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A SYNOPSIS OF AOTEAROA/NEW ZEALAND *LEJEUNEA* (LEJEUNEACEAE: JUNGERMANNIOPSIDA) AND NEW SPECIES IN THE *LEJEUNEA EPIPHYLLA* COLENSO COMPLEX

ОБЗОР РОДА *LEJEUNEA* (LEJEUNEACEAE: JUNGERMANNIOPSIDA) В АОТЕАРОА/НОВОЙ ЗЕЛЕНДИИ, С НОВЫМИ ВИДАМИ ИЗ КОМПЛЕКСА *LEJEUNEA EPIPHYLLA* COLENSO

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Abstract

We present a summary of the Aotearoa/New Zealand *Lejeunea* flora in a synopsis covering 21 species, 19 of which have been, or are here, formally described and two tag-named. Four species are described as new (*L. amphinephea* M.A.M.Renner*, L. demissa* M.A.M.Renner*, L. perichymidia* M.A.M.Renner and *L. thalassoides* M.A.M.Renner & Glenny) all have been previously treated as a complex under the illegitimate name *Lejeunea epiphylla* Colenso. These four species exhibit complicated patterns of morphological variation and overlap in both size and shape as has been quantified in other liverwort species complexes. *Lejeunea hawaikiana* is proposed as a new synonym of *L. apiculata*, while *Lejeunea gracilipes* is retained at species rank. The 21 species comprise nearly the entire Aotearoa/New Zealand *Lejeunea* diversity, but at least two other entities not encompassed by our synopsis are known from the North Cape region, and their affinities and identity remain to be resolved. The aim of this synopsis is to formally document our current state of knowledge regarding New Zealand *Lejeunea*, to pave the way for a full resolution of the diversity of this genus in Australasia.

Резюме

Приводится конспект флоры рода *Lejeunea* Аотеароа/Новой Зеландии, включающий ключ для определения видов, детальные описания морфологии, диагностические признаки, распространение, экологию, рисунки 19 описанных видов и 2 таксонов, намеченных к описанию. Четыре вида описаны как новые для науки (*L. amphinephea* M.A.M.Renner*, L. demissa* M.A.M.Renner*, L. perirothidia* M.A.M.Renner и *L. thalassoides* M.A.M.Renner & Glenny). Эти виды представляют собой сложный комплекс морфотипов форм, перекрывающихся как по размерам, так и форме, что нередко встречается и в других группах печеночников. Ранее эта группа рассматривались как комплекс под незаконным названием *Lejeunea epiphylla* Colenso*. Lejeunea hawaikiana* предлагается в качестве нового синонима *L. apiculata*, в то время как *L. gracilipes* сохраняется в ранге вида. Двадцать один вид включает почти все разнообразие рода в Новой Зеландии, однако, по крайней мере два других вида, не охваченных этим кратким обзором, известны из региона Нордкап, их родство и идентичность еще предстоит выяснить. Данный краткий обзор отражает настоящее состояние знаний о роде *Lejeunea* в Новой Зеландии и является основой для дальнейшего изучения этого рода в Австралазии.

KEYWORDS: liverworts, new species, new synonyms, biodiversity

Introduction

The Lejeuneaceae is the largest family of leafy liverwort, comprising more than 1500 species in around 72 genera (Gradstein, 2020), though this number remains in a state of limited flux as a result of the recognition of phylogenetic novelties (Zhu *et al.,* 2017*,* 2018a,b, 2019), and the reduction of others in response to novel phylogenetic insights (Renner & de Lange, 2020). *Lejeunea* Lib. may be the second largest genus within the Lejeuneaceae, after *Cololejeunea* (Spruce) Steph., with c. 500 species worldwide (including *Taxilejeunea* (Spruce) Steph.) (Söderström *et al.,* 2016). *Lejeunea* exhibits high species richness in wet tropical regions, and a Neotropical origin for the genus has been inferred (Heinrichs *et al.,* 2013; Lee *et al.,* 2020). No comprehensive review of *Lejeunea* has ever been undertaken for New Zealand, though recent studies informed by molecular data suggest that New Zealand has a distinct, if not overly diverse, suite of *Lejeunea* species with levels of endemism comparable with the liverwort flora as a whole (Renner *et al.,* 2009a, 2011). Currently 16 *Lejeunea* species are recognized from New Zealand, of which 8 are endemic.

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The Lejeuneaceae is one of the more challenging leafy liverwort families with regards species circumscription and identification. Complicated patterns of morphological variation have contributed to a long history of confusion among species, both in New Zealand and overseas (Renner *et al.,* 2010, 2013), such that Lejeuneaceae diversity within New Zealand is incompletely documented and, compared to other diverse families, such as the Lophocoleaceae, Lepidoziaceae, or Radulaceae, the Lejeuneaceae is relatively understudied. Over the past two decades several publications have tackled species circumscription issues on a case by case basis, both in response to discovery of genuine novelties (Glenny, 1996; Glenny & Renner, 2019; Renner, 2010; Renner & de Lange, 2020), and in an effort to resolve more challenging species (Renner *et al.,* 2010, 2011, 2013; Beveridge & Shepherd, 2019; Beveridge *et al.,* 2019). In particular, quantitative studies have shed light on what constitutes patterns and parameters of morphological variation that are significant for species circumscription, and have produced a body of empirical evidence that addresses directly the underlying structural factors contributing to morphological variation, which underpin the challenging nature of the Lejeuneaceae (Renner *et al.,* 2013). As such, we are now better able to understand and explain patterns of morphological variation in terms of the underlying hierarchy of contributing factors, from intra-individual plasticity to inter-species difference, to the benefit of our species circumscriptions. This was not always the case, and historically variation among herbarium specimens was often attributed to environmentally induced inter-individual variation, an explanation that often neglected an absence of supporting experimental evidence for such an explanation and which, in a herbarium setting, overlooked the fact that each observation of morphological variation is confounded by genotype, given each herbarium specimen comprises a different individual.

Within New Zealand *Lejeunea*, some species such as *L. exilis* (Reinw., Blume & Nees) Grolle, *Lejeunea flava* (Sw.) Nees and *L. gracilipes* (Taylor) Spruce comprise homogeneous and discrete morphological entities, whose circumscription is without dispute. Others such as *Lejeunea tumida* Mitt. and *L. epiphylla* Colenso have been, or still are, morphologically heterogeneous species, which reflects more our lack of understanding than underlying reality. What was *Lejeunea tumida* now comprises four species in two separate lineages (Renner *et al.,* 2010, 2011), all of which are endemic to Aotearoa/New Zealand. Another problematic species is *Lejeunea epiphylla* Colenso which, though an 'accepted' name in common use in New Zealand and Australia, is an illegitimate later homonym of *Lejeunea epiphylla* Mitt.

Colenso's (1888) protologue of *Lejeunea epiphylla* provides little in the way of distinctive detail, which is not a deficiency in Colenso's descriptive capacity, rather it is a reflection on the characters manifest in the plants comprising his type. Colenso's description could apply equally well to any species with sessile, pentacarinate perianths and large ovate underleaves. As a result, the name *Lejeunea epiphylla* Colenso has been applied to a range of plants that do not have tumid perianths or conspicuous granular leaf cell surface ornamentation. Plants conforming to this rather loose operational circumscription occupy a wide range of microsites including soil, rock including basalt, limestone and calcareous mudstone, tree trunks, branches, and leaves and fronds of a range of vascular plant species including *Beilschmiedia* Nees and *Hymenophyllum* Sm., and occur from Northland to the Auckland Islands, and west to Tasmania. Not surprisingly given this breadth of microhabitat diversity, plants currently attributed to *Lejeunea epiphylla* Colenso comprise a range of morphologies, two of which are actually admixed on the *Hymenophyllum demissum* (G.Forst.) Sw. fronds within Colenso's type specimen. One of these has ovate-triangular leaf lobes, and lobules with a two-celled first lobule tooth, the other has rotund leaf lobes and a one-celled first lobule tooth. There are other differences in underleaf size and shape, all of which are consistent within shoots. Other forms are correlated with microsite and substrate, plants found on calcareous or basalt rocks also have triangular ovate leaf-lobes, but unlike the plant in Colenso's type produce stipitate perianths on short lateral branches, whose subfloral innovations are reduced in stature. Another form with large inflated lobules, underleaves with a broad sinus, and long-stipitate perianths occurs on Auckland Island.

We have collected *Lejeunea epiphylla* Colenso throughout New Zealand, and examined herbarium material from Australia and New Zealand. Though the set of herbarium specimens of this species are variable in form and expression, consistent correlations in character expression and microsite occupancy lead us to hypothesize that *Lejeunea epiphylla* Colenso comprises four species. As far as we can ascertain from study of type specimens in Geneva (G), Natural History Museum, London (BM), Te Papa Tongarewa (WELT), and Farlow Herbarium (FH), no other names are available for any of these four species. That diversity within the *Lejeunea epiphylla* Colenso complex has been overlooked for so long reflects the conjunction of a number of historical factors coupled with difficulties intrinsic to the plants themselves. These problems, involving morphological continuity and overlap among species, and preservation of historical ontological variation in contemporary form have been described previously (Renner *et al.,* 2013).

Collecting effort in under-explored habitats, particularly the north of Te Ika a Maui/the North Island, and offshore islands, continues to add species to the New Zealand bryophyte flora. In this paper we present, but do not formally describe, a fifth new species which has been confused with *Lejeunea primordialis* (Hook.f. & Taylor)

Gottsche, Lindenb. & Nees. This new tag-named entity occurs as a trunk epiphyte in lowland forests of Te Ika a Maui/the North Island. It is often found on pűriri (*Vitex lucens* Kirk) trunks and branches. We do not formally describe this plant because Covid-19 and the move of the NSW herbarium have prevented the first author from accessing material for formal description. We also present a synopsis whose aim is to summarise current knowledge of this diverse genus in New Zealand. We provide a key to the 21 *Lejeunea* species, including 19 formally described and two tag-named species currently recognized for New Zealand. Four of these species are newly described; the remaining 15 have been previously documented from New Zealand in published literature. The aim of this synopsis is to communicate current knowledge of this challenging genus, to pave the way for future discoveries of new species and new records that will complete our understanding of the diversity of this predominantly tropical lineage in southern temperate Australasia. A with some other predominantly tropical Lejeuneaceae lineages, there appears to be a strong southern temperate Australasian endemic element to New Zealand's *Lejeunea* flora (Renner & de Lange, 2020), alongside other tropical components.

