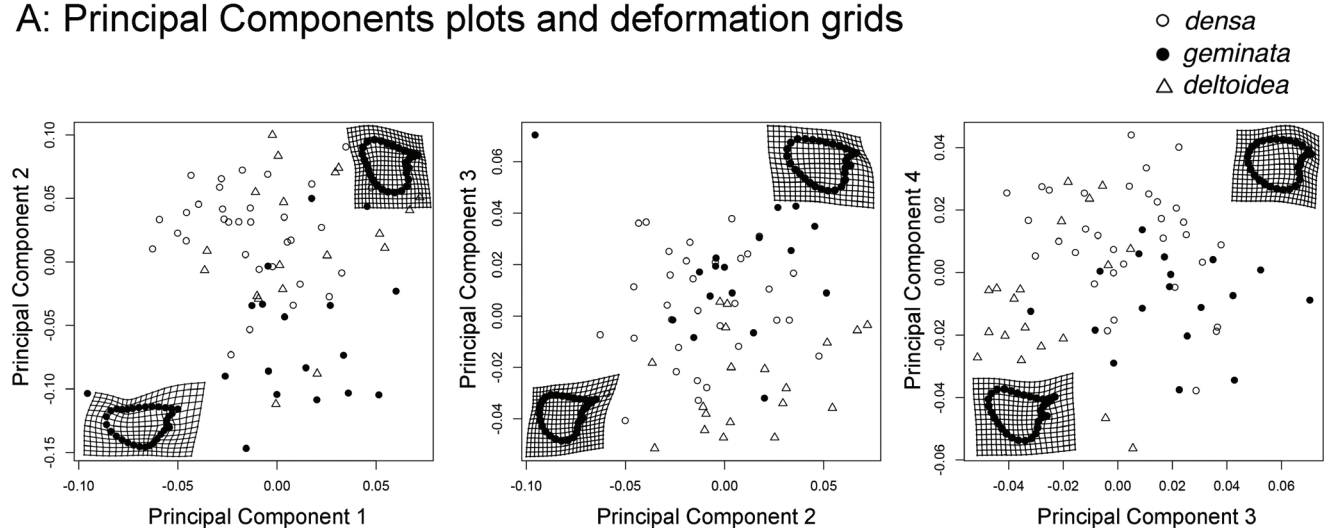
In a Principal Components Analysis (PCA) of leaf shape the first principal component (PC) described a change from elliptic-ovate to broadly obovate associated with leaf base ampliation and relative depth of the stem insertion line, which accounted for 51.2% of variation in leaf shape (Fig. 5). There was no separation of species along this axis. The second PC described a change in leaf shape from broadly obovate to ovate, both with an ampliate leaf base. In ovate leaves part of the ventral margin was straight whereas this was continuously curved in obovate leaves. This change described 15.8% of variation in leaf shape. The combination of first and second principal components achieved partial separation of *P. deltoidea* var. *densa* and *P. geminata*, while *P. deltoidea* var. *deltoidea* overlapped with both. The third PC described changes in leaf shape associated with the length of the leaf insertion and shape of the dorsal leaf margin, with more rotund leaves in positive values and more obovate leaves with a concave dorsal stem margin in negative

values. Species again overlapped along the second principal component, but *P. geminata* occupied mostly positive values and *P. deltoidea* var. *deltoidea* negative values. The third component described 10.9% of leaf shape variation, and cumulatively the first three components described 77.9% of total shape variation. Deformation grids comparing species mean shapes illustrated that all three species have similar average shapes (Fig. 5). However, on average *P. geminata* had a more convex dorsal leaf margin and a less ampliate base; *P. deltoidea* var. *deltoidea* had a deeper leaf insertion and a wider separation between landmarks at the ventral end of the stem insertion reflecting the presence of the ventral decurrent wing, and a broad ampliate base. In other respects the average leaf shapes of *P. deltoidea* var. *densa* and *P. deltoidea* var. *deltoidea* were similar. The test for homogeneity of slopes for a linear model fitted for each species was rejected (Table 2). Within the multivariate multiple regression, shape variation was significantly correlated with both size and lineage, and the interaction between size and lineage was also significant.

Sums of squares indicated that size explained around 23% of leaf shape variation, differences between lineages explained 25% of variation, and their interaction 6% of variation, leaving 46% of shape variation unexplained by the independent variables. The plot of residual shape component on log centroid size showed most *P. deltoidea* var. *deltoidea* leaves were separated from the other two lineages, and a partial separation between leaves of

P. deltoidea var. *densa* and *P. geminata* (Fig. 6). Subtle differences in the shape of the smallest leaves sampled for each lineage were indicated, those of *P. deltoidea* var. *densa* were obovate to nearly spatulate, those of *P. geminata* were narrow ovate, and those of *P. deltoidea* var. *deltoidea* were more broadly ovate (Fig. 6). These differences were consistent with qualitative appraisal of a wider range of leaves from specimens of each lineage.

A: Principal Components plots and deformation grids



B: Deformation grids for species mean shapes

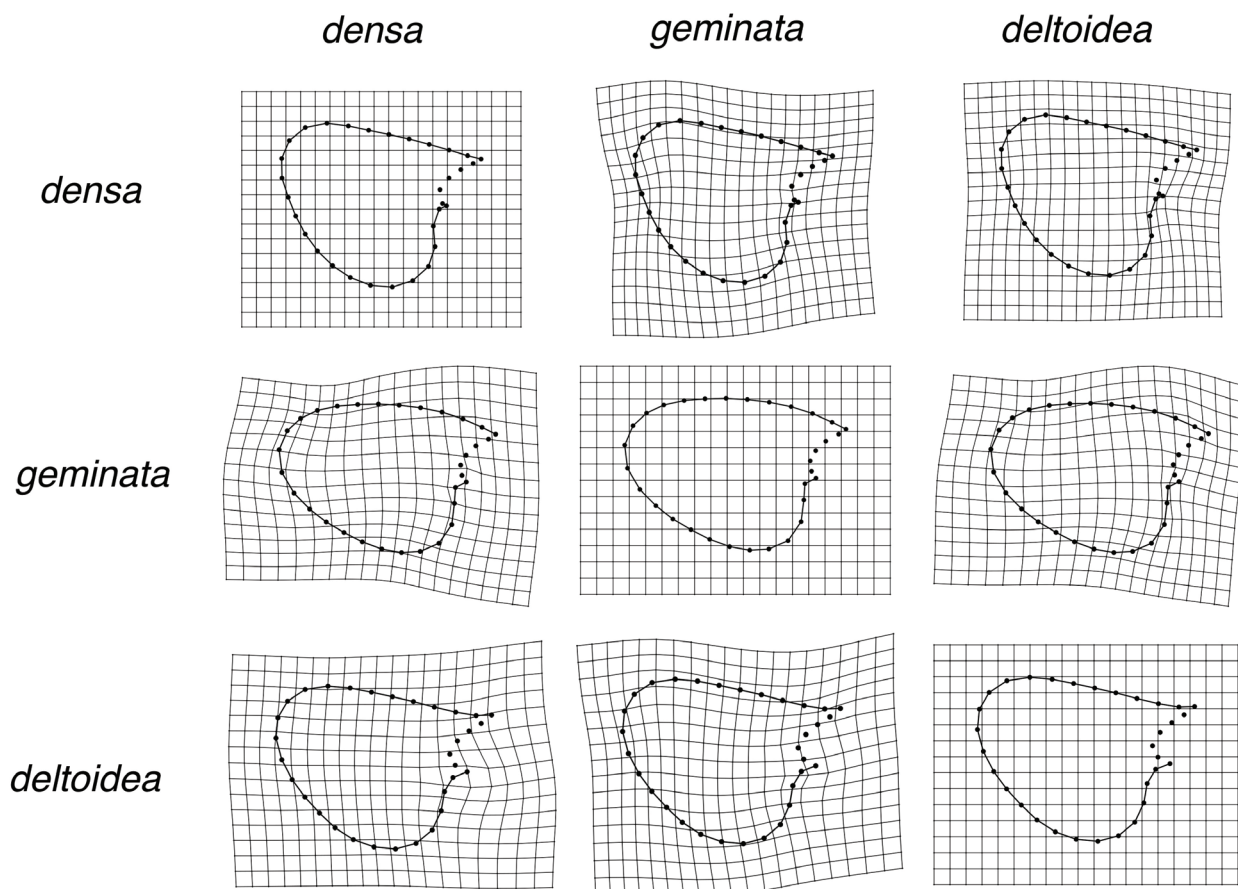


Figure 5. A. Shape Principal Components Analyses, with biplots for the first four principal components and thin plate splines illustrating deformations associated with the x axis within each plot. B. Thin plate splines illustrating deformations between the mean leaf shapes for each species. The rows show the mean leaf shape for each taxon.

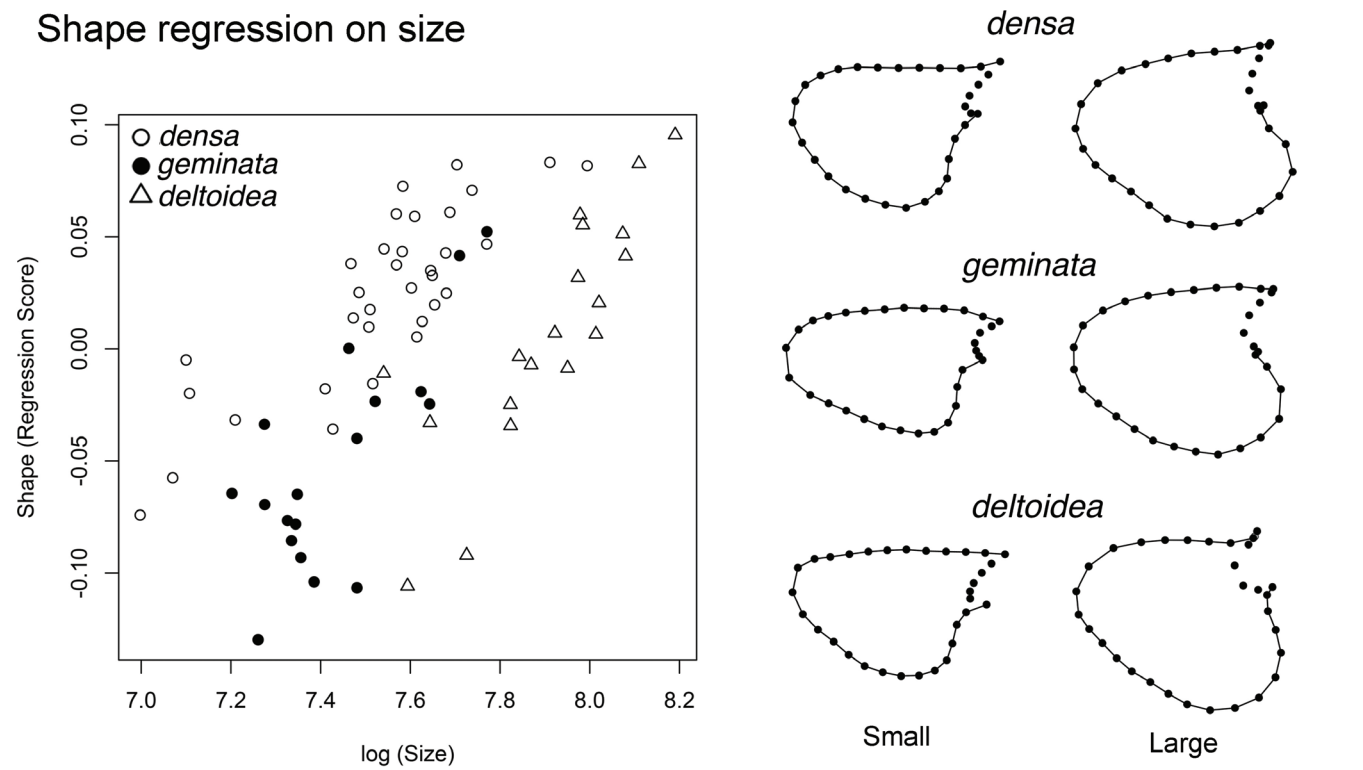


Figure 6. Regression plot of the shape regression score on log leaf centroid size, and landmark configurations for the smallest and largest leaves of each species included in the analysis.

Table 2. Homogeneity of slopes and Procrustes ANOVA testing hypotheses regarding the relationship between shape, size and taxon membership.

Homogeneity of Slopes Test

Df	SSE	SS	R2	F	Z	Pr(>F)
Common Allometry	68	0.3567				
Group Allometries	64	0.2152	0.1415	0.3038	10.52	6.2639 0.001 **

ANOVA table

	Df	SS	MS	Rsqr	F	Z	Pr(>F)
log(Size)	1	0.1091	0.1091	0.2343	32.4534	11.7596	0.001 **
Taxon	2	0.1157	0.0578	0.2483	17.1984	9.5578	0.001 **
log(Size):Taxon	2	0.0258	0.0129	0.0555	3.8415	3.3966	0.001 **
Residuals	64	0.2152	0.0034				
Total	69	0.4658					

Waxes

The film, the membranous platelet-like projections, and the water-repellent properties of the outer capsule surface were all removed from the two capsule valves washed in chloroform. Those on the un-dipped capsule valves remained (Fig. 7).

Discussion

Surface waxes are rare in bryophytes (Proctor 1979), and in liverworts are known on gametophytes of a few genera including *Anthelia*, *Marchantia*, and *Plagiochila* (Schönherr and Ziegler 1975, Heinrichs *et al.* 2000). Even in *Plagiochila* the frequency of expression is relatively low, waxes were detected on only 8 of 81 species surveyed by Heinrichs *et al.* (2000). In none of these *Plagiochilaceae* species were leaf surfaces waxes visible by

light microscopy. This contrasts with the wax, in the broad sense of that term (Barthlott *et al.* 1998), on the outer valves of the sporophyte of *P. deltoidea* var. *deltoidea*. At 400× magnification, the surface bears conspicuous ornamentation of membranous, triangular platelets projecting from a near continuous film, the film itself is cracked and lifted in loose sheets in places (Fig. 7). There is no detectible wax ornamentation on the gametophyte of *P. deltoidea* var. *deltoidea*, consistent with results for *P. deltoidea* obtained by Heinrichs *et al.* (2000), based on Reif C199D, though the identity of that specimen should be confirmed.

The three lineages comprising *Plagiochila deltoidea* as broadly circumscribed exhibit subtle morphological differences, primarily in quantitative characters, all of which exhibit overlapping ranges of variation. These characters include leaf cell size, expression

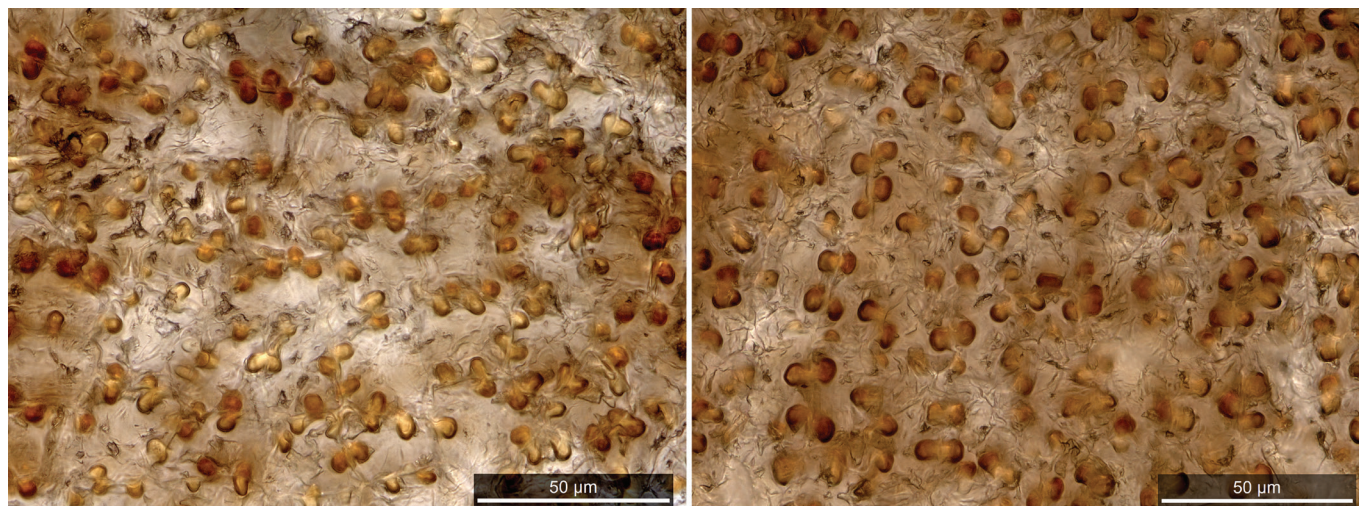


Figure 7. Surface of capsule valves of *Plagiochila deltoidea* var. *deltoidea* showing irregular membranous platelet-like ornamentation projecting from a basal film that is cracked, fissured, and lifted in irregular sheets in places, as viewed with a light microscope, from AK290978.

of the leaf vitta, leaf size and shape, the number of leaf teeth, leaf imbrication, plant stature, and the number and size of teeth on the perianth mouth. The degree of morphological difference is incongruent with the degree of phylogenetic divergence among the three lineages. This poses challenges to both circumscription and ranking of any taxa proposed to accommodate this phylogenetic diversity within *P. deltoidea* sens. lat. Characters identified as diagnostic of the three lineages during the analysis of molecular voucher specimens do hold across the set of herbarium voucher specimens examined as part of this study, for the most part. However, variation within specimens in characters such as the size and extent of the vitta within the leaf base, cell size, the number and stature of teeth on the leaf margin and perianth mouth, complicate diagnosis of each lineage on morphological grounds, and several herbarium specimens were observed that could not be assigned to a lineage, being intermediate between the two recognised varieties of *P. deltoidea*. By contrast, despite morphological variation and overlap, individuals belonging to *P. geminata* are consistently different from *P. deltoidea* by their smaller shoot size, widely spaced leaves that are rolled around their longest axis when dry and have fewer teeth on average, and perianth mouth with more numerous smaller triangular teeth and other characters (see taxonomic treatment below) and both herbarium specimens and living plants are readily recognisable on the basis of these morphological features. Further, individuals of *P. geminata* form a well-supported, phylogenetically discrete lineage, suggesting they share a unique history. Their distribution is more or less allopatric from the other two lineages, being confined to the upper North Island with an outlying occurrence on the Chatham Islands, where it is sympatric with *P. deltoidea* var. *densa*. *Plagiochila geminata* is also ecologically distinct from the other two lineages, inhabiting coastal and lowland broadleaf forests between sea level and 460 masl. *Plagiochila geminata* fulfils a combination of criteria indicating species status, including phenotypic, phylogenetic, and ecological distinctiveness.

Recognising *Plagiochila geminata* as a distinct species introduces two scenarios to explain the paraphyly of the re-circumscribed *P. deltoidea*. Either *P. deltoidea* is paraphyletic or the paraphyly reflects a knowledge problem. Either is plausible given available evidence and both are discussed below following an assessment of the evidence supporting the recognition of *P. geminata* as a

separate species. Further investigation may demonstrate that the two varieties within *P. deltoidea* represent cryptic species (see Renner 2020) that warrant recognition at species rank, and the morphological and molecular data available to date do not exclude that possibility. The two varieties of *P. deltoidea* can usually be discriminated on their gross morphology and leaf architecture. *Plagiochila deltoidea* var. *deltoidea* is often a very large plant, with shoot systems up to 7.5 mm wide, with leaves obliquely spreading and distinctly succubously orientated. The vitta is single, not divided and fairly narrow. *Plagiochila deltoidea* var. *densa* is a smaller plant, with shoot systems to 4.5 mm wide whose leaves are transversely orientated and adpressed against the stem. The vitta is double, being divided at the base of the cnemis. These and other characters define two groups of specimens, corresponding with the two lineages, in most cases but some specimens possess characters intermediate in their expression, and attribution of these individuals to one of the two varieties is not possible. Hybridisation may explain the morphological intermediacy of these individuals, though hybridisation among liverwort species is thought uncommon as there are few documented examples. The other possibility is that, given the strongly supported monophyly and inferred age of the species, *P. deltoidea* preserves considerable, ancient, allelic diversity, perhaps supported by maintenance of large population sizes through geological time. Population genetic analysis targeting the two varieties of *P. deltoidea* may inform future decisions over what rank is most appropriate for them.

The challenge of lack of morphological divergence is neither unique to the *P. deltoidea* complex, nor particularly unusual within bryophytes. Taxon circumscription at species rank and below relies heavily on continuous characters in many genera, including *Hygroamblystegium* Loeske (Vanderpoorten *et al.* 2003), *Rhynchostegium* Schimp. (Hutsemékers *et al.* 2012), *Orthotrichum* Hedw. (Medina *et al.* 2012, 2013), and *Homalothecium* Schimp. (Hedenäs *et al.* 2014), and when overlap in gametophytic traits occurs this complicates species delimitation and identification (Hedenäs *et al.* 2014). In these and other genera such as *Lejeunea* Lib., multiple lineages previously attributed to single species have been recovered by molecular data, and these were often separated by subtle morphological differences only, particularly those associated with continuous traits (Heinrichs *et al.* 2009,

2010, 2015; Renner *et al.* 2013; Aranda *et al.* 2014). The *P. deltoidea* complex may present an instance of crypsis in broad sympatry due to incipient divergence in trait means without separation of trait distributions, such that the degree of divergence fails to yield morphological discontinua, and a general lack of qualitative differences. Variation within and overlap between species in gametophytic traits is problematic for taxon circumscription and identification within *P. deltoidea*, as noted above, as it is in other bryophytes including *Oligotrichum* DC. (Bell and Hyvönen 2012) and *Homalothecium* (Hedenäs *et al.* 2014).

Morphologically weakly differentiated taxa at species rank and below result from a range of processes, including hybridization, for example the allopolyploid *P. britannica* Paton (Barbulescu *et al.* 2017), and possibly a lineage within *Hygroamblystegium* (Vanderpoorten *et al.* 2004); vicariant divergence, as exemplified by cryptic lineages within *Metzgeria furcata* (L.) Corda (Fuselier *et al.* 2009); and also possibly by ecological divergence, for which cryptic species of *Conocephalum* Hill with their apparently differential tolerance of desiccation and micro-morphological differences associated with gas exchange (Szweykowski *et al.* 2005), are candidates. At least some degree of ecological differentiation has been inferred between cryptic species within the *Aneura pinguis* (L.) Dumort. complex as well (Bączkiewicz and Buczkowska 2016). Further study may identify ecological differentiation among the three lineages within *P. deltoidea* that support the recognition of cryptic species.

Plagiochila deltoidea var. *deltoidea* and *P. deltoidea* var. *densa* are both widespread throughout cool hyper-humid environments, from the Coromandel Range in the North Island to South Westland, and Stewart Island, with *P. deltoidea* var. *densa* extending east to the Chatham Islands. *Plagiochila geminata* is confined to warm temperate forests of the northern North Island and the Chatham Islands. This northern North Island – Chatham Islands disjunction is broadly equivalent to that exhibited by the fern *Asplenium pauperequitum* Brownsey and P.J.Jacks (Cameron *et al.* 2006). The Chatham Islands vascular flora comprises three broad elements, one with affinities to northern New Zealand, Australia, and the Pacific, one with affinities to southern New Zealand, and a third derived from New Zealand with no clear center of origin (Cameron *et al.* 2006). The same broad distributional patterns are present in the non-vascular Chatham Islands flora; examples of northern element bryophytes include, as noted above the mosses *Fissidens oblongifolius* var. *oblongifolius* and *Archidium elatum* Dixon and Sainsbury, and the liverworts *Cheilolejeunea trifaria* (Reinw., Blume and Nees) Mizut., *Radula javanica* Gottsche, and *P. geminata*. The lichen *Heterodea muelleri* (Hampe) Nyl. has been recorded in New Zealand only from the far north of the North Island, and Chatham Island.

Plagiochila deltoidea var. *deltoidea* expresses a relationship between leaf size and shape different from *P. deltoidea* var. *densa* and *P. geminata*, and was nearly completely separated in plots of leaf residual shape component on leaf size (Fig. 6). Different allometric relationships in sister taxa suggest lability in leaf ontogeny within *P. deltoidea*. The capacity to vary size, shape, and the relationship between size and shape may contribute to the success of *Plagiochila* if leaf size, shape, orientation and spacing have functional significance in relation to different microsites, habitats, and plant sizes.

Taxonomic Treatment

Key to taxa of the *Plagiochila deltoidea* complex

1. Leaf medial cells 9–17 µm wide; rows of elongate and heavily thickened cells of the basal vitta extending to near mid-leaf leaf, and occupying more than half of the stem insertion length, often with a separate dorsal ‘sub-vitta’ of three or four tiers of cells extending a short distance into the leaf cnemis; leaf margins bearing 7–25 (average 15) teeth; leaves imbricate when dry, rolled along the cnemis only, smallest leaves obovate; female bracts usually with large triangular-laciniate teeth; perianth mouth with 11–22(–27) long triangular teeth on each labium *P. deltoidea* var. *densa*
- 1: Leaf medial cells 10–24 µm wide; rows of elongate and heavily thickened cells of the vitta confined to the leaf base, not extending to close to mid-leaf, occupying the ventral half of the leaf insertion at most, never extending dorsally into the cnemis; leaf margins bearing 5–31 teeth; leaves contiguous or remote when dry, often rolled along their entire width into a cone; smallest leaves ovate; female bracts with small to large triangular teeth; perianth mouth with short triangular teeth, or with large laciniate teeth 2
2. Perianth mouth with 10–22 (average 13) laciniate teeth on each labium; leaf margins bearing (7–)12–31 (average 23) teeth; leaves 2.5–4.6 mm long by 1.7–3.4 mm wide; plants robust, shoots to 7.5 mm wide when hydrated *P. deltoidea* var. *deltoidea*
- 2: Perianth mouth with 14–24 (average 18) short triangular teeth on each labium; leaf margins bearing 5–21 (average 13) teeth; leaves 1.8–3.3 mm long by 1.3–2.3 mm wide, plants medium, shoots 4.5 mm wide when hydrated *P. geminata*

Plagiochila deltoidea Lindenb., Species Hepaticarum 5: 132. 1843.