We dedicate this synopsis to the late Prof. Rudolph Mathias Schuster, who applied his intuitive understanding of variation to the resolution of challenging species complexes in a range of New Zealand liverwort genera, coupling that understanding with a sound understanding of morphology, anatomy, and homology and an unmatched illustrative prowess.

MATERIAL AND METHODS

Grouping individuals

Character analysis identified qualitative morphological differences among individuals of the *Lejeunea epiphylla* Colenso complex that circumscribed four morphological groups (Table 1). These groups form the basis for our investigation of the partitioning of morphological variation.

Morphometric data

Morphometric data was collected from 24 specimens from Tasmania and New Zealand that encompassed the range of geographic and morphological variation expressed by *Lejeunea epiphylla.* Eleven to fifteen shoots from each specimen were removed and soaked at room temperature in lactic acid for 2h (Zander, 1997) to partially clear cell contents, after which they were slide-mounted with the ventral side uppermost in glycerol/glycerine. For each specimen, 19 lobule pairs and associated leaves were selected haphazardly from mature shoot sectors – two or three leaf pairs below the shoot apex – to avoid ontogenetic effects. Nine were on different shoots, and 10 on another haphazardly selected shoot, making a total of 10 modules from the same shoot, and 10 modules from different shoots per individual, with one module filling both categories.

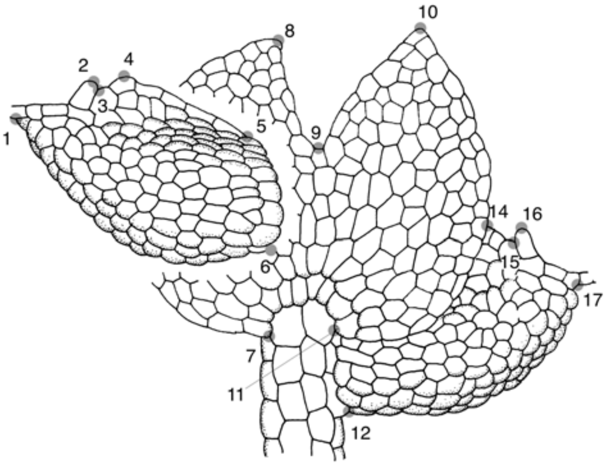

Fig. 1. Landmarks used in this study, not shown is landmark 13, which is beneath the underleaf, at the opposing end of the same stem insertion as landmark 12, corresponding to landmark 5 on the other lobule.

Images were captured on a Photomakroskope M 400 with IM1000 software attached to a Leica IM300 compound microscope (Leica Microsystems, Wetzlar, Germany). Files for data digitisation and manipulation were created using the Thin-Plate Spline (TPS) series, including tpsUtil (Rohlf, 2010a) and tpsDig2 (Rohlf, 2010b). See http://life.bio.sunysb.edu/morph/ (accessed 12 November 2010). Measurements of seven linear dimensions, describing leaf, lobule and underleaf lengths and widths, and underleaf sinus depth, were captured from these images using ImageJ (Abramoff *et al.,* 2004).

Seventeen two-dimensional landmarks were located on lobules and underleaves to provide comprehensive coverage of lobule shape, lobule spacing, underleaf sinus depth and width, and shoot symmetry using homologous points (Fig. 1). Landmarks 1–6 were located on the antical lobule, 7–11 on the underleaf and 12–17 on the postical lobule. The landmarks were (1) lobule–lobe

Table 1. Qualitative characters circumscribing species belonging to the *Lejeunea epiphylla* complex.

Character	*L. amphinephea*	*L. demissa*	*L. perichymidia*	*L. thallasoides*
First lobule tooth, at full expression	unicellular	two-celled, moniliform	unicellular	two-celled, moniliform or side-by-side, or unicellular
Leaf-lobe apex	rounded	broadly obtuse	rounded	obtuse
Gynoecium production	on leading shoots	on short lateral branches	on leading shoots	on short lateral branches
Subfloral innovation stature	Normal	Normal	Normal	Reduced or absent
Perianth base	Stipitate	Sessile	Sessile or short stipitate	Stipitate

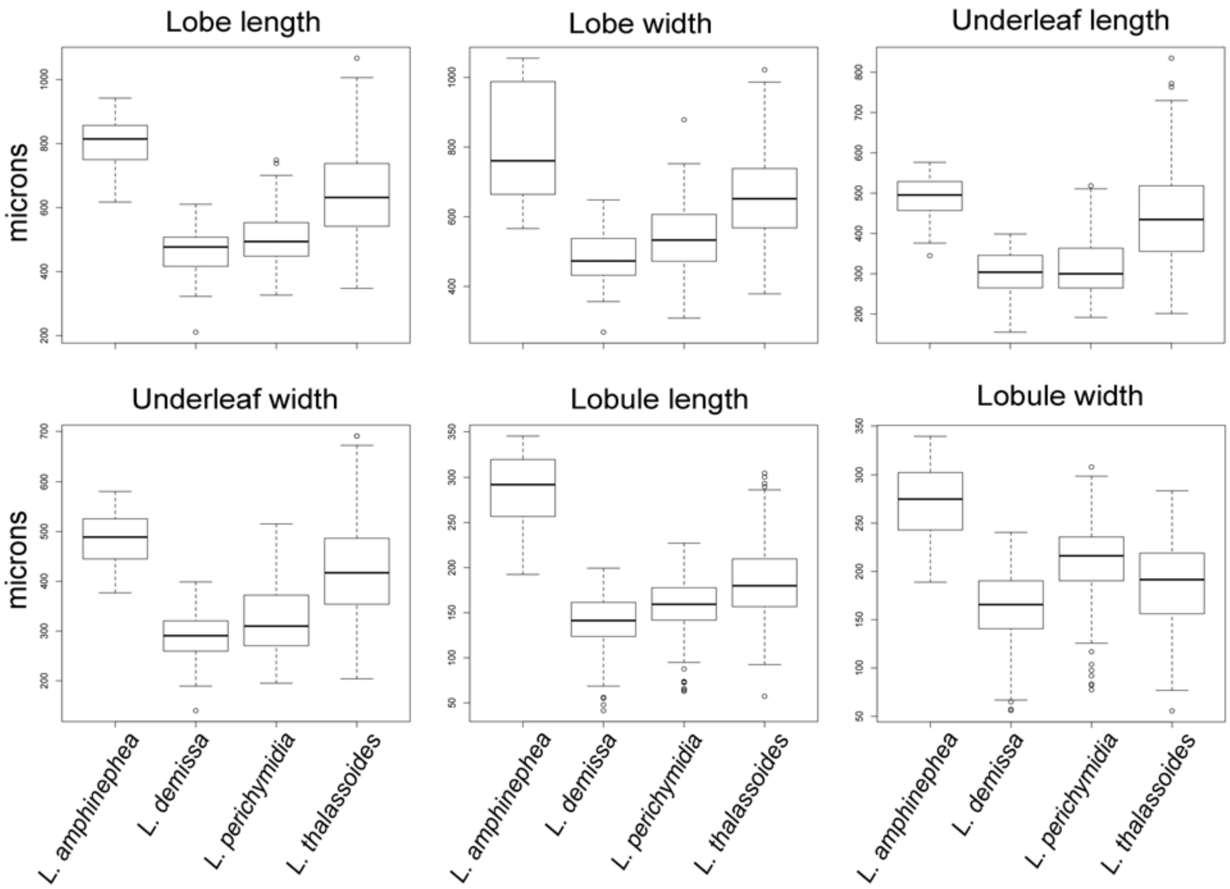

Fig. 2. Boxplots illustrating variation in leaf-lobe, lobule, and underleaf lengths and widths within species belonging to the *Lejeunea epiphylla* Colenso complex.

juncture (2) apex of first lobule tooth (3) base of first lobule tooth (4) apex of second lobule tooth (5) antical lobule–stem junction (top of lobule stem insertion) (6) postical lobule–stem junction (bottom of lobule stem insertion) (7) left (true right (where the shoot apex is 'downstream' and the shoot has dorsal side uppermost) end of underleaf insertion (8) left (true right) underleaf lobe apex (9) base of underleaf sinus (10) right (true left) underleaf lobe apex (11) right (true left) end of underleaf insertion (12) postical lobule–stem junction (bottom of lobule stem insertion) (13) antical lobule–stem junction (top of lobule stem insertion) (14) apex of second lobule tooth (see Renner, 2012) (15) base of first lobule tooth (16) apex of first lobule tooth and (17) lobule–lobe juncture (Fig. 1). A total of 389 landmark configurations were captured from the 24 specimens.

Quantifying and describing shape variation

We used Generalised Procrustes superposition (Rohlf & Slice, 1990) to align landmark configurations. Previous studies using the same landmark set in related organisms found correlation between Procrustes and Tangent space distances of 1.0 about a slope of 0.986 (Renner *et al.,* 2013), meaning the linearized approximation provided by Kendall's shape space was likely to be excellent, as has also been found in other biological systems studied to date (Klingenberg, 2020). We used principal components analysis on the resulting Procrustes coordinates to summarise the major axes of shape variation within and among our species. We reduced the landmark dataset to those describing the shape and spacing of lobule pairs, and then to those landmarks describing the shape of individual lobules to examine patterns of variation in those structures separately from the entire module to which they belong. All landmark analyses were performed in the geomorph package (Adams & Otárola-Castillo, 2013) in R, ver. 3.5.2 (R Core Team, 2017).

RESULTS

Size variation

All seven lengths and widths exhibited overlap among the four species, with no pair of species exhibiting discrete ranges of variation for any variable. Boxplots for each dimension illustrate a general trend across the four species in that the largest species, *L. amphinephea*, has the longest lengths and widths on average, while the smallest species *L. perichymidia* has the shortest lengths and widths, with the exception of lobule width, for which *L. perichymidia* has the second widest lobules, on average (Fig. 2).