= *Jungermannia deltoidea* (Lindenb.) Hook.f. and Taylor, Choix de Plantes de la Nouvelle-Zélande: 36. 1846.

Type citation: in portu Dusky Bay dicto Novae Zeelandiae; in terra van Diemen (*Fraser. Herb. Hookeri*); in Barbadoes insula (*Herb. Neesii ab Es.*)

Type: New Zealand, Dusky Bay, without collector (lectotype designated by Inoue and Schuster (1971): STR!; isolectotype: W!)

= *Plagiochila caespitosa* Colenso, Transactions and Proceedings of the New Zealand Institute 20: 244. 1887 [1888]. Colenso, non Steph. Stephani 1892, fide Hamlin 1972, syn fide Engel and Merrill 2010.

Type citation: Forming small thick cushion-like tufts on branches of trees in low, wet, and dark woods, “Forty-mile Bush”, near Norsewood, County of Waipawa; October 1886: W.C.

Type: n.v.

= *Plagiochila howeana* Steph., Bulletin de l’Herbier Boissier, sér. 2 4: 783. 1904 = Species Hepaticarum 2: 461. 1904.

Type citation: New Zealand, ubique communis.

Type: New Zealand, Kelly Range, T.W.N. Beckett 335 (lectotype designated by Inoue and Schuster 1971: NY n.v.)

= *Plagiochila axillaris* Colenso, Transactions and Proceedings of the New Zealand Institute 20: 246. 1887 [1888] Colenso, non J.B.Jack and Steph., Stephani 1892 fide Inoue and Schuster 1971, Hamlin 1972.

Type citation: ‘On trees and logs, in woods with the preceding species, *P. trispicata*; 1887: W.C.’

Type: New Zealand, Wood Creek, DVK, 10 Feb. 1887, W. Colenso a.1342 (lectotype designated by Engel and Merrill (2010): WELT-H007775!)

=*Plagiochila spenceriana* Colenso, Transactions and Proceedings of the New Zealand Institute 21: 50. 1889.

Type citation: On trees, forests near Dannevirke, County of Waipawa, near Dannevirke, 1888, H. Hill

Type: Dannevirke, County of Waipawa, 1888, H. Hill, sub Colenso 1427 ex hb K in hb G (lectotype designated by Bonner (1962): G; isolectotypes (?): WELT-H007774!d BM)

Typification: The typification of *P. deltoidea* is not straightforward. Pearson (1923) restricted application of the name *P. deltoidea* to New Zealand plants. Inoue and Schuster (1971 p. 97) cited a specimen of *P. deltoidea* ‘in herb. Lindenberg’ held in STRAS, thereby possibly lectotypifying the taxon. However, the citation of their lectotype specimen is not without significant ambiguity because Lindenberg’s herbarium is held in Vienna (W) (Stafleu and Cowan 1981). If Inoue and Schuster (1971) were referring to a duplicate from the Lindenberg herbarium held in STRAS they should have cited this as ‘ex herb. Lindenb.’ rather than ‘in’. So is this citation of the STRAS herbarium an error? Engel and Merrill (2010) thought so, though they provided no helpful commentary on their decision. The error would be easily identified if there were no specimens from Dusky Bay in STRAS that might be part of the original material of *P. deltoidea*. However, there is a specimen from Dusky Bay in STRAS, that may be derived from the original material of *P. deltoidea*. Therefore, a decision regarding what the lectotype of *P. deltoidea* hinges on two issues. First, was the citation of the herbarium STRAS by Inoue and Schuster (1971) an error and did they mean W, consistent with their statement ‘in herb. Lindenb.’, or did they simply err by stating ‘in’ rather than ‘ex’? Second, is the specimen in STRAS part of the original material? Both points are difficult to address, the authors of the 1971 publication are both dead, and neither felt subsequent published clarification of their intent necessary. The specimen from ‘Dusky Bay’ in STRAS may imply that Inoue and Schuster’s (1971) lectotypification on a specimen in that herbarium was intended, and not an error; however, the specimen was not annotated by Inoue or Schuster and bears no annotation that it comes from the Lindenberg herbarium. In fact, it is labelled “*Ramulus Plagiochila deltoideae* nov. Zeeland Dusky Bay” and contains a single sterile shoot.

The second point is no easier, except that if the specimen in STRAS is not part of the original material then it is ineligible to serve as a lectotype. In herb. Lindenberg in Vienna there are two specimens from Dusky Bay bearing Hooker numbers 47 and 54 respectively, which were likely collected by Menzies in 1791 (Engel and Merrill 2010). These comprise part of the original material and indicate that Dusky Bay plants were stored as different specimens, of which 54 includes male and 47 female plants. Was the single sterile shoot in STRAS derived from one of these specimens or another portion of the Dusky Bay material of *P. deltoidea*? All duplicates of syntype specimens are part of the original material, even if they were not seen by the describing author. Lindenberg did not cite a collector of New Zealand

material, only the locality ‘Dusky Bay’. Both Inoue and Schuster (1971) and Engel and Merrill (2010) inferred that their respective lectotypes were collected by Menzies. The STRAS specimen bears the same evidence as those in W for supporting its inclusion within the original material.

Engel and Merrill (2010) made no mention of Inoue and Schuster’s (1971) lectotypification, except to note that ‘until now the species has not been evaluated with reference to the original material studied by Lindenberg (1839–1843)’ (Engel and Merrill 2010 p. 505).

There are few early collecting events at Dusky Bay. Subsequent to Menzies in 1791, Lyall collected at Dusky Bay between 1847 and 1851 when he served as surgeon-naturalist on HMS Acheron (Engel and Glenn 2008). This implies that only Menzies’ gatherings were available from Dusky Bay when *P. deltoidea* was described; they were widely distributed by Hooker. The replication of locality information, absence of collector, proximity, and content (specimens in W and STRAS contain the same entity) are all consistent with the STRAS specimen being a duplicate from one of the W specimens or another portion of the original material.

Given both the STRAS and W specimens are part of the original material of *P. deltoidea* (Article 9.3) and Inoue and Schuster’s statement “in herb. Lindenberg” is considered a negligible error then Inoue and Schuster’s (1971) inadvertent lectotypification must be followed, because their citation of the type specimen was clear and direct (Renner 2021). There is no provision for rejecting a lectotype because another better, more representative, or ideal specimen is available. Indeed, the nomenclatural type is not necessarily the most typical or representative element of a taxon (Article 7.2). However, despite perceived or real issues with the lectotypifications, application of the name *P. deltoidea* will not change regardless of which lectotype is accepted, because both STRAS and W specimens contain the same entity, whose agreement with the protologue was already established by Engel and Merrill (2010).

A lectotype for *P. spenceriana* Colenso was inadvertently designated by Bonner (1962), whose treatment often fulfills the requirements of effective lectotypification, given comment 3 in his introduction (Renner 2021). Engel and Merrill (2010) proposed a redundant lectotype using a possible isolectotype in WELT.

The types of both *P. axillaris* and *P. spenceriana* have leaves with succubous insertion, and a decurrent ventral wing. The shoot stature is relatively large, the teeth are low in stature, triangular and of relatively even size. As noted above, two syntype specimens of *P. howeana* also share these features.

I have not seen the lectotype of *P. howeana*. However, in Genève there are two residual syntypes of *P. howeana*: Nova Zelandia, ins merid. Waimate (Canterbury) damp bush, May 1901, T.W.N. Beckett, ex herb Levier 2792, (G00121950!); and Nova Zelandia, ins merid. Waimate (Canterbury) damp bush, May 1898, T.W.N. Beckett, ex herb Levier 1183, (G00121967!). These two residual syntypes contain plants with large, succubously inserted, sparsely and evenly toothed leaves with a low decurrent wing on the ventral stem insertion; and male branches terminal and single – characters which are a good match with *P. deltoidea* var. *deltoidea*. Critical features described by Stephani included

the large leaf size (4 mm long), the ampliate leaf base, and the coarsely toothed perianth mouth, which broadly agree with these original materials, and I have inferred that the same entity is represented in the lectotype.

I have not seen the type of *P. caespitosa* Colenso but details in the protologue are consistent with its synonymy with *P. deltoidea* var. *densa*, in particular 1) the close, sub-imbricate, obliquely cordate-orbicular leaves, 2) the nearly straight dorsal leaf margin, 3) the comment ‘small and sub-orbicular at base.’ This third comment is difficult to interpret, as it follows a description of the stem-leaf junction but it seems most likely that Colenso is referring to the small leaves at the base of leafy shoots, which are indeed sub-orbicular in *P. deltoidea*. The entire male bract lobe margins mentioned by Colenso unambiguously assign this name to the *P. deltoidea* complex. Until the original material of *P. caespitosa* is examined, its synonymy with *P. deltoidea* is retained, and synonymy with any of the infraspecific taxa is not made.

Recognition: When sterile, *P. deltoidea* can be distinguished from other similar but unrelated species by its predominantly ventral-intercalary stolon production and exclusively lateral-intercalary vegetative branching. Male specimens are distinctive in their entire male bract lobes. In combination these features are sufficient to distinguish all varieties of *P. deltoidea* from species with which the species has been persistently confused. Species of the *P. fasciculata* species complex, which includes *P. baylisii* Inoue and R.M.Schust., *P. conturbata* Steph., *P. fasciculata*, *P. hartziana* Pearson, and *P. subflabellata* Colenso, all produce stolons by lateral-intercalary branching, have leafy shoots produced by *Frullania*-type vegetative branches, and have dentate male bract lobes. *Plagiochila colensoi* Hook.f. Taylor also produces stolons by lateral-intercalary branches and has dentate male bract lobes.

Plagiochila deltoidea and *P. strombifolia* have been confused from the time *P. deltoidea* was first described. Differences between the two species were elucidated by Inoue and Schuster (1971), who concluded that the species were easily separated by 1) the more numerous narrow-based, usually shorter, fine, sometimes aciculate marginal teeth possessing an elongated terminal cell in *P. strombifolia*; 2) leaves longer than wide in *P. strombifolia*; 3) the basal leaf cells more elongate in *P. deltoidea*; 4) the homogeneous oil-bodies of *P. strombifolia*; and 5) male branching by *Frullania*-type branches in *P. strombifolia*. All five of these characters successfully separate these two species, in addition to the presence of ventral-intercalary stolon branching in *P. deltoidea* versus lateral-intercalary stolon production in *P. strombifolia*. Distribution is an aid to identification because *P. deltoidea* is endemic to New Zealand (Renner 2018). Specimens of *P. deltoidea* of Tasmanian origin are absent from Australasian herbaria, and the species has not been observed in Tasmania despite several lengthy and dedicated field campaigns since 2007.

In New Zealand *P. deltoidea* has been confused with *Chiastocaulon flamabile* M.A.M.Renner, on account of their shared possession of deltoid leaves, stolon production by ventral-intercalary branches, and lack of terminal vegetative branching. *Chiastocaulon flamabile* differs in leaf dentition, most leaves have an obviously bifid leaf apex and few teeth on a nearly straight ventral margin, and in the male bracts, which are dentate, rather than entire.