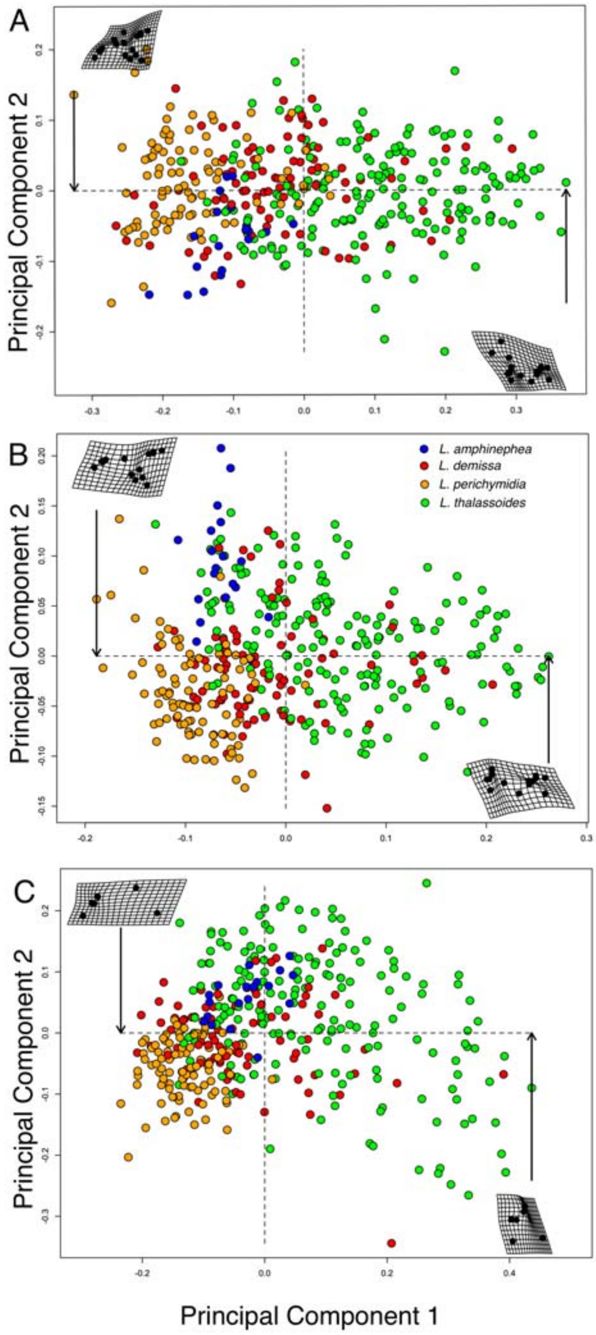

Fig. 3. Principal Components plots showing variation within and among species belonging to the *Lejeunea epiphylla* Colenso complex, as captured by landmark sets quantifying A: module shape including lobules and underleaves; B: pairs of lobules belonging to a single module without the associated underleaf; and C: single lobules.

Shape variation

The first principal component describing the distribution of whole-module landmark sets in shape space accounted for 61.6% of variation, which was associated with changes in the relative stature of the underleaf and lobules, relatively large underleaves with small lobules in a module being one extreme and relatively small underleaves with large lobules the other, as illustrated by the thin-plate splines associated with the positive and negative ends of the first principal component (Fig. 3A). There was little clustering or separation of species along this axis, though *L. thalassoides* dominated the positive side of the plot. The first principal component describing the distribution of lobule pair landmark sets in shape space (Fig. 3B) accounted for 53.2% of variation, which was associated with changes in the relative spacing of the lobules in the pair, and the lobule shape itself. The landmark configuration at the negative end of the first principal component has the lobules overlapping on the stem, and the lobules landmarks have a rectangular configuration. The landmark configuration at the positive end of the first principal component has the lobules separated on the stem, and the lobule landmarks have a trapezoid configuration. Again, there was little separation among species though two, *L. perichymidia* and *L. amphinephea* do exhibit clustering and restriction to one part of the plot. The first principal component describing the distribution of lobule landmark sets in shape space (Fig. 3C) accounted for 54.5% of variation, which was associated with a change from a trapezoid shape whose longest side was along the lobule keel, to a trapezoid shape whose longest side was the stem insertion. There was little separation among species but again *L. perichymidia* and *L. amphinephea* both formed reasonably distinct, but not separate clusters, though there was little overlap between this pair of species in lobule shape.

DISCUSSION

The *Lejeunea epiphylla* complex provides another demonstration that comprehensive quantification of morphology reveals spectrum like patterns of size and shape variation among similar, possibly closely related, *Lejeunea* species such that strict discontinuity among species in size and shape of vegetative structures is lacking. *Lejeunea epiphylla* is not unusual in this regard, similar patterns of continuity and overlap among species has been observed in other liverwort species complexes including those in the genera *Lejeunea* and *Plagiochila* (Dumort.) Dumort. (Renner *et al.,* 2013, 2018), by studies where molecular data corroborated phylogenetic divergences among putative species. In the absence of molecular data to substantiate species status, the significance of qualitative, often micromorphological, differences among species risks being overshadowed by extensive intra-individual variation resulting in continuity and overlap in size and shape among species. As a result, it then seems entirely natural to interpret qualitative character differences as also being the product of intra-specific polymorphism or environmentally induced variation. However, claims of environmentally induced variation must be made with caution because without reciprocal transplant studies or other experimental evidence, it is often the case that each observation of morphological variation is confounded by genotype, therefore a single cause for the expression of any differences cannot be derived.

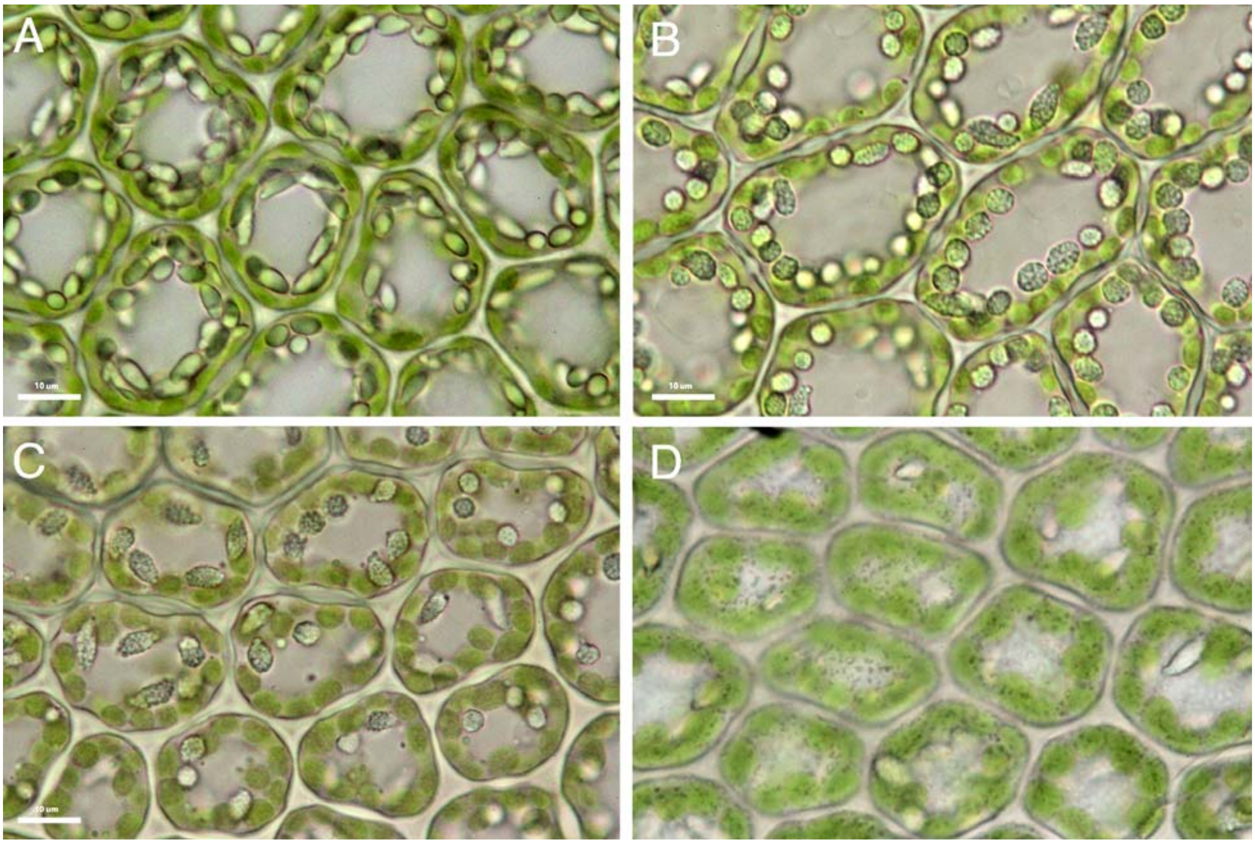

Fig. 4. A: Oil-bodies of *Lejeunea thalassoides (Glenny 14482)*. B: Oil-bodies of *Lejeunea primordialis (Glenny 14464)*. C: Oil-bodies of *Lejeunea flava (Glenny 14457).* D: Leaf-lobe cell surface of *Lejeunea flava (Glenny 14457),* please note the focal plane of this image is on the leaf cell surface, not the middle of the cell lumen, the associated intereference effects and blurring of background objects explains the *apparent* differences in oil-body morphology between this figure and Fig. 4C. Compare the oil-bodies in this image with those in the background of Fig. 4C for demonstration of this point. All images to same scale, 10 micron scale bar indicated in A, B, C.

The attribution of intra-individual variation to phenotypic plasticity or polymorphism within species over inter-specific difference therefore represents an error of inference to the detriment of species circumscriptions.

Studies that explain morphological differences among individuals assigned to the same species in terms of environmentally induced variation or phenotypic plasticity in the absence of experimental evidence should therefore be regarded skeptically especially when studies that bring data on inter-individual relationships to bear find broadly circumscribed species do not adequately encapsulate the relationships found, usually because they under-represent real diversity.