Plagiochila deltoidea* var. *deltoidea (Figs 8, 9)

Description: Plants forming long pendulous turfs or short pendants of sparingly branched leafy shoots arising from a sharply differentiated creeping, branched, system of basal stolons bearing highly reduced leaves; leafy shoots mid-green in life, light brown in herbarium, to 100 mm long and 5,000–7,300 mm wide, leafy shoots monomorphic, stature reduced at base close to stolons; flagellae absent. Branching within stolons predominantly ventral-intercalary, rarely lateral-intercalary, always giving rise to other stolons; within leafy sectors by lateral- and ventral-intercalary branching, giving rise to leafy shoots only. Stems on stolons and primary shoots in leaf sectors reddish-brown, to 400 mm diameter, transversely elliptic, surfaces smooth; cortical cells in 3 or 4 layers, cortical smaller than medullar, with strong continuous reddish-brown thickenings on cell walls constricting cell lumina, except in a wedge of unpigmented cell walls from the ventral merophyte, medullar cell walls with small triangular trigones at cell junctions otherwise without thickening, pale yellow pigmented; stems on leafy shoot similar without the ventral wedge of unpigmented walls. Rhizoids on stolons arising in loose fascicles from the base of leaves, also scattered along the lateral and ventral stem surfaces. Leaves on leafy shoots remote when dry, contiguous when wet, postically secund, broadly ovate to elliptic, 2549–4579 mm long by 1774–3393 mm wide, succubously orientated when dry or wet, dorsal and ventral margins strongly inrolled when dry, dorsal margin straight, entire or with a few scattered teeth on the outer half; apex broadly rounded, postical margin shallowly curved in outer half then broadly ampliate in basal half; with (9–)14–31 narrow-triangular teeth of fairly even size and spacing distributed from the apex to the basal quarter of the postical margin, teeth on the basal part of the postical margin rare; teeth triangular 2–6(–8) cells wide at base and 3–12(–14) cell tiers high, uniseriate for 1–4(–5) cells, upper cells quadrate to rectangular, capped by a single rounded to acute cell; insertion J-shaped, oblique, recurved and decurrent ventral end, decurrency bearing an indistinct wing as low as 2 cell tiers high, not attaining ventral stem midline, leaving two cortical cell rows leaf-free, dorsally attaining the stem midline but not decurrent, stem visible between leaves. Marginal cells short-rectangular or quadrate, 12.6–21.1 mm long by 8.7–19.5 mm wide, long axis parallel with margin, free external wall heavily thickened, thickening convex, bulging into cell lumen medially, not sharply differentiated from medial cells; cells in median leaf elliptic, 12.4–28.4 mm long by 10.6–21.8 mm wide, walls with discrete convex to nodular, rarely elongate and confluent, trigones; medial wall thickenings rare, thickenings above and below trigones along junction of transverse walls with free dorsal and ventral exterior walls absent, transition to basal cells more or less abrupt, particularly dorsally where isodiametric medial cells and rectangular cells are juxtaposed, medially and ventrally transitional cells have slightly coarser trigones and longer lengths relative to width; cells in leaf base rectangular to long rectangular, 25.3–66.6 mm long by 11.8–23.5 mm wide, trigones nodular to block-like, rounded rather than angular, discrete, not confluent with adjacent medial thickenings, 0 or 1 medial wall thickenings present; leaves on stolons remote, appressed, ovate, unlobed, entire. Cell surfaces smooth and unornamented. Oil-bodies not observed. Underleaves vestigial, several cells, irregularly arranged, often ciliate, produced consistently on leafy sectors. Asexual reproduction absent.

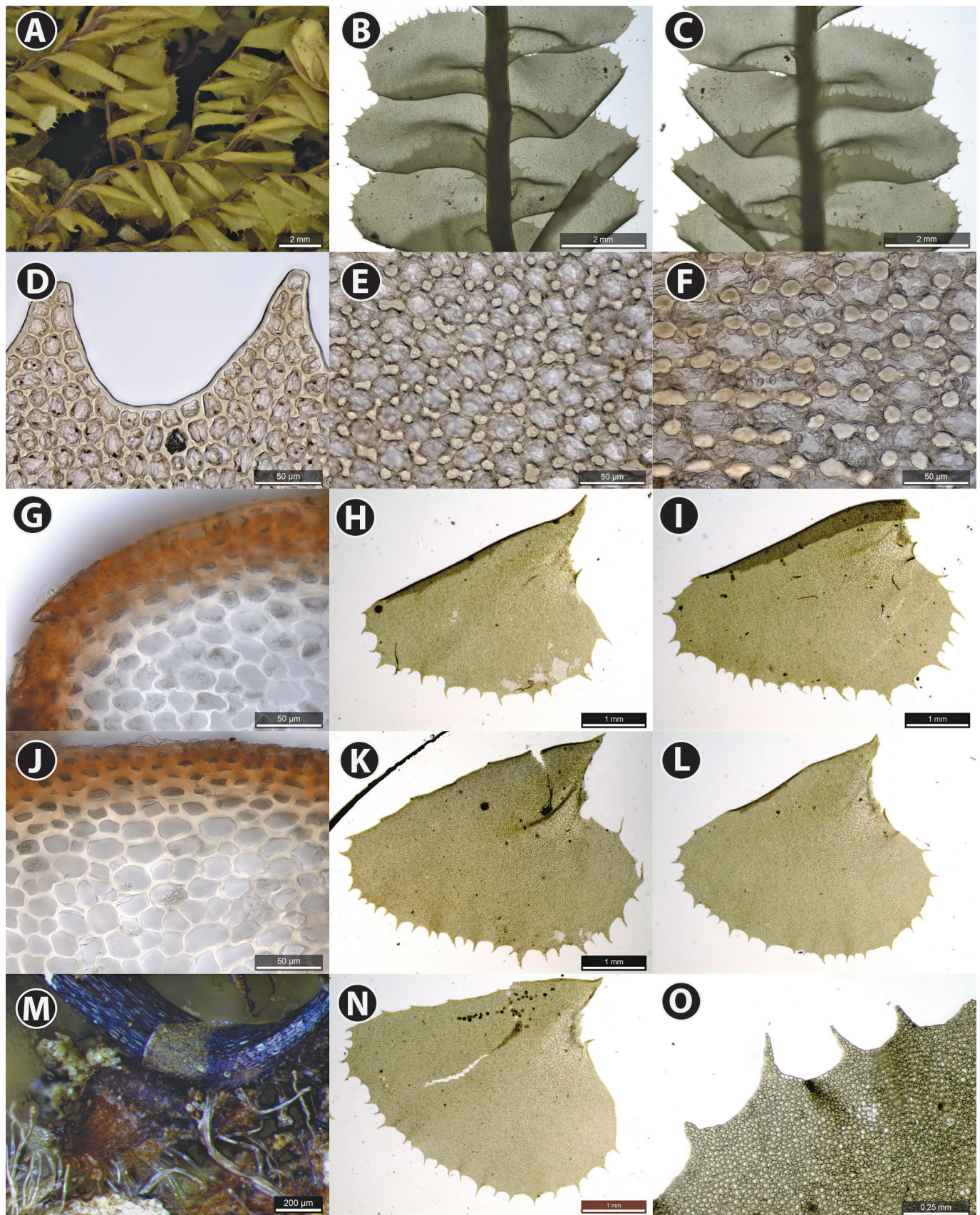


Figure 8. *Plagiochila deltoidea* var. *deltoidea*. A. Habitus, dried. B. Shoot in dorsal view. C. Shoot in ventral view. D. Leaf marginal cells. E. Leaf medial cells. F. Leaf basal cells. G. Transverse section of leafy shoot stem. H, I, K, L, N. Primary shoot leaves. J. Transverse section of stolon stem. Primary shoot leaves. M. O. Leaf margin. A–C, M from CANB9408642; D–F, O from AK290978; G–L, N from F1141750.

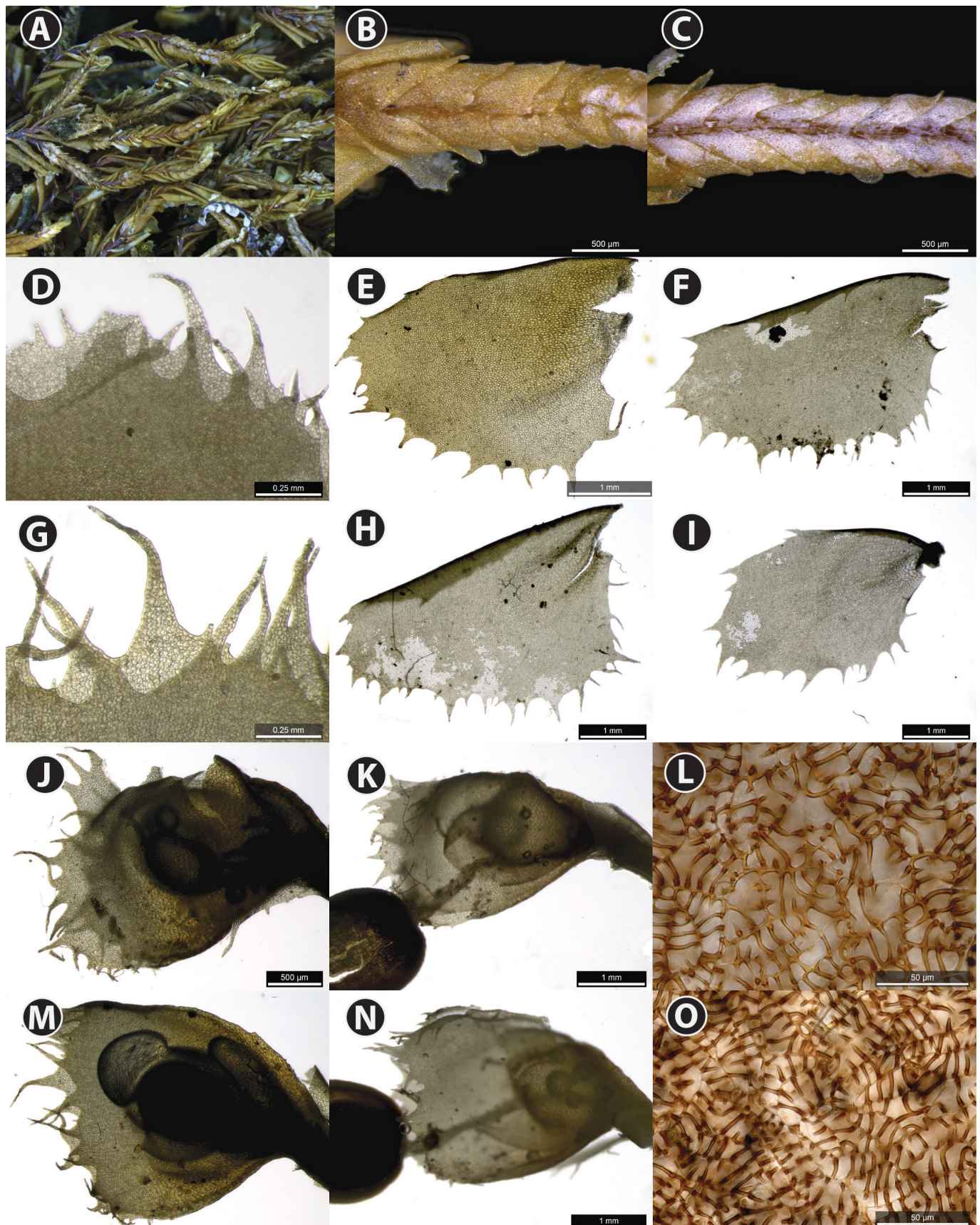


Figure 9. *Plagiochila deltoidea* var. *deltoidea*. A. Habitus, male plants. B–C. Androecia in ventral view. D, G. Perianth mouth. E, F. Female bracts. H, I. Female bracts. J, K, M, N. Perianths in lateral view. L, O. Innermost capsule valve cell layer ornamentation, viewed with interior surface uppermost. A–C, E, L, O from AK290978; D, F, H, I, K, N from F1141750; G, J, M from CANB9408642.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, solitary, growth of androecial branch neutrally geotropic, continuing axis of leafy shoot, not inclined downward; androecial bracts in (3–)7–11 pairs, bract lobes orbicular, entire, margins weakly recurved toward ventral base, transversely orientated, obliquely spreading; free, unfused; antheridia 1 per bract, stalk biseriate. Gynoecia at apices of leafy shoots; bracts ovate, larger than preceding leaves, 2317–4055 mm long by 1345–3059 mm wide (including teeth); base truncate; median base not or weakly inflated; dorsal margin strongly reflexed, bearing 1–3 small triangular teeth 2–4 cells broad at their base and 2–6 cells high, capped by a uniseriate row of 2–4 cells; apex and ventral margin lacinate, bearing 10–19 teeth, 3–14 cells broad at their base and up to 20 tiers high, radiating, more or less straight, separated by truncate sinus formed by the continuation of the leaf, or U-shaped sinus when teeth are closely spaced; bract cells as for leaf cells; cell surfaces smooth and unornamented; female bracteole not observed; gynoecial disc bearing about 10 archegonia. Subfloral innovations by lateral-intercalary branching from the antio-ventral end of the leaf insertion line, two or more present, rarely ventral-intercalary subfloral innovations are produced subsequent to lateral innovations; additional lateral-intercalary branches from the base of the subfloral innovation may be present; production of subfloral innovations seems curtailed by fertilisation of the gynoecium, in sporophyte-bearing plants a single innovation may subtend the perianth. Perianth wedge-shaped, 2220–2720 mm long and 1932–2628 mm wide at mouth, drooping, with prominent dorsal and ventral keels, dorsal keel with a low wing in basal half, ventral keel rounded; perianth laterally compressed, lateral walls plane; mouth bilabiate, labia curved, each with 10–17 lacinate teeth, uniseriate at apex, at least biseriate for most of their length; cells of perianth walls as for female bracts. Fertilised perianth with coelocaul precursor. Sporophytes shortly exserted, capsule short ellipsoidal, 1.2–1.5 times longer than wide; valves (5)6 stratose, epidermal layer cells largest, inner layer cells rectangular, haphazardly arranged, with 4–7 strong, regularly spaced, red-brown pigmented semi-annular bands on inner wall. Outer surface of capsule cells with irregular ornamentation. Spores and elaters not seen.