In this study, shape variation in lobules, which are among the best sources of micromorphological character differences for both identifying individuals and circumscribing species, is such that discrete clusters (species) do not manifest within the spectrum-like variation that results when lobule shape is quantified, even by sophisticated methods for capturing shape. This may reflect on the relatively coarse quantification of lobule shape achieved by only 6 landmarks. Even with this caveat the quantification of shape achieved still illustrates the broader point, that the failure to detect discrete clusters within a particular dataset, while necessary for the refutation of species circumscriptions, is insufficient evidence against separate species status. Previous quantitative studies of bryophytes have shown that we can move past this difficulty simply by accepting that absolute morphological discontinuity is simply an inappropriately strict criterion (Medina *et al.,* 2012, 2013; Renner *et al.,* 2013, 2018). This study interprets morphological data as those studies suggest is appropriate, by giving due consideration and weight to micromorphological differences that occur, while being attentive to size-correlated patterns of expression in those and other characters such as the shape of lobes, lobules and underleaves. The result is that differences among individuals apparent in the field by virtue of the correlation between form and microsite occupancy, become realized in the herbarium through circumscriptions that respect the modularity and developmental flexibility of the plants, and ultimately better reflect their phylogenetic diversity through a nuanced appreciation for morphological variation. We hope that Prof. Schuster would approve of this perspective.

TAXONOMIC TREATMENT

KEY TO *LEJEUNEA* OF NEW ZEALAND AND TASMANIA

Tips for using the key to Lejeunea *species.*

1. Check whether or not the specimen is a mixed gathering. *Lejeunea* species may form mixed patches, so always be aware of whether or not your specimen comprises one species, as this will save a lot of time and confusion. Differences among species may be subtle, involving differences in underleaf and lobule shape, in addition to leaf cell surface ornamentation and oil-bodies, so several shoots from across the specimen should be checked.

2. Choose several of the largest shoots for examination. Character expression within *Lejeunea* species is often correlated with size, such that diagnostic features are borne on the largest shoots only. Two studies have explicitly addressed allometric patterns of quantitative character expression in leafy liverworts, and both have found significant allometric relationships in which diagnostic shape variation is maximally expressed on the largest structures (Renner *et al.,* 2013, 2018). The point is that patterns of expression are critical and require nuanced understanding not adequately captured by the reduction of variation to simple ranges, including the allometric components to the expression of variation in both qualitative and quantitative variation. Just because, due to their structural simplicity and allometric variation, small shoots of different species are indistinguishable does not mean the species to which those shoots belong are the same. The complex realities of morphological variation expressed by leafy liverworts is itself an argument against overly typological and formulaic operational species criteria, in particular those based on simple morphological discontinuity. The expression of diagnostic characters associated with lobule shape and dentition may be variable within and among shoots, and it is often necessary to search a number of shoots for lobules whose expression is optimal before an effective assessment of character manifestation can be made.

3. Count oil-bodies close to the shoot apex. Oil-body number in *Lejeunea* and *Cololejeunea* species can increase with distance from the shoot apex. In some *Lejeunea* species with granular oil-bodies 5-7 oil-bodies are present in cells of mature leaves at the shoot apex, while 12-24 oil-bodies are present in cells of leaves further down the shoot. Oil-body number in the key refers to counts from cells close to the shoot apex. The difference between homogeneous and granular oil-bodies in *Lejeunea* is somewhat subtle. Homogeneous oil-bodies have smooth surfaces, and no discernible internal structure, they also tend to be fusiform in shape. These homogeneous oil-bodies tend to be numerous within each cell, and are often arranged in a distinct submarginal ring (Fig. 4A). Granular oil-bodies, on the other hand, have a finely granular surface and discernable internal structure. Granular oil-bodies tend to be few in number, usually less than 20, per cell and may be scattered or arranged in a loose submarginal ring (Fig. 4B-C). Granular oil-bodies occur in species which also possess a granular leaf-lobe cell surface ornamentation, which can be fine and indistinct (Fig. 4D).

4. Two of the couplets in the key are based solely on whether perianths are carinate or not. In specimens where perianths are absent, we recommend the following proceedure. Firstly check through older portions of the specimen, including those overgrown by younger shoots, for old perianths. These are sometimes present, but buried within, the specimen. Failing that try keying the specimen in both directions. Subsequent couplets contain sufficient detail that the forcing of your specimen through one, or the other, should become clear through the mismatch between characters described in each and those borne by the plant at hand.

5. It has been claimed that perianth stipe expression in Lejeuneaceae is variable within individuals, and even within single shoots, and that this inconsistency of expression renders this feature worthless for species circumscription. While at face value the observation of variable perianth stipe expression is correct, extending that claim to inconsistency is incorrect because it neglects ontogenetic patterning in the expression of perianth stipes. The perianth stipe character requires careful interpretation, the stipe evidently develops during the later stages of perianth growth, perhaps close to the maturity of the sporophyte enclosed by the perianth. This delayed development means that on a single shoot perianths with and without stipes may be present, but the perianths without stipes will always be the youngest, containing inconspicuous sporophytes. Perianth stipe length may be variable on perianths in close proximity, see for example Fig. 5L, this is due to differences in perianth age, which themselves likely relate to differences in when the archegonium was fertilized, the event which ultimately triggers perianth development. Within the New Zealand *Lejeunea* flora variation in stipe length at perianth maturity is rare, and known only to occur in *Lejeunea rhigophila*, in which perianths bearing erupted sporophytes may or may not have a stipe (Renner *et al.,* 2010). The demonstration of true variability in stipe expression against common ontogenetic markers is, however, rare for Lejeuneaceae. For the purposes of this key, perianth maturity is reached when the enclosed sporophyte has ceased cell division. In practical terms, this means that mature perianths are those from which the sporophyte has emerged, or is at the point of rupturing the calyptra, in other words the sporophyte is conspicuous, swollen, and dark if the calyptra remains intact.

1. Leaf cell surfaces bearing granular ornamentation, sometimes sparse; oil-bodies (where known) granular, generally fewer than 10 per leaf lobe cell; plant colour often whitish-green, opaque 2

— Leaf cell surfaces smooth, without ornamentation; oil-bodies (where known) homogeneous, fusiform, small, numbering upward of 30 per leaf-lobe cell and often arranged in a sub-marginal ring; plant colour green, yellow-green, or brown-green, clear 11

2\. Perianth inflated, carinae faint or absent 3

— Perianth inflated or compressed, pentacarinate but always at least four carinae conspicuous 5

3\. Underleaves ovate, divided from 0.5 to 0.75 their length; plants usually comprised loose, radiating patches; shoots mid-green, or if white-green then small, up to 0.6 mm wide 4

— Underleaves more or less rotund to ovate, divided to 0.5, usually less, underleaf lobes triangular; plants usually comprised long, sparingly branched shoots arranged in parallel, positively geotropic and often forming pure turfs on tree or palm trunks; shoots bright pale green when fresh, drying to a whitish brown .... 9. *Lejeunea gracilipes*

4\. Perianth with remnants of 5 carinae, each taking the form of 2 rows of raised and paired cells; mature perianths usually weakly pentagonal in end-view; lobe–lobule junction lying postical to the base of the first lobule tooth; lobule arch (the lobule margin between the lobe-lobule insertion and the base of the first lobule tooth) of 3 or 4 cells (for illustrations of this character compare the following figures in Renner *et al.,* 2010: Fig. 8B, 8C, 9B); a trunk epiphyte in lowland (<300 m) forest from Northland south to Nelson– Marlborough . ... 21. *Lejeunea tumida*

— Perianth without carinae remnants as described above, laterally dilated with suture or grove on median dorsal surface, ventral surface smooth; lobe–lobule junction lying antical to the apex of the first lobule tooth; lobule arch of 4–7 cells; epiphytic or epiphyllous on trunks, branches, twigs and leaves in lowland through montane forest and scrub from North Auckland to South Westland ....4. *Lejeunea colensoana*

5\. Leaf apex acuminate 6

— Leaf apex rounded 7

6\. Leaves contiguous, apex spreading at right angles to shoot axis; shoots typically comprising either all normal or explanate leaves, without abrupt and numerous transitions among lobule forms within a single shoot ....2. *Lejeunea apiculata*

— Leaves remote, apex spreading toward shoot apex; shoots comprised a mixture of explanate and normal leaves ....7. *Lejeunea exilis*

7\. Leaf lobe elliptic-ovate, nearly parallel sided close to the stem, tapering gradually to a more or less tightly rounded apex, overall wider than long; lobules small in comparison to leaf lobe size; underleaves ovate, on larger shoots imbricate, and obscuring lobules in entirety in ventral view .... 8. *Lejeunea flava*

— Leaf lobe ovate-rotund, margins more or less continuously curved, progressively and evenly rounded at apex, approximate as long as wide, or slightly wider; lobules small or large in comparison to leaf lobe size, but not obscured by underleaves in ventral view; underleaves various 8

8\. Leaves dislocating from stem 16. *Lejeunea schusteri*

— Leaves not dislocating from the stem 9

9\. Leaf cells bulging, leaf lobe margin crenulate with bulging cells; plants not flattened against the substrate; underleaves rotund, divided to less than 0.5×, sinus narrow, underleaf lobes triangular .... 18. *Lejeunea* sp. (s) (AK306857; Surville Cliffs)

— Leaf cells not bulging, leaf lobe margin entire; plants flattened against substrate; underleaves ovate, divided to 0.5× or more, sinus narrow or broad, if broad then lobes spreading, underleaf lobes lanceolate 10

10\. First lobule tooth multicellular on larger lobules ... . 11. *Lejeunea hodgsoniana*

— First lobule tooth always unicellular regardless of lobule size .... 3. *Lejeunea anisophylla*

11\. Lobules nearly uniformly explanate; underleaves rotund, remote to contiguous; plants on basalt, soil, or decaying wood within and alongside streams .... 19. *Lejeunea subelobata*

— Plants without the above combination of characters; lobules at least sometimes fully developed, or if not then variable in size and not uniformly explanate; underleaves rotund or, more often, ovate 12

12\. Plants with lobule first tooth at least sometimes multicellular, formed by two or three moniliform cells, at least on the largest lobules 13

— Plants with lobule first tooth consistently unicellular, including on the largest lobules 16