Recognition: Separating *P. deltoidea* var. *deltoidea* from the other two taxa is a challenge. Assessing the presence, or absence, of a suite of quantitative morphological characters is often necessary to achieve accurate identifications, and this can take time, and requires leaves to be dissected and slide-mounted for critical examination of micro-morphological and anatomical details, which are summarised in Table 3.

In addition to the features described in the key to taxa above, particularly those associated with the leaf vitta, *P. deltoidea* var. *deltoidea* differs from *P. deltoidea* var. *densa* in a number of features. In general aspect it is distinct in its succubously orientated, contiguous to remote leaves, whereas *P. deltoidea* var. *densa* has transversely orientated, imbricate leaves. *Plagiochila deltoidea* var. *deltoidea* is generally a larger plant than *P. deltoidea* var. *densa*. The perianth mouth of *P. deltoidea* var. *deltoidea* bears fewer, larger triangular-lacinate teeth than in *P. deltoidea* var. *densa*. The leaves of *P. deltoidea* var. *deltoidea* are succubously orientated, the leaf insertion is J-shaped, with the dorsal end postical to the ventral end, the ventral leaf insertion line is decurrent on the ventral stem surface, upon which there is a low wing of tissue. This low decurrent wing is absent from *P. deltoidea* var. *densa*, whose leaves are transversely orientated from a U-shaped insertion in which the dorsal and ventral ends often lay nearly over the top of one another. The leaves of *P. deltoidea* var. *densa* have 9–23 variably sized triangular teeth with long and short teeth admixed around the apex and on the postical margin. The leaves of *P. deltoidea* var. *deltoidea* have 14–31 smaller, evenly sized teeth.

Plagiochila deltoidea var. *deltoidea* is generally a larger plant than *P. geminata*, *P. deltoidea* var. *deltoidea* shoots are 5.0–7.3 mm wide when hydrated whereas *P. geminata* shoots are 2.7–4.7 mm wide. The leaves of *P. deltoidea* var. *deltoidea* have more teeth on their margin, 9–31 versus 2–24 on the leaves of *P. geminata*. The perianth mouth of *P. deltoidea* var. *deltoidea* has 10–17 large triangular-lacinate teeth on each labium, whereas the perianth mouth of *P. geminata* has 14–24 smaller triangular to narrow-triangular teeth on each labium. The ventral end of the leaf insertion may be decurrent in both varieties, but this is more pronounced and consistent in *P. axillaris*.

Table 3. Characters distinguishing the three taxa within *Plagiochila deltoidea*. Numbers are given as average counts, with the range in brackets.

Character	<i>Plagiochila deltoidea</i> var. <i>deltoidea</i>	<i>Plagiochila deltoidea</i> var. <i>densa</i>	<i>Plagiochila geminata</i>
Maximum shoot width	7.5	4.6	4.5
Leaf teeth number	23 (12–31)	15 (7–25)	13 (5–21)
Vitta	confined to the leaf base, not extending to close to mid-leaf, occupying the ventral half of the leaf insertion at most, never extending dorsally into the cnemis	extending to near mid-leaf leaf, and occupying more than half of the stem insertion length, often with a separate dorsal 'sub-vitta' of three or four tiers of cells extending a short distance into the leaf cnemis	confined to the leaf base, not extending to close to mid-leaf, occupying the ventral half of the leaf insertion at most, never extending dorsally into the cnemis
Leaf medial cell width (mm)	11–22	9–17	10–22
Leaf teeth number	13 (10–22)	17 (11–22)	18 (14–24)
Labium teeth	lacinate	long triangular	short triangular

Distribution and Ecology: *Plagiochila deltoidea* var. *deltoidea* is endemic to New Zealand, where it is distributed south from the Coromandel Range of the North Island, and throughout the South Island in wet forest and scrub on river terraces, gullies, faces, ridges, and mountain tops. *Plagiochila deltoidea* var. *deltoidea* grows as an epiphyte on tree trunks, and on stumps of dead trees, and has been collected in a diverse range of situations, including wind pruned scrub dominated by *Coprosma* spp., and *Melicytus ramiflorus* J.R.Forst and G.Forst.; within the interior of *Nothofagus*-podocarp forest on slopes and river terraces and within *Nothofagus* forest. *Plagiochila deltoidea* var. *deltoidea* tends to form pure or near-pure long pendulous turfs or short pendants, and occurs in association with a wide range of epiphytic bryophyte, lichen, and fern species.

Notes: The irregular ornamentation on the outer surfaces of the capsule wall cells is removed by dipping in chloroform, which is consistent with it being wax-based. Ornamentation in form of a narrow film that cracks and lifts in places, giving the capsule surface a ragged appearance.

Specimens examined: New Zealand: North Island: Whirinaki Forest Park, Waterfall Loop track near Whirinaki River, SSW of Minginui, 38°41'S 176°43'E, 380 m, J.J. Engel 20706, 30 Jan 1995 (F 1141750). South Island: Richmond Ecological Reserve, Pelorus Ecological District, Brown River Reserve on SH6 north of Rai Valley township, 41°12'37"S 173°34'46"E, 60 m, J.E. Braggins 04/055C, 28 Oct 2004 (AK 290978); Shenandoah Valley, 1 km N of Shenandoah Saddle, 32 km SSW of Murchison, 42°01'S 172°14'E, 680 m, H. Streimann 51257, 3 Feb 1993 (CANB 9306707); Waimate (Canterbury) damp bush, T.W.N. Beckett, ex herb. Levier 2792, May 1901 (G 0012195, residual syntype of *P. howeana*); Waimate (Canterbury) damp bush, T.W.N. Beckett, ex herb. Levier 1183, May 1898 (G 00121967, residual syntype of *P. howeana*); Limestone Cavern track, upper reaches of a tributary of Pig Creek, 10 km NW of Monowai Power House, 45°45'S 167°30'E, 335 m, J.A. Curnow 3556, 18 Nov 1990 (CANB 9408642).

Plagiochila deltoidea* var. *densa J.J.Engel and G.L.Merr., Nova Hedwigia 91: 506. 2010. Figs 10, 11.

Type citation: Holotype: New Zealand, South Is., Westland Prov., Westland Natl. Park, Franz Josef Glacier Valley, Roberts Point, SW of Mt. Gunn, ca. 620–670 m, Engel 18116 (F); isotype: (CHR).

Description: Plants forming long pendulous turfs or short pendants of sparingly branched leafy shoots arising from a sharply differentiated creeping, branched, system of basal stolons bearing highly reduced leaves; leafy shoots mid-green to bronze-green in life, light brown in herbarium, to 100 mm long and 2677–4651 mm wide, leafy shoots monomorphic, stature reduced at base close to stolons; flagellae absent. Branching within stolons predominantly ventral-intercalary, rarely lateral-intercalary, always giving rise to other stolons; within leafy sectors by lateral- and ventral-intercalary branching, giving rise to leafy shoots only. Stems on stolons and primary shoots in leaf sectors reddish-brown, to 280 mm diameter, transversely elliptic, surfaces smooth; cortical cells in 4 layers, cortical much smaller than medullar, with strong continuous reddish-brown thickenings on cell walls constricting cell lumina, except in a wedge of unpigmented cell walls from the ventral merophyte,

medullar cell walls with small triangular trigones at cell junctions otherwise without thickening, pale yellow pigmented; stems on leafy shoot similar without the ventral wedge of unpigmented walls and with outer walls within the medulla layer with thin continuous thickening. Rhizoids on stolons, arising in loose fascicles from the base of leaves, also scattered along the lateral and ventral stem surfaces. Leaves on leafy shoots imbricate, obliquely orientated, postically secund, deltoid, 1794–2965 mm long by 1614–2803 mm wide, transversely oriented when dry, succubously orientated when wet, dorsal margin straight, strongly recurved when dry, entire or with 1 or 2 small teeth; apex broadly rounded, postical margin broadly amplate toward base; with 7–24 narrow triangular teeth of varying size and spacing distributed from around the apex, rarely on the outer part of the dorsal margin, to the base, though teeth on the straight, basal part of the postical margin rare; teeth narrow-triangular (1–)2–9(–10) cells wide and 3–10(–20) cell tiers high, uniseriate for 2–5 cells, upper cells rectangular, capped by a single acute cell; insertion J-shaped, oblique, recurved at ventral end but not decurrent, not attaining ventral stem midline, leaving two cortical cell rows leaf-free, dorsally decurrent and attaining the dorsal stem midline, but stem visible between leaves. Marginal cells quadrate to rectangular, 8.1–11.3 mm long by 6.7–9.6 mm wide, rectangular cells have long axis parallel with margin, free external wall heavily thickened, thickening convex, bulging into cell lumen medially, not sharply differentiated from medial cells; cells in median leaf isodiametric to elliptic 8.3–23.9 mm long by 8.3–17.2 mm wide, walls with discrete convex to nodular trigones, medial wall thickenings rare, thickenings above and below trigones along junction of transverse walls with free dorsal and ventral exterior walls absent, transition to basal cells more or less abrupt, particularly dorsally where isodiametric medial cells and rectangular cells are juxtaposed, medially and ventrally transitional cells have progressively coarser trigones and longer lengths relative to width; cells in leaf base rectangular to long rectangular, 22.2–67.4(–86.2) mm long by 10.5–18.8 mm wide, trigones bulging, discrete or confluent with adjacent medial thickenings, 1 or 2 bulging medial wall thickenings present, occasionally confluent with each other and adjacent trigones; leaves on stolons remote to contiguous, appressed, ovate, unlobed but with triangular teeth. Cell surfaces smooth and unornamented. Oil-bodies not observed. Underleaves vestigial, amorphous aggregations of several cells, produced consistently on leafy sectors. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, solitary, growth of androecial branch positively geotropic, inclined downward from leafy shoot, becoming negatively geotropic at transition back to vegetative growth; repeated transition between androecia and vegetative shoots results in oscillating shoots when the androecia in *P. deltoidea* are produced in series at shoot apices, possibly as a result of fluctuating positive and negative geotropism in shoot apices producing androecia and vegetative sectors, respectively.; androecial bracts in 4–11 pairs, bract lobes orbicular, entire, margins weakly recurved toward ventral base, transversely orientated, obliquely spreading; connate across the dorsal stem surface or not, fused with the preceding bract or not; ventral leaf-free strip present, underleaves present throughout spike, small, ciliate, disc distinct; antheridia 1 per bract, stalk biseriate. Gynoeceia at apices of leafy shoots; bracts elliptic-

obovate, smaller than preceding leaves, 1696–3334 mm long by 1188–2268 mm wide; base truncate; median base inflated forming a prominent pocket; dorsal margin not reflexed, bearing 1–3 small spinose dentate teeth 2–4 cells broad at their base and 2–6 cells high, capped by a uniseriate row of 2–4 cells; apex and ventral margin lacinate, bearing 10–16 lacerate teeth, 3–14 cells broad at their base and up to 30 tiers high, radiating, more or less straight to weakly curved, separated by narrow to broad U-shaped sinus, rarely V-shaped; bract cells as for leaf cells; cell surfaces smooth and unornamented; female bracteole when present bifid, closely pressed against the prominent, rounded, protruding ventral perianth keel; gynoeceal disc bearing about 10 archegonia. Subfloral innovations by lateral-intercalary branching from the antio-ventral end of the leaf insertion line, two or more present, rarely ventral-intercalary subfloral innovations are produced subsequent to lateral innovations; additional lateral-intercalary branches from the base of the subfloral innovation may be present; production of subfloral innovations seems curtailed by fertilisation of the gynoeceum, in sporophyte-bearing plants a single innovation may subtend the perianth; in contrast, proliferation of subfloral innovations and repeated pulses of synchronous gynoeceum production by each shoot may result in a flabellate shoot system in female plants whose gynoecea are not fertilised. Perianth campanulate when immature and unfertilised, elliptic-oblong, 2738–3548 mm long and 2113–2660 mm wide at mouth, drooping, with prominent wing on basal half of dorsal and ventral keels, dorsal keel curved at base and longer than ventral; laterally compressed except near base, lateral walls plane; mouth bilabiate, labia curved, each with 11–22(–27) long triangular teeth, uniseriate in upper half, biseriate in lower half and 3 or 4 cells wide at base; cells of perianth walls as for female bracts. Fertilised perianth with coelocaul precursor, calyptral perigynium present, archegonia elevated on surface around base. Sporophytes shortly exerted or not, capsule short ellipsoidal, 1.2–1.5 times longer than wide; valves 5 or 6 stratose, epidermal layer cells 9.6–12.8 mm deep, inner layers cells 5.2–7.9 mm deep; inner layer cells elongate, tapering, haphazardly arranged, with 5–9 brown-pigmented semiannular bands on inner cell wall, confluent along the upright cell walls. Spores 11.5–14.3 mm diameter, 2-celled when released from dehiscent capsule, with stout echinate ornamentation.