13\. Perianth tumid, without carinae 14

— Perianth pentacarinate 15

14\. Leaf lobes squarrose when dehydrated, markedly altered from hydrated conformation; underleaves remote to contiguous, underleaf bases not cordate; lobules with antical margin around the first lobule tooth visible in ventral view, not strongly inrolled; the first lobule tooth consistently with 2 cells, usually inclined outward, away from the shoot apex, lobe–lobule junction lying postical to the base of the first lobule tooth, lobule arch usually of 3 (ranging from 2 to 4) cells ....12. *Lejeunea oracola*

— Leaf lobes maintaining hydrated conformation when dry, not squarrose; underleaves imbricate, underleaf bases cordate; lobules with antical margin inrolled, margin around the first lobule tooth not visible in ventral view; the first lobule tooth consistently of 3 or 4 cells, usually inclined inward, towards the shoot apex, lobe–lobule junction lying above the base of the first lobule tooth, lobule arch consistently of 4 cells .... 15. *Lejeunea rhigophila*

15. First lobule tooth variably 1- to 3-celled, when three celled orientated nearly parallel with the stem axis, antical lobule margin strongly inrolled and obscured in ventral view; leaf apex evenly rounded, keel half the lobe width or more; underleaves remote, rotund to elliptic, about twice the stem width .... 10. *Lejeunea helmsiana*

— First lobule tooth variably 1- or 2-celled, antical lobule margin inflated but not inrolled, and so visible in ventral view; leaf apex broadly obtuse, keel half the lobe width or less; underleaves remote to contiguous, elliptic to ovate, about three times the stem width .... 6. *Lejeunea demissa*

16. Plants with blue oil-bodies 5. *Lejeunea cyanophora*

— Plants with hyaline or pale grey oil-bodies 17

17. Shoots 1.2 mm or more wide across leaves when hydrate 18

— Shoots less than 1.0 mm wide across leaves when hydrated, typically 500–600 µm 20

18. Subfloral innovations absent, or small-stature in comparison to parent shoot; underleaves on large shoots ovate, imbricate, wider than lobules, which are obscured in ventral view; leaf lobes ovate-triangular, apex often obtuse, lobule keel straight to slightly curved; lobules trapezoidal, keel nearly straight; ventral merophyte 2 to 4 cells wide .... 20. *Lejeunea thalassoides*

— Subfloral innovations present and similar in stature to the parent shoot; underleaves on large shoots nearly rotund, narrower than the lobules, which are visible in ventral view; leaf lobes elliptic, apex rounded; ;obules broadly ovate, lobule keel curved; ventral merophyte 2 cells wide 19

19. Mature perianths (those containing a sporophytes whose cell divisions are completed, or nearly completed) sessile or with a short, inconspicuous stipe; bracteole narrow ovate to nearly rectangular; plants dark green to brown green, on rocks or tussock bases on Auckland Islands ...... 1. *Lejeunea amphinephea*

— Mature perianths (those containing a sporophytes whose cell divisions are completed, or nearly completed) sessile or with a short, inconspicuous stipe; bracteole ovate; plants mid- to bright-green, on soil, tree trunks, branches, and leaves in the North and South Islands of New Zealand, and Tasmania .... 13. *Lejeunea perichymidia*

20. Cladia present, produced by lateral-intercalary branching, and dislocating leaving the basal collar of leaf-like appendages intact on the parent shoot; lobe apex sometimes obtuse; underleaves as long as wide, appearing squat on larger shoots with a wide sinus .... 14. *Lejeunea primordialis*

— Cladia not produced; lobe apex always rounded; underleaves longer than wide, appearing ovate on larger shoots with a narrow sinus .... 17. *Lejeunea* sp. (p) (AK286681; Mangere).

SYNOPSIS

In the species treatments below we quote the 'Original material' from the protologue for older literature where type specimen designation was not necessarily explicit, and the 'Type' provides more detail on type specimens and typifications published after the original species description. The simultaneous presentation of both 'original material' and 'type' citations provides useful information, and facilitates assessment of the status of cited type specimens. This form is standard practice in Australia (see for example *Australian Systematic Botany*) and is particularly relevant for liverwort taxonomy given the avoidable errors in type specimen citation that are occasionally made, and subsequently propagated, in literature (see Renner, 2021). For more recently described species where type specimens were explicitly cited by describing authors, we cite a 'Type' only.

1. **Lejeunea amphinephea** M.A.M.Renner sp. nov. Fig. 5.

Diagnosis: *Lejeunea amphinephea* is distinguished by its rotund underleaves with a broad sinus with obtuse to rounded vertex; the round to ovate leaf-lobes whose apex is rounded; the smooth leaf cell surfaces; the lobules with a keel deeply and nearly continuously curved through 90 degrees, with a first lobule tooth always composed of a single-cell; the dimorphic shoot systems with branches smaller in stature than the primary shoot; gynoecia borne on short lateral branches subtended by a single subfloral innovation that continues vegetative growth; and the perianths with a long stipe.

Type: New Zealand, Auckland Island, Hanfield Inlet near waterfall on southern side, 50°45'S 166°10'E, 23.II.1973, *P.N. Johnson 23/5* (holotype: WELT-H006349)

Description: Plants mid- to brown-green, primary shoots large for genus, 30–40 mm long 1.2–2.0 mm wide, sparingly and irregularly branched, branching exclusively lateral-intercalary, branches with conspicuous irregularly lobed basal collar, loosely prostrate forming extensive patches on soil and rocks, in association with seepages and waterways or outcrops. Stems with seven or eight rows of larger cortical cells surrounding around 11–25 rows of smaller medullary cells; free external cell wall thickened, as are longitudinal radial cortical cell walls; medullar cell walls unthickened. Leaves contiguous to loosely imbricate, insertion attaining dorsal stem midline and overlapping across the dorsal-most cell row, dorsal leaf-free strip absent; lobes 617–942 (796 ± 90) µm long by 566–1055 (805 ± 172) µm wide, rotund to ovate, moderately convex, not obliquely spreading, outer portion arching ventrally, apex rounded to broadly obtuse, weakly falcate and obtusely notched at junction with keel; antical margin flared, not auriculate but crossing

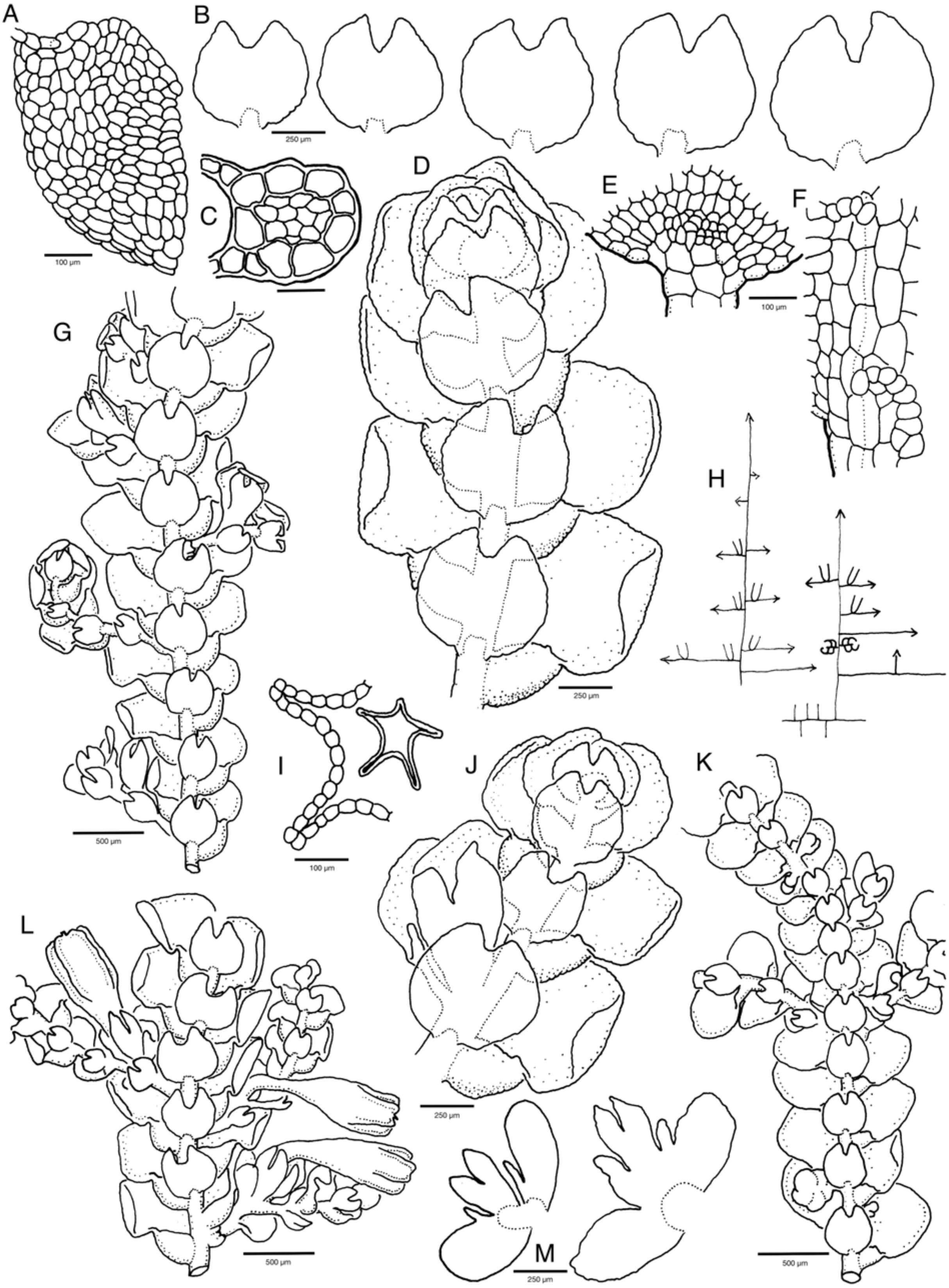

Fig. 5. *Lejeunea amphinephea* A: Lobule detail. B: Five underleaves showing size variation within a single shoot. C: Stem transverse section. D: Shoot in ventral view. E: Underleaf base. F: Dorsal stem surface showing leaf insertion lines, with dorsal stem midline indicated. G: Shoot in ventral view showing gynoecia production on small stature lateral branches. H: Cladograms, not to scale. I: Perianth transverse sections. J: A normal stature gynoecium bearing shoot showing normal leafy subfloral innovation. K: shoot bearing male branches. L: Shoot sector with gynoecia on small stature lateral branches, with long-stipitate perianths and small stature subfloral innovations. M: Two sets of female bracts and bracteoles. All from WELT-H6349, except K from WELT-H6135.

opposite stem margin, and overlapping adjacent lobes so obscuring the stem in dorsal view; margins entire. Lobules 192–345 (282 ± 44) µm long by 188–339 (271 ± 43) µm wide, 0.125–0.2× lobe area, not dimorphic though variable in size, carinal region broadly inflated, antical margin at most only weakly appressed against the lobe, keel evenly and continuously arched through 80–90° in maximally developed lobules, less arched to occasionally straight in others. Lobule first tooth single-celled, long axis orientated toward shoot apex, fused along all of its basal margin with a cell of similar size, and along 0.75 of the interior margin with a slightly larger cell, whose free margin defines a shallow notch between the first lobule tooth and the broadly rounded, indistinct second tooth; lobule antical margin interior of the second lobule tooth straight, marginal cells slightly elongate with long axes parallel with margin. Underleaves remote, at most contiguous on the largest shoots, rotund to ovate, 345–576 (485 ± 65) µm long by 377–580 (479 ± 58) µm wide, bifid to 0.3×, sinus broadly V- to U-shaped, vertex rounded, sinus 109–209 (155 ± 32) µm deep, lobes triangular, obtuse, not spreading, margins entire to weakly and irregularly crenulate; underleaf insertion shallowly arched, on 2 stem cortical cells. Oil-bodies not seen. Asexual reproduction absent.

Paroicous. Androecia on short determinate lateral-intercalary branches, bearing two to three pairs of hyaline fertile bracts. Gynoecia produced on leading leafy shoots and lateral intercalary branches, subtended by a single Lejeuneoid innovation (Pycnolejeuneoid innovations were recorded for this species during the preparation of this description, but have not been confirmed due to restricted specimen access during the current pandemic — their presence would be anomalous within the Lejeuneinae). Female bracts rounded, bract lobules ligulate, apex rounded or obtuse; bracteole elliptic-oblong, bifid to 0.5×, lobes linear, not spreading, fused with bract lobules at base on one or both sides. Female bracteole similar to vegetative underleaves. Perianth 1152–1311 µm long overall with free perianth 593–690 µm long, equally pentacarinate, carinae unarmed, extending to near the base, rostrum 4–6 cells high. Immature perianths estipitate, mature perianths with a long, hyaline, basal stipe 530–621 µm long, comprised of leptodermous cells.

Distribution and Ecology: Currently known only from subantarctic Auckland Island and Adams Island, where it has been collected between sea level and 400 m elevation in a range of microsites, including on steep rocks of a lightly vegetated slip; on rocks in coastal stream; on dead stipes of *Polystichum vestitum* (Sw.) C.Presl; on rocks in water of stream outfall, and on the eastern side of Cloudy Peak on a rock outcrop, partly sheltered by short scrub and *Chionochloa antarctica* (Hook.f.) Zotov. It is possible that *Lejeunea amphinephea* is endemic to the Auckland Islands, but as the Lejeuneaceae and the genus *Lejeunea* is generally poorly known and collected, the possibility that this species occurs elsewhere, including New Zealand, where it may yet be discovered in comparable microhabitats within the alpine zone, and southern South America cannot be excluded.

Recognition: A combination of characters will serve to distinguish *L. amphinephea* from other *Lejeunea* known from the New Zealand Botanical Region, and all should be checked to confirm the identity of plants under examination. The leaf cell surfaces are smooth; they do not bear a fine to coarse granular ornamentation as if found in some other large *Lejeunea* species such as *L. flava* and *L. gracilipes.* The leaf surface ornamentation of *L. flava* and *L. gracilipes* can be seen under around 400 times magnification on a compound microscope with appropriate diaphragm settings, and especially where air-bubbles are trapped between the leaf surface and cover-slip, they appear as small, usually scattered granules on the cell surface; and in life contribute to the opaque appearance of some, but not all, of the species that possess them. The leaf-lobes are rotund to ovate, and have a broadly and continuously rounded margin including the exterior margin, which is often reflexed. There is never a distinct obtuse apex as occurs in species with more ovate-triangular leaf lobes, for example *L. thallasoides* M.A.M.Renner & Glenny. The lobules of *L. amphinephea* are, when fully developed, distinctive in their relatively large size in comparison with the leaf-lobes, being around a sixth to an eighth the area of the lobe, and in their deeply and continuously curved keel, which is evenly cambered through nearly 90°, and whose base extends at right angles from the stem. The junction between the keel apex and the leaf-lobule forms a right angle, but is not notched. Shoot stature in *L. amphinephea*, as in many *Lejeunea*, is variable and diagnostic features associated with lobule shape are expressed best by the largest shoots, so these should be preferentially selected for inspection. Smaller-statured shoots often do not express diagnostic features, and tend to bear strong resemblance to the smaller shoots of other species, to the extent that plants comprising exclusively small-statured shoots may be difficult to assign to a species. Another distinctive feature of *L. amphinephea* is the long stipe at the base of fertilized perianths, this comprises half the overall perianth length and is 500–600 µm long and 6 or 7 tiers of leptodermous, hyaline, and inflated cells tall. The perianths are borne in gynoecia that are subtended by a single subfloral innovation that continues vegetative growth.

Among New Zealand *Lejeunea* species, *Lejeunea amphinephea* is most likely to be confused with *L. thalassoides*, because the two species are similar in stature, both have large underleaves with a broad sinus and the smaller stature shoots of both species bear a strong resemblance to one another. A useful feature for distinguishing smaller stature shoots of *L. amphinephea* from those of *L. thalassoides*, is found in the subfloral innovation, which in *L. thalassoides* are rudimentary and abortive; they do not continue vegetative growth while in *L. amphinephea* they do. The leaves of *L. amphinephea* have a continuously rounded free external margin, within which there is no trace of an obtuse apex, whereas the leaf lobe has a distinct obtuse apex in *L. thallasoides*, this character is best assessed by dissecting and slide-mounting leaf lobes so that their outline is unambiguous. The stem section may also provide assistance in distinguishing *L. amphinephea* from *L. thalassoides;* the stems of *L. amphinephea* have seven cortical cell rows, or eight in the vicinity of stem insertion lines, whereas in *L. thalassoides* the larger stems have up to 10 cortical cell rows.

Etymology: from the ancient Greek ἀμφικνεφής 'wrapped in darkness' referencing both the long winter nights, expanse of surrounding deep open ocean, and dark green colour of the plants in herbarium material.

Conservation: *Lejeunea amphinephea* was listed as *Lejeunea* aff. *flava* (b) (WELT H006349; Auckland Islands) in de Lange *et al.* (2020). This species is currently known only from Auckland Island, where it has been collected at several localities in the early 1970's.

Specimens examined: New Zealand, Auckland Island, Carnley Harbour, Camp Cove, 50°51'S 166°01'E, 30 m, 21.II.1973, *P.N. Johnson 21/53* (WELT-H006135); Waterfall Inlet 5049'S 166°12'E, 12.II.1973, *P.N. Johnson 12/22* (WELT-H004955); Cloudy Peak, 50°53'S 166°09'E, 400 m, 14.II.1973, *P.N. Johnson 14/41* (WELT-H005213) Adams Island, 1 mile east of Fairchild's Garden, 50°51'S 165°56'E, 18.II.1973, *P.N. Johnson* (WELT-H005510)

2. **Lejeunea apiculata** Sande Lac., Ned. Kruidk. Arch. 3: 421. 1854[1855].

Original material: none cited, but published in a treatment of new species from Java collected ('detexit') by Dr. F. Jughuhn.

Type: Java (L) *non vidimus.*

=*Lejeunea hawaikiana* M.A.M.Renner & de Lange, New Zealand J. Bot. 49: 431. 2011 *nom. nov. pro Stenolejeunea acuminata* R.M.Schust., Journal of the Hattori Botanical Laboratory 89: 156 (2000) non *Lejeunea acuminata* (Lehm. & Lindenb.) Lehm. & Lindenb., Synopsis Hepaticarum 3: 354 (1845) *syn. nov.*

Type: New Zealand, North Island, Northland, Radar Bush, *R.M. Schuster 95-503* (holotype: F ex herb. R. M. Schuster).

Schuster (2000) described *Stenolejeunea acuminata* as distinct from *S. apiculata* (Sande Lac.) R.M.Schust. due to it's autoicy, short sterile subfloral innovations, dentate repand female bracts, and asperulate cuticle. Schuster's (2000) concept of *L. apiculata* was based entirely on the treatment of Eifrig (1936), and it is significant that neither Eifrig nor Schuster examined the type(s) of *L. apiculata* (Schuster 2000 p.159). Schuster claimed that *L. apiculata* is dioicous based on his interpretation of Eifrig's (1936) illustration, which showed a plant with serial gynoecia production and no androecia. However, one of the two New Zealand specimens that Schuster himself attributed to his autoicous *Stenolejeunea acuminata* similarly bore gynoecia and no androecia, though the gynoecia were not produced in series as in Eifrig's plant (Schuster, 2000). Schuster's interpretation that *L. apiculata* has a smooth cuticle may be explained by this feature simply being overlooked by Eifrig, and the differences in female bract morphology to variation within and among specimens, the subtle expression of this character, and the difficulties in interpreting the relatively shallow, irregular dentition expressed by *L. apiculata* (see Lee, 2013), and the fact that Eifrig's (1936) illustrations were relatively coarse.