Recognition: *Plagiochila deltoidea* var. *densa* can be recognised by the characters given in the key to taxa above, including the smaller leaf lobe cells, which is one of the distinctive features of this taxon (Fig. 12). For characters separating *P. deltoidea* var. *densa* from *P. deltoidea* var. *deltoidea*, see the recognition section of the latter, above. *Plagiochila deltoidea* var. *densa* tends to have more closely spaced leaves than *P. geminata*. When dry the leaves of *P. deltoidea* var. *densa* remain transversely orientated, plane, and obscure the stem in lateral view. In contrast, the leaves of *P. geminata* become tightly rolled when dry so that the stem is clearly visible from all sides. The perianth mouth has narrowly triangular teeth tapering to a long uniseriate apex up to 10 cells long in *P. deltoidea* var. *densa*, and has broadly triangular teeth dentate that narrow to a sharp point, uniseriate for two cells, and up to five cells in *P. geminata*. The leaves of *P. deltoidea* var. *densa* are ovate-elliptic except small leaves that can be obovate, while in *P. geminata* the leaves are ovate tending elliptic when small. Large leaves of both species are nearly the same shape except that the dorsal margin in *P. deltoidea* var. *densa* is straight,

whereas in *P. geminata* it is often shallowly convex. Although observations of sporophytes are limited, there are differences between *P. deltoidea* var. *densa* and *P. geminata* in the patterns of secondary thickening in the inner cell layer of the capsule valve. In *P. deltoidea* var. *densa* the inner cells bear strong, complete and regularly spaced semi-annular thickenings, whereas in *P. geminata* the semi-annular thickenings are weak, taper toward the cell middle and may be incomplete, often bifurcate, and are irregularly spaced and arranged.

Variation: Within *P. deltoidea* var. *densa* there is variation in the stature of male plants. Most male plants are smaller than female plants, but three collections (F1140885 and F1141063, and one in NSW) are of male plants as large and robust as females. All three collections were from upper montane forests, the first two from the mountains of the central South Island, the third from Waikaremoana.

Female bracts exhibit variation in size and dentition that may cause confusion. Usually leaves and bracts increase in size toward the gynoeceum, so that the female bracts are the largest 'leaves' on the shoot. In some instances though, the female bracts closest to the gynoeceum are around half the area of the previous leaf pair, which are the largest. The dentition of these half-sized bracts is particularly coarse, thus their overall appearance is rather different from normal bracts. Variation in bract stature can be observed within individuals. There is also variation in the size and number of teeth on perianth labia, with one specimen (F1141748) having as many as 28 narrow triangular teeth on each labium. More typical specimens have fewer, larger teeth that are often curved.

Branch types are fairly consistent, but in one instance a lateral intercalary vegetative branch was observed from which issued a positively geotropic stolon of ventral-intercalary origin, in the manner similar to the branching within *Chistocaulon dendroides*.

Leaf cells in *Plagiochila deltoidea* var. *densa* are smaller than in the other two varieties, which was the basis for the recognition of *P. deltoidea* var. *densa* J.J.Engel and G.L.Merr. While there is greater variation in cell size than reported by Engel and Merrill (2010) within *P. deltoidea* var. *densa*, and consequently more overlap with the cell sizes observed in the other two varieties, the smaller leaf cells of *P. deltoidea* var. *densa* stand as one of the most distinctive features of the taxon.

The dimensions of medial cells measured here differ in range from those reported by Engel and Merrill (2010). This difference may be explained by the fact that the size of medial cells size increases progressively from the leaf margin to the end of the vitta. In this study cell sizes were measured halfway between the end of the vitta and the leaf apex, which may not be the same location from which previous measurements were made. Other studies may have measured cells from the middle of the leaf, but the varying length of the vitta among species in combination with the trend for decreasing cell size, will mean that measured cell sizes will be larger at mid-leaf, and hence larger than the range reported in this study. Having a standardised point of location is an important element of accommodating the variation in cell size from the base to the apex of the leaf, and the influence of vitta length on the realised patterns within and among species.

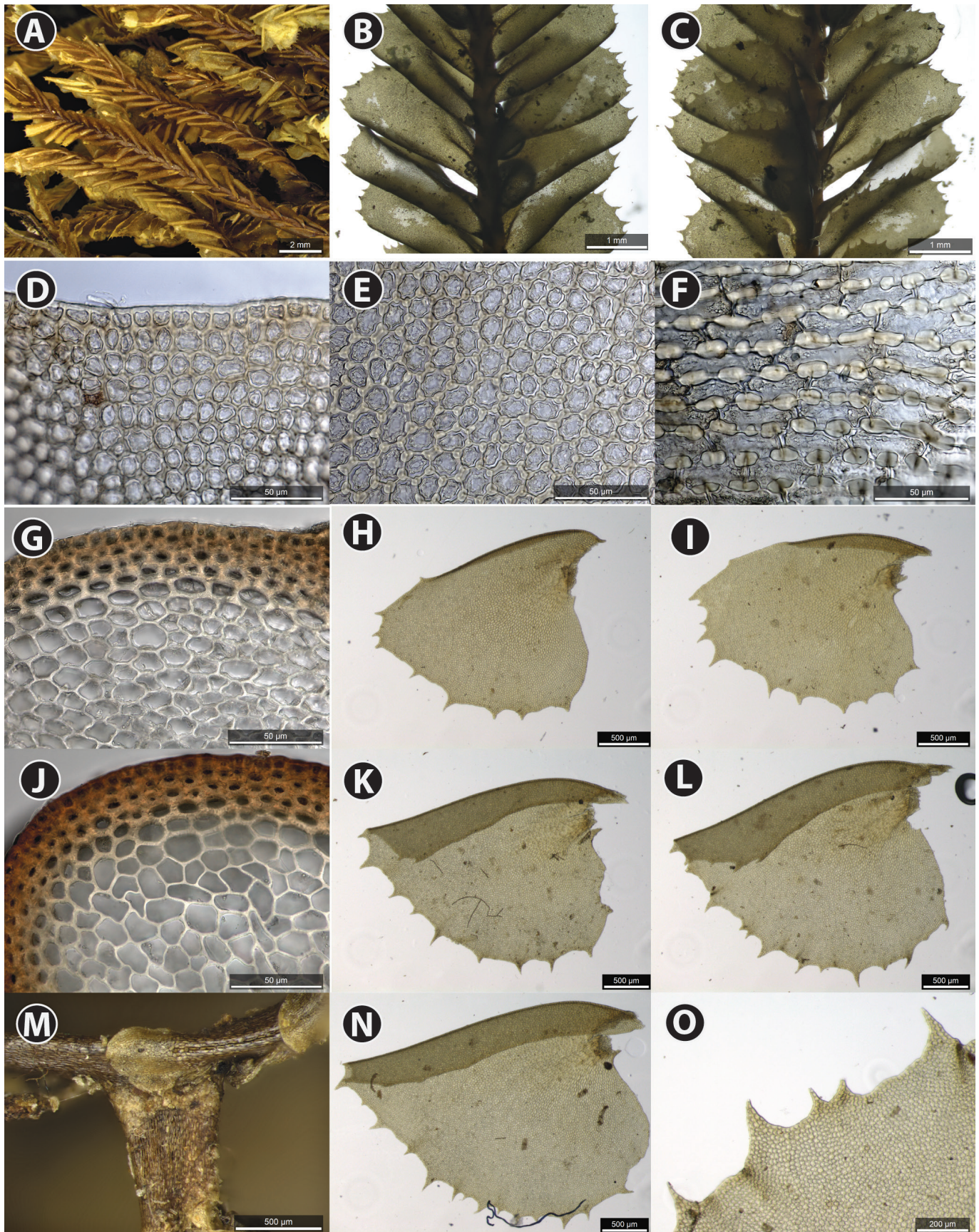


Figure 10. *Plagiochila deltoidea* var. *densa*. A. Habitus, dried. B. Shoot in dorsal view. C. Shoot in ventral view. D. Leaf marginal cells. E. Leaf medial cells. F. Leaf basal cells. G. Transverse section of leafy shoot stem. H, I, K, L, N. Primary shoot leaves. J. Transverse section of stolon stem. M. Ventral-intercalary stolon. O. Leaf margin. A, D–F, H, I, K–O from AK287128; B, C from NSW899342; G, J from F1141080.

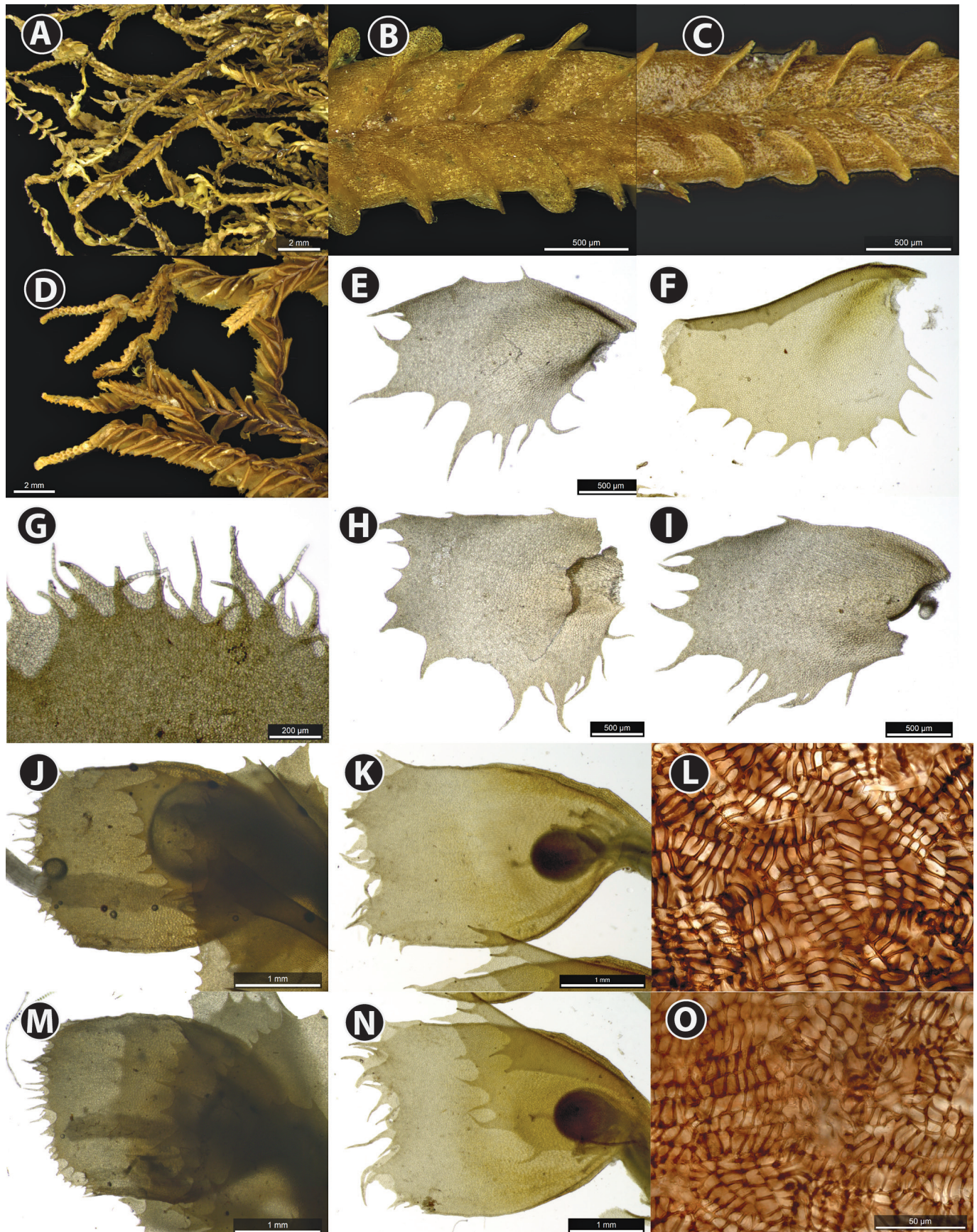


Figure 11. *Plagiochila deltoidea* var. *densa*. A. Habitus, small male plants. B. Androecia in ventral view. C. Androecia in dorsal view. D. Habitus, large male plants. E, F. Female bracts. G. Perianth mouth. H, I. Female bracts. J, K, M, N. Perianths in lateral view. L, O. Innermost capsule valve cell layer ornamentation, viewed with interior surface uppermost. A from F1141064; B–D from F1140885; E, G–I from NSW899342; F, K from F1141724; J, L, M, O from AK287128; N from F1141748.