Although *L. apiculata* has been reported for Australia, plants from south-eastern Australia agree more with *L. hawaikiana* in their autoicy, female bract morphology, and asperulate cuticle. Similarly, the account of Malaysian *L. apiculata* in Lee (2013) is more compatible with *L. hawaikiana* as we understand that taxon in New Zealand, than it is with *L. apiculata* sensu Schuster (2000), given the Malaysian plants are autoicous, have irregularly dentate female bracts and bracteole and an asperulate cuticle (see Fig. 96, 98 and 99 in Lee (2013) contra the description). Our experience of Australian and New Zealand plants is that the distinctions between *L. apiculata* and *L. hawaikiana* presented by Schuster (2000) do not hold, and plants of *L. apiculata* and *L. hawaikiana* from Australia and New Zealand are compatible on morphological grounds. Further, our experience of Australian *L. apiculata* as an autoicous plant with asperulate leaf cell surface ornamentation, having irregularly and shallowly dentate female bracts and bracteole is shared more broadly by other observers from across the distribution of *L. apiculata* (e.g. Zhu & So, 2001; Lee, 2013). On this basis the fundamental distinctions between *L. apiculata* and *L. hawaikiana* break down such that *L. hawaikiana* cannot be maintained as a separate taxon. Therefore we propose formal synonymy here, and accept that the species present in New Zealand is *L. apiculata*.

Lejeunea apiculata is widely distributed in Asia, Australasia, and the Pacific including the Cook Islands. In New Zealand *Lejeunea apiculata* occurs in Northland, and on the Kermadec and Chatham Islands, the latter of which represents the global southern limit at nearly 44°S. *Lejeunea apiculata* is often encountered as a lithophyte within stream beds, though Schuster (2000) characterised it as an epiphyte. Its acuminate leaf lobe apex orientated perpendicular to the shoot axis and the deeply divided underleaves are both distinctive features.

3. **Lejeunea anisophylla** Mont., Ann. Sci. Nat., Bot., sér. 2, 19: 263. 1843.

Original material: Hab. ad cortices inter muscos in insulis Sandwich ŕ celeb. Gaudichaud collectos inveni.

Type: Hawaii 'ad cortices inter muscos in insulis Sandwich' (holotype: PC; isotypes: BM, G-18236) *fide* Zhu & So (2001).

Lejeunea anisophylla is widespread in Africa, Indomalesia and Oceania, extending east to Hawaii (Pócs, 2010, 2011; Zhu & So, 2001). The recently proposed synonymy of *L. anisophylla* with *L. adpressa* Nees, which has priority (Gradstein, 2021), would extend the distribution of this taxon to tropical America. We have not had the opportunity to evaluate this proposal, so retain use of the name *Lejeunea anisophylla. Lejeunea anisophylla* is known in the New Zealand Botanical Region from the Kermadec and Chatham Islands, the latter of which may be the world southern limit for the species. The distribution in both Australia and New Zealand is poorly documented, and it is possible the species occurs on the north-east coast of the North Island, and associated islands.

4. **Lejeunea colensoana** (Steph.) M.A.M.Renner, Aust. Syst. Bot. 23: 455. 2010.

Basionym: *Taxilejeunea colensoana* Steph. Hedwigia 35: 132. 1896.

Original material: Hab. Nova Zelandia (Colenso)

Type: New Zealand. Corticolous, Colenso comm. Curnow (lectotype designated by Grolle (1982): G00060673!; isolectotype: Hb. Hodgson 14490 MPN).

Lejeunea colensoana is endemic to New Zealand, where it is common in cool hyperhumid forests in the North and South Islands. For description, illustration, and details on ecology and recognition see Renner *et al.* (2010).

5. **Lejeunea cyanophora** R.M.Schust., J. Hattori Bot. Lab. 26: 246. 1963.

Original material: South Island, Westland, ca. 0.6 mi. N of Haast Pass (RMS; mixed among *Radula*, *Plagiochila pleurota*; thin soil over shaded moist rocks).

Type: F ex herb. R.M.Schuster

Lejeunea cyanophora is the only *Lejeunea* known to have blue oil-bodies (Schuster, 1963). Besides this distinctive feature the plant in the type specimen is rather non descript, but does not immediately match any other species known from New Zealand, so we continue to accept it as distinct. The collection details provided by Schuster suggest the plant was collected where the Haast River intersects the Haast Pass-Makarora Road. The species is known only by the type, which grew in association with *Dinckleria pleurata* (Hook.f. & Taylor) Trevis. and *Radula plicata* Mitt. The co-occurrence of these species suggests an epiphytic microsite, rather than a lithophytic one, as recorded on the specimen packet, as both species are more frequently epiphytic especially in their co-occurrence. In lowland forests of the West Coast of Te Wai Pounamu/South Island *Dinckleria pleurata* and *Radula plicata* often co-occur on *Dacrydium cupressinum* Sol. ex G.Forst. trunks, and in many other epiphytic settings. Dedicated searches to date have failed to relocate this species in the wild in the vicinity of Haast Pass, and possibly a wider search area including lower elevation forests and encompassing a greater diversity of microsites should be considered for future efforts to relocate this enigmatic entity.

6. **Lejeunea demissa** M.A.M.Renner sp. nov. Fig. 6, 7.

Diagnosis: *Lejeunea demissa* is distinguished by its ovate underleaves with a V-shaped sinus with obtuse to acute vertex; the ovate leaf-lobes whose apex is broadly obtuse to acute; the smooth leaf cell surfaces; the lobules with a keel shallowly curved, with a first lobule tooth composed of two cells and moniliform; the dimorphic shoot systems with branches smaller in stature than the primary shoot; gynoecia borne on short lateral branches subtended by a single subfloral innovation that continues vegetative growth; and the perianths with a short stipe.

Type: New Zealand, North Island, Coromandel Ecological Region, Te Aroha Ecological District, Mt Te Aroha summit, along track to Dog Kennel Flat, SW side of summit, in *Nothofagus menziesii* (Hook.f.) Oerst. and *Griselinea littoralis* Raoul forest, 37°32'S 175°45'E, 940 m, 12.III.1995, *J.E. Braggins 95/201* (holotype: AK255268)

= *Lejeunea epiphylla* Colenso Trans. & Proc. New Zealand Instit. 21: 73. 1889. *nom illeg. non* Mitten J. Proc. Linn. Soc., Bot. 5: 118. 1861. *pro parte.*

Original material: Hab. Epiphytical on *Hymenophyllum* (sps.), woods, Dannevirke, County of Waipawa; 1888, W. C.

Description: Plants forming mostly pure patches on tree trunks and branches, also epiphyllous, particularly on *Hymenophyllum demissum* (G.Forst.) Sw. Shoots yellow green, to 25 mm long, medium sized for genus (1.0–) 1.2–1.6(–2.0) mm wide, irregularly pinnately branched. Stems with external and internal walls unthickened except for weak concave trigones of primary wall around cell wall junctions, seven cortical cells and around 10 medullary cell rows, cortical cell walls evenly and continuously thickened, medulla cell walls unthickened, hyaline. Leaves imbricate, insertion reaching the dorsal stem mid-line, dorsal leaf free strip absent. Lobes ovate, 211–610 (464 ± 68) µm long by 269–648 (483 ± 78) µm wide, imbricate to contiguous, obliquely spreading and patent, not squarrose when dry, convex, margin entire, apex rounded to obtuse. Lobules 41–200 (136 ± 35) µm long and 56–240 (160 ± 42) µm wide, with explanate and normal morphs, lobules not strictly dimorphic, typically intergrading along shoots, explanate morphs infrequent, normal lobules barely extending beyond the width of the underleaves, mostly obscured, keel straight at antical and postical ends, mostly arched in the middle, through 80° in total; lobule arch 4 cells, angle between arch and keel 50–90° at lobe-lobule juncture, arch meeting base of lobule tooth in plane with lobule; first lobule tooth variably 1 cell, or two moniliform cells, pointing in direction of shoot apex, all lobules on a shoot may have one-celled teeth, or two-celled first teeth; first tooth basal cell fused with two or three subtending cells, the

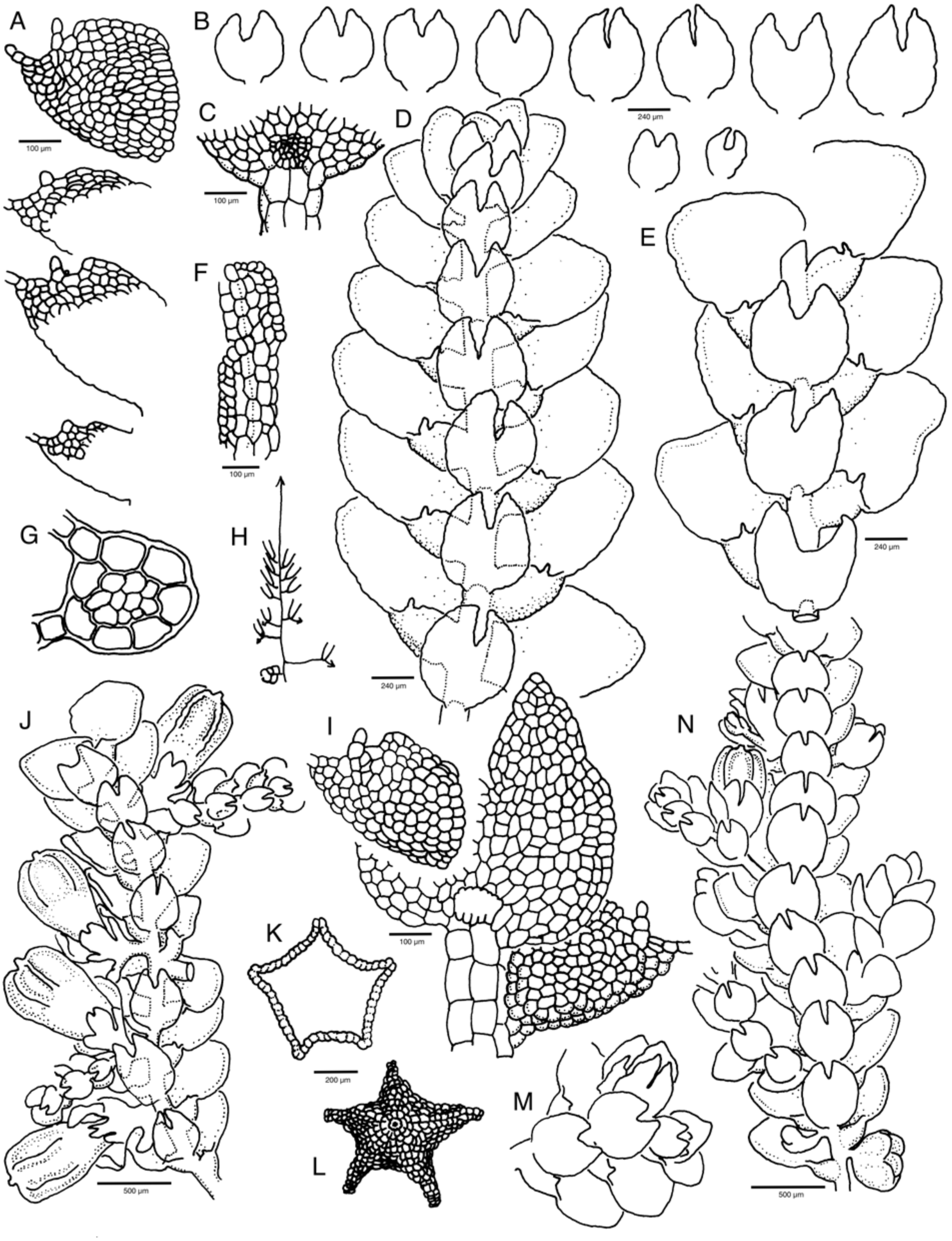

Fig. 6. *Lejeunea demissa* A: Four lobules showing variation in lobule teeth. B: Ten underleaves showing size and shape variation within a single shoot. C: Underleaf base. D: Shoot in ventral view. E: Shoot in ventral view, note difference in size and stature of underleaves and lobules. F: Dorsal stem surface showing leaf insertion lines, with dorsal stem midline indicated. G: Stem transverse section. H: Cladogram, not to scale. I: Lobule pair and underleaf comprising a single module, with underleaf partially cut away. J: Shoot sector with gynoecia on small stature lateral branches. K: Perianth transverse section. L: Perianth viewed from above, same scale as K. M: Shoot sector with gynoecia on lateral branch, with subfloral innovation. N: Shoot sector bearing gynoecia and androecia. A, B, C, E, H, K, M from WELT-H10971; D, F G, I, J, N from AK255268; L from AK300050; N from CHR589304.

Fig. 7. *Lejeunea demissa* Four shoot sectors showing variation in lobule stature and teeth, and underleaf size and shape, within a single specimen, WELT-H10971

marginal of which are larger than surrounding cells, the interior of which is situated in a shallow rectangular notch that separates the first and second lobule teeth; second lobule tooth of one or two cells, obtuse; antical margin beyond first tooth plane or weakly in-rolled, straight then curved toward stem insertion at interior end; carinal region inflated primarily along the keel. Explanate lobules of 10–14 cells bearing a single-celled apical tooth. Underleaves contiguous to imbricate, ovate, broadest at or slightly below mid-point, 155–399 (302 ± 52) µm long and 140–399 (284 ± 46) µm wide, one third to one half the shoot width, bifid to 0.3×, sinus 64–168 (107 ± 27) µm deep, broadly to narrowly V-shaped, vertex rounded to acute, lobes not divergent, acute when small, increasingly obtuse and rounded as stature increases, rounded on largest underleaves. Underleaves attached to 2 or 3 ventral cortical cells, insertion transverse to weakly arched, underleaf base not cordate. Lobe cell walls with small triangular trigones and 1 or 2 small but distinct medial wall thickenings per wall. Lobe cell surface unornamented. Oil-bodies 16–35 per cell, small, ellipsoidal, internally homogeneous, colourless, smooth, in a loose submarginal ring. Asexual reproduction lacking.

Paroicous. Antheridia on short, determinate, achlorophyllous lateral branches bearing 3 bracts, 2 of which contain a single antheridia each, with an underleaf at branch base. Gynoecia produced on lateral branches immediately after branch initiation, the female bracts being the first leaf gyre produced by the branch, the branch then terminating, gynoecia also produced occasionally in the middle of leafy axes. Gynoecia subtended by one Lejeuneoid subfloral innovation of smaller stature than main leafy shoot that continues vegetative growth. Female bracts fused with bract underleaf on both sides. Perianths 805–983 µm long overall, with free perianth 760–910 µm long, pentacarinate, carinae with crenulate ridges through bulging cells, extending from apex one half to two thirds the way down the perianth sides; rostrum relatively short but distinct; with a short basal stipe 46–80 µm long, of two or three cell tiers. Sporophytes not seen.

Distribution and Ecology: *Lejeunea demissa* is endemic to New Zealand, where it is widely distributed throughout the North and South Islands with known records from the Bay of Islands in Northland to south Westland, however *Lejeunea demissa* is likely to be more widely distributed to the north and south of these northern and southern reports. *Lejeunea demissa* is an epiphyte or facultative epiphyll on tree trunks, branches, twigs and leaves between sea level and 1000 m. Common host species for epiphyllous growth are *Beilschmiedia tawa* (A.Cunn.) Kirk and *Hymenophyllum demissum.* At Coromandel *L. demissa* grew on the trunk of *Dacrydium cupressinum* in *Agathis* Salisb. forest, with *Lopholejeunea* (Spruce) Steph. and *Radula allisonii* Castle. At Mt Te Aroha *L. demissa* was collected as an epiphyte on a trunk of *Schefflera digitata* J.R.Forst. & G.Forst. At Rangitata River *L. demissa* was an epiphyte in low stature broadleaf forest, and at South Westland an epiphyte on tree trunks in alluvial forest.

Recognition: *Lejeunea demissa* is a fairly characteristic plant that is unlikely to be confused with other *Lejeunea* species in New Zealand, so long as it is examined carefully. Microhabitat provides a good first clue to identity, *L. demissa* is an epiphyte or epiphyll, it is not known to grow on rock, soil, or leaf litter and this, in combination with the smooth leaf lobe cell surfaces, the two-celled first lobule tooth and pentacarinate perianths are sufficient for confidant identification. Lobules, when *well developed* bear a 2-celled moniliform first lobule tooth that spreads away from the shoot axis, often at 45° or more. Above the first lobule tooth is a prominent triangular second lobule tooth. Sometimes explanate lobules also produce a 2-celled moniliform first lobule tooth. Some searching may be required along shoots to find lobules whose apex is visible, alternatively focusing up and down within clean shoot sectors may suffice to detect the first lobule tooth. Three of the other *Lejeunea* species in New Zealand with a moniliform first lobule tooth (*L. colensoana*, *L. oracola* and *L. rhigophila*) have inflated, ecarinate perianths while the fourth (*L. helmsiana*) has a first lobule tooth of three of four cells and has smaller, rotund, and remote to contiguous underleaves. The only species that is likely to be confused with *L. demissa* is *L. perichymidia*, especially when smaller plants expressing a high percentage of explanate lobules are at hand. Small and large shoots of *Lejeunea demissa* can be distinguished from those of *L. perichymidia* by the leaf-lobes having a distinct rounded to obtuse apex, whereas the leaf-lobes of *L. perichymidia* are continuously rounded; and the underleaves of *L. demissa* are ovate while those of *L. perichymidia* tend to be more rotund. It may co-occur with *L. perichymidia*, and with it form mixed patches, in which case identification may be challenged if the mixture is overlooked.

Etymology: From Latin demissa, hanging, applied in reference to the frequent colonisation of leaves of the fern *Hymenophyllum demissum*, where it co-occurs with *Radula demissa*.

Conservation: *Lejeunea demissa* is widely distributed throughout cool wet forests of both main islands, so we suggest it may be suitable for listing as 'Not Threatened' following criteria in Townsend *et al.* (2008).

Specimens examined: New Zealand: North Island: Eastern Northland and Islands Ecological Region and District, Bay of Islands, Russell State Forest, Waihaha Stream, 35°21.323'S 174°12.129'E, 45 m, 14.I.2009, *M.A.M. Renner 4150 & D.S. Glenny* (AK314701); Coromandel Peninsula, Horomanga Block, Waiwawahi Stream, 36°54'S 175°31'E, 25.II.1973, *N.M. Adams* (WELT-H011249); South Island: Canterbury, Rangitata River, Rata Stream, 760 m, 25.VII.2013, *M. Crowe* (CHR 589304); South Westland, 2 miles above Haast River Bridge, 11.VII.1969, *R.K. Dell* (WELT-H003005, WELT-H003007); New Zealand, without specific locality, *Colenso a.2127* (WELT-H003133).

7. **Lejeunea exilis** (Reinw., Blume & Nees) Grolle, J. Hattori Bot. Lab. 46: 353. 1979.

Basionym: *Jungermannia exilis* Reinw., Blume & Nees, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 227. 1825.

Original material: none cited, but published in Hepaticae Javanicae.

Type: Java (neotype designated by Bischler *et al.* (1962): STR sub. *Microlejeunea erectifolia* (Spruce) Steph.; isoneotype: W Lindenb. Hep. 6724 p.p. sub. *Microlejeunea cucullata* (Reinw., Blume & Nees) J.B.Jack & Steph., PC-MONT, S)

Lejeunea exilis is widespread in Malesia, Australia, and the Pacific as an epiphyte or epiphyll, and in the New Zealand Botanical Region occurs only on the Kermadec Islands, where it has been collected as an epiphyll on *Rhopalostylis* H.Wendl. & Drude. This is another species that may occur on the north-east coast of the North Island and associated inshore and offshore islands. For a description and illustration see Renner & de Lange (2011).

8. **Lejeunea flava** (Sw.) Nees, Naturgesch. Eur. Leberm. 3: 277. 1838.

Basionym: *Jungermannia flava* Sw., Prodr. 144. 1788.

Original material: Jamaica.

Type: Jamaica, *Swartz* (lectotype designated by Grolle (1976): UPS; isolectotypes: BM, S)

=*Lejeunea sinclairii* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 262. 1884. *nom. illeg. non* Mitten, Bonplandia 10: 19. 1862.

Original material: *N. Zelandia*.

Lejeunea flava has a pantropical distribution, with extension into southern temperate Australasia, where it is widespread throughout Tasmania and New Zealand in forest habitats. It is a distinctive species in the field due to its opaque green or yellow-green colour, in combination with pentacarinate perianths and large, imbricate, ovate underleaves. Molecular phylogenetic studies resolve *L. flava* paraphyletic, suggesting this species comprises a complex that requires detailed investigation (Heinrichs *et al.,* 2013). The illegitimate name *L. sinclairii