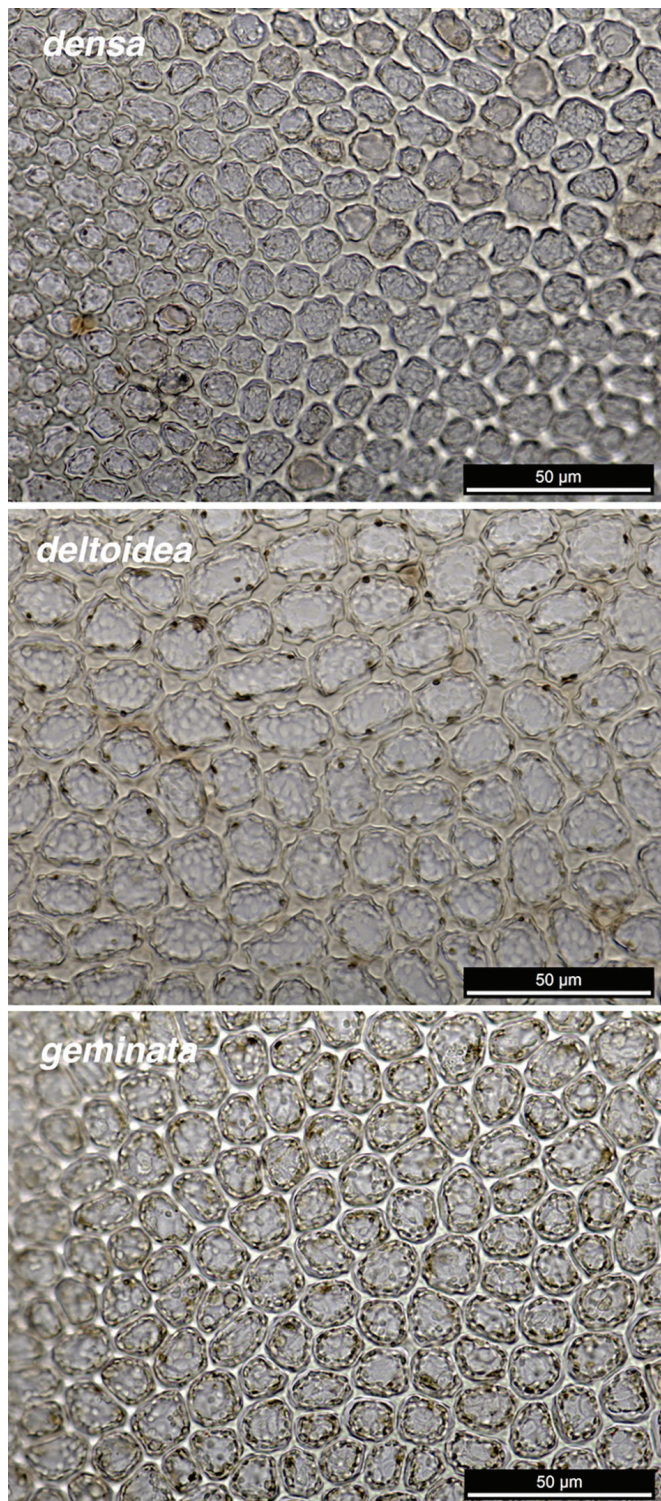


Figure 12. Comparison of medial leaf lobe cells in representative examples of *Plagiochila deltoidea* var. *densa* (F1141064) *P. deltoidea* var. *deltoidea* (CANB9708642) and *P. geminata* (AK327793).

Distribution and Ecology: *Plagiochila deltoidea* var. *densa* is endemic to New Zealand, where it occurs south from the Coromandel Range in the North Island, throughout the South Island, and east to the Chatham Islands. *Plagiochila deltoidea* var. *densa* grows in beech forests and podocarp-broadleaf forests, within which it occupies a wide variety of microsites, including tree trunks, tree branches, soil on banks of mossy stream-sides, raised areas on the forest floor, and within bryophyte turfs on steep slopes.

Specimens examined: New Zealand: North Island: Lake Waikaremoana, E.A. Hodgson, 10 Feb 1936 NSW; Tongariro National Park, Central Plateau, Ruapehu, Mangawhero River catchment, Ohakune Mountain Road, 1048 m, M.A.M. Renner 6780, 23 Nov 2013 (NSW 899341); *ibid.*, M.A.M. Renner 6776b, 23 Nov 2013 (NSW 899342); Urewera National Park, crest trail from Highway 38 towards Whakataka summit, N of northern extremity of Lake Waikaremoana, 38°42'S 177°03'E, 930–1030 m, J.J. Engel 20652, 29 Jan 1995 (F 1141748); Urewera National Park, Panekiri Range, summit area of Pukenui in vicinity of Pukenui Bluff, S of Lake Waikaremoana, 38°47'S 177°04'E, 1180 m, J.J. Engel 23325, 24 Mar 1997 (F 1141064); *ibid.*, J.J. Engel 23329, 24 Mar 1997 (F 1141186); Urewera National Park, Huiairau Range, summit area of Te Rangaakapua, 38°33'S 177°13'E, 1265–1320 m, J.J. Engel 23428, 25 Mar 1997 (F 1141729). South Island: North West Nelson Ecological Region, Arthur Ecological District, start of track to Harwoods Hole, 40°56'37"S 172°53'22"E, 740 m, J.E. Braggins 04/092A, 30 Oct 2004 (AK 290693); North Westland Ecological Region, Blackball Ecological District, Sewell Peak, in *Nothofagus* forest near top of road to first peak, 42°24'32"S 171°20'24"E, 780 m, J.E. Braggins, 6 Dec 2000 (AK 287128); Nova Zelandia, ins. merid. Westland, Kelly's Range, Bruce's Creek, T.W.N. Beckett, det. F. Stephani n.4348, 30 Jan 1903 (M); Nelson Province, Nelson Lakes National Park, off Lakehead Track near junction with southern end of Loop Track, NE of Lake Rotoiti, SSE of St. Arnaud, 41°49'S 172°51'E, 630 m, J.J. Engel 22727, 1 Mar 1997 (F 1141080); Arthurs Pass National Park, Bridal Veil Track, E side of Bealey River and just N of town of Arthurs Pass, 42°56'S 171°33'E, 760–825 m, J.J. Engel 22920, 7 Mar 1997 (F 1140885); Mt Cook National Park, Governors Bush, SW of town of Mt Cook, 43°44'S 170°05'E, 760–800 m, J.J. Engel 18207, 1 Jan 1983 (F 1141063).

Plagiochila geminata M.A.M. Renner, sp. nov. (Figs 13, 14)

Type: New Zealand: North Island: Te Pahi, Radar Bush, 34°28'03"S 173°51'15"E, 160 m, P.J. de Lange 9989 & M.A.M. Renner, 19 Sep 2011 (holotype: AK 327793)

Diagnosis: Similar to *Plagiochila deltoidea* var. *deltoidea* in having leaves succubously inserted and orientated that are remote when dry; however *P. geminata* is a smaller plant with shoots 2.7–4.7 mm wide when hydrated, the leaves bear 5–21 teeth (average ~13), and the perianth bears 14–24 (average 18) triangular to narrow triangular teeth on each labium; in contrast *P. deltoidea* var. *deltoidea* is a large plant with shoots 5.0–7.3 mm wide when hydrated, the leaves bear 9–31 teeth (average ~22), and the perianth bears 10–17 (average 13) lacerate teeth on each labium.

Description: Plants forming long pendulous turfs or short pendants of sparingly branched leafy shoots arising from a sharply differentiated creeping, branched, system of basal stolons bearing highly reduced leaves; leafy shoots mid-green to bronze-green in life, light brown in herbarium, to 70 mm long and 1850–3400 mm wide, leafy shoots monomorphic, stature reduced at base close to stolons; flagellae absent. Branching within stolons predominantly ventral-intercalary, rarely

lateral-intercalary, always giving rise to other stolons; within leafy sectors by lateral- and ventral-intercalary branching, giving rise to leafy shoots only. Stems on stolons and primary shoots in leaf sectors reddish-brown, to 280 mm diameter, transversely elliptic, surfaces smooth; cortical cells in 4 layers, cortical much smaller than medullar, with strong continuous reddish-brown thickenings on cell walls constricting cell lumen, except in a wedge of unpigmented cell walls from the ventral merophyte, medullar cell walls with small triangular trigones at cell junctions otherwise without thickening, pale yellow pigmented; stems on leafy shoot similar without the ventral wedge of unpigmented walls and with outer walls within the medulla layer with thin continuous thickening. Rhizoids on stolons, arising in loose fascicles from the base of leaves, also scattered along the lateral and ventral stem surfaces. Leaves on leafy shoots remote when dry, contiguous when wet, postically secund, broadly ovate to subdeltoid, 1858–3224 mm long by 1376–2286 mm wide, succubously orientated when dry or wet, dorsal and ventral margins strongly inrolled when dry, dorsal margin straight to weakly curved, entire; apex broadly rounded, postical margin shallowly curved in outer half then ampliate in basal half; with 5–21(–24) triangular to narrow-triangular teeth of varying size but fairly even spacing distributed from the apex to the basal quarter of the postical margin, teeth on the basal part of the postical margin rare; teeth triangular (1)2–5(–8) cells wide and 3–10(–12) cell tiers high, uniseriate for 2–5 cells, upper cells quadrate to rectangular, capped by a single rounded to acute cell; male plants with stronger leaf-dentition than female plants; insertion J-shaped, oblique, recurved at ventral end but not decurrent, not attaining ventral stem midline, leaving two cortical cell rows leaf-free, dorsally attaining the stem midline but not decurrent, stem visible between leaves. Marginal cells short-rectangular or quadrate, 11.7–18.2 mm long by 9.8–16.3 mm wide, long axis parallel with margin, free external wall heavily thickened, thickening convex, bulging into cell lumen medially, not sharply differentiated from medial cells; cells in median leaf isodiametric to broadly elliptic, 13.0–24.3 mm long by 10.0–21.6 mm wide, walls with discrete convex to nodular trigones, medial wall thickenings rare, thickenings above and below trigones along junction of transverse walls with free dorsal and ventral exterior walls absent, transition to basal cells more or less abrupt, particularly dorsally where isodiametric medial cells and rectangular cells are juxtaposed, medially and ventrally transitional cells have slightly coarser trigones and longer lengths relative to width; cells in leaf base rectangular to long rectangular, 28.0–54.0 mm long by 16.5–22.6 mm wide, trigones nodular discrete, not confluent with adjacent medial thickenings, 0 or 1 medial wall thickenings present; leaves on stolons remote, appressed, ovate, unlobed, entire. Cell surfaces smooth and unornamented. Oil-bodies not observed. Underleaves vestigial, several cells forming low fused ciliate projections, produced consistently on leafy sectors. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, solitary, growth of androecial branch positively geotropic, inclined downward from leafy shoot, becoming negatively geotropic at transition back to vegetative growth; repeated transition between androecia and vegetative shoots results in oscillating shoots; androecial bracts in 10–16 pairs, bract lobes orbicular, entire, margins weakly recurved toward ventral base, transversely orientated, obliquely spreading; a single spinose tooth present at base of antical

lobe margin at the stem insertion, stem insertion apparently leaving a dorsal leaf-free strip, unbroken line of dorsal stem visible between male bracts; underleaves present throughout spike, small, few-celled, disc indistinct, lobes ciliate; antheridia 1 per bract, stalk biseriate. Gynoecia at apices of leafy shoots; bracts ovate, larger than preceding leaves, 2147–2650 mm long by 1722–2398 mm wide (including teeth); base truncate; median base not or weakly inflated but not forming a prominent pocket; dorsal margin strongly reflexed, bearing 1–3 small triangular teeth 2–4 cells broad at their base and 2–6 cells high, capped by a uniseriate row of 2–4 cells; apex and ventral margin lacinate, bearing 12–22 triangular teeth, up to 12 cells broad at their base and up to 15 tiers high, radiating, separated by broad U-shaped sinus; bract cells as for leaf cells; cell surfaces smooth and unornamented; female bracteole when present deeply bifid, lobes ciliiform, against the prominent, rounded, protruding ventral perianth keel; gynoecial disc bearing about 10 archegonia. Subfloral innovations by lateral-intercalary branching from the antico-ventral end of the leaf insertion line, two or more present, rarely ventral-intercalary subfloral innovations are produced subsequent to lateral innovations; additional lateral-intercalary branches from the base of the subfloral innovation may be present; production of subfloral innovations seems curtailed by fertilisation of the gynoecium, in sporophyte-bearing plants a single innovation may subtend the perianth; in contrast, proliferation of subfloral innovations and repeated pulses of synchronous gynoecium production by each shoot may result in a flabellate shoot system in female plants whose gynoecia are not fertilised. Perianth wedge-shaped, 3112–3292 mm long and 2551–2810 mm wide at mouth, drooping, with prominent dorsal and ventral keels, dorsal keel with a low wing in basal half, ventral keel rounded; perianth laterally compressed, lateral walls plane; mouth bilabiate, labia curved, each with (14–)16–24 triangular to narrow-triangular teeth, uniseriate toward apex, at least biseriate for most of their length; cells of perianth walls as for female bracts. Fertilised perianth with coelocaula precursor. Sporophytes shortly exserted, capsule short ellipsoidal, 1.2–1.5 times longer than wide; valves 6 stratose, epidermal layer cells 10.5–16.4 mm deep, others 3.8–6.6 mm deep; inner layer cells rectangular, haphazardly arranged, with semi-annular bands on inner wall weak, often incomplete, and irregular, red-brown-pigmented. Spores 2-celled at capsule dehiscence, ellipsoidal, 16.2–21.1 mm on longest axis with low, sparse aculeate to tuberculate ornamentation.

Etymology: *geminata* (adj.) twinned, in reference to its resemblance to *P. deltoidea* var. *densa*.

Notes: Teeth on perianth mouth are variable among and within individuals, from triangular to narrow triangular.

Recognition: *Plagiochila geminata* is similar to *P. deltoidea* var. *densa*, and the two taxa overlap in some important characters such as leaf shape and dentition. Differences between these two taxa are subtle and may be inconsistent, so all available features must be considered to achieve an identification. For details on recognition of *P. geminata*, see the treatments of *P. deltoidea* var. *deltoidea*, and *P. deltoidea* var. *densa* above.

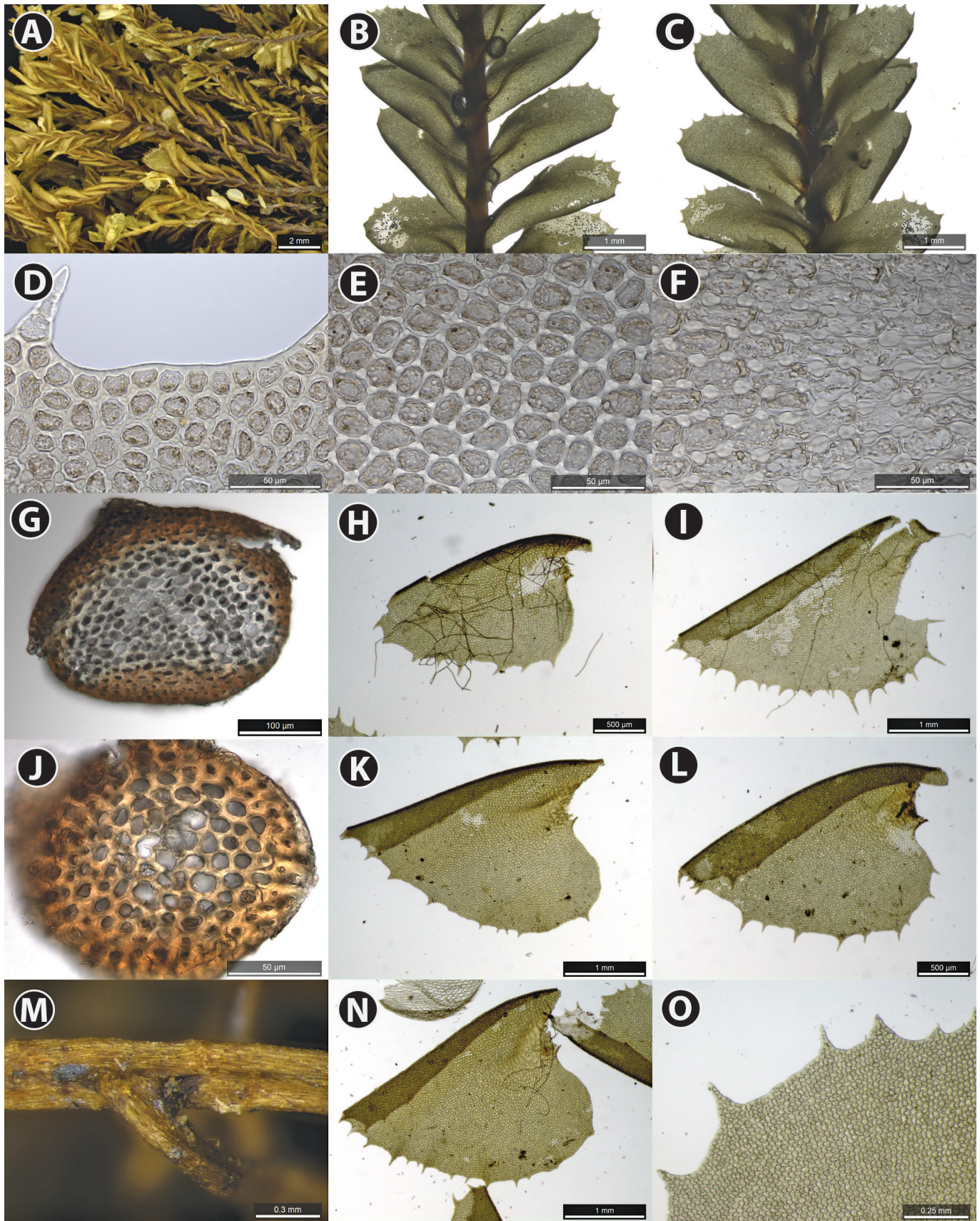


Figure 13. *Plagiochila geminata*. A. Habitus, dried. B. Shoot in dorsal view. C. Shoot in ventral view. D. Leaf marginal cells. E. Leaf medial cells. F. Leaf basal cells. G. Transverse section of leafy shoot stem. H, I, K, L, N. Primary shoot leaves. J. Transverse section of stolon stem. M. Ventral-intercalary stolon. O. Leaf margin. A–C, G–L, N from F1141749, D–F, M, O from AK298125.

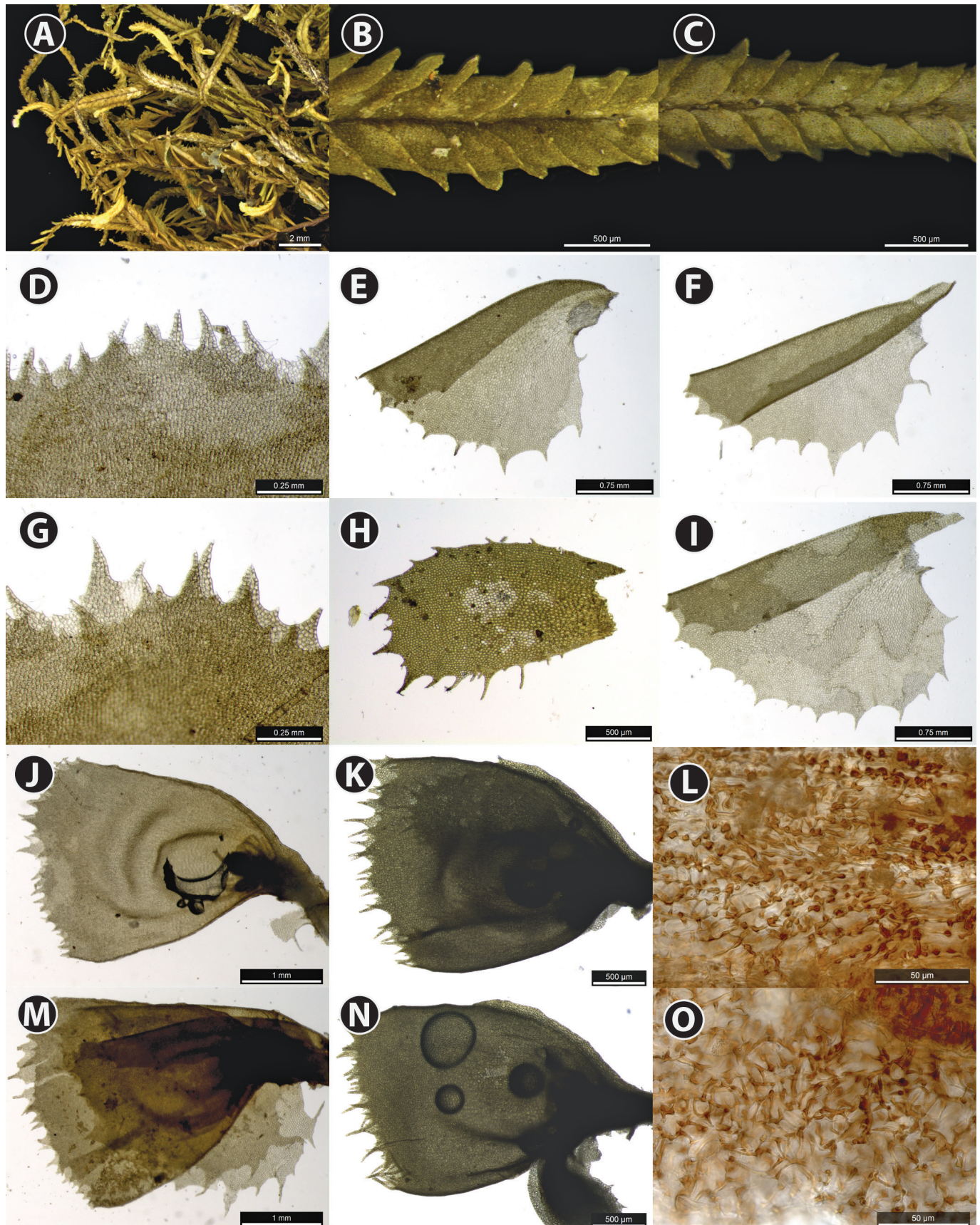


Figure 14. *Plagiochila geminata*. A. Habitus, male plants. B–C. Androecia in ventral view. D, G. Perianth mouth. E, F. Female bracts. H, I. Female bracts. J, K, M, N. Perianths in lateral view. L, O. Innermost capsule valve cell layer ornamentation, viewed with interior surface uppermost. A–C, K, N, from F1141788; D–J, L, M, O from AK298125.

Distribution and ecology: *Plagiochila geminata* is endemic to New Zealand, where it is known from the northernmost North Island from the Auckland Region, including the islands of the Hauraki Gulf, north to the northern tip of the Aupouri Peninsula, and east to the Chatham Islands. *Plagiochila geminata* grows as an epiphyte on tree trunks, on decaying logs, and as a lithophyte on basalt and breccia. It has been collected as a trunk epiphyte within forests with a strong broadleaf component, including dense podocarp-broadleaf forest with *Agathis* Salisb., *Halocarpus* Quinn, and *Kunzea* Rchb. at Radar Bush; broadleaf forest with *Beilschmiedia* Nees, *Vitex* L., and *Hoheria* A.Cunn. in a steep sided valley at Herekino; *Metrosideros* Banks ex Gaertn. on Rangitoto; and *Coprosma chathamica* Cockayne, *Dracophyllum* Labill. and *Myrsine chathamica* F.Muell. forest on Chatham Island. *Plagiochila geminata* grows on living and dead broadleaf and treefern trunks, including *Cyathea dealbata* (G.Forst.) Sw.

Specimens examined: New Zealand: North Island: Radar Bush, WSW of Cape Reinga, S of Mt Te Paki, 34°28'S 172°46'E, 100 m, J.J. Engel 20837, 6 Feb 1995 (F1141749); Northern edge of Herekino Forest S of quarry, Kiwanis Reserve, junction of Okahu Stream and unnamed stream, c 5 miles S of Kaitaia, 35°10'S 173°16'E, 60–80 m, J.J. Engel 20913, 7 Feb 1995 (F 1141788); Western Northland Ecological Region, Hokianga Ecological District, Okahau, 35°19'S 173°46'E, H.B. Matthews 315a, Nov 1925 (AK18808); Whangarei, Mt Manaia, base of peak down, 35°49'S 174°31'E, J.E. Braggins s.n., 7 Jul 1980 (AK320980); Hauraki Gulf, Little Barrier Island, track 18, just N of Mt Whেকauwhেকau, 36°14'S 175°6'E, J.E. Braggins 80/733 & R.E. Beever, 26 Jan 1980 (AK322142); Little Barrier Island, East Cape hut, 36°12'S 175°6'E, 6 m, J.E. Braggins 80/411b & R.E. Beever, 24 Jan 1980 (AK322147); Little Barrier Island, summit track, 36°12'S 175°4'E, 460 m, J.E. Braggins 82/243b, 15 Jun 1984 (AK322137); Rangitoto Island, along track to base of cone, J.E. Braggins 84/314c, 21 Jul 1984 (AK293689); Hunua Ranges, catchment behind Milnes Creek, 37°7'S 175°10'E, W.B. Sylvester, 22 Apr 1972 (AK313292); Chatham Islands: Rekohu, Alfred Preece farm, east of Rangaika Reserve, 44°04'04"S 176°25'00"W, R.E. Beever and J.E. Beever 108-14c, 6 Jan 2007 (AK 298125).

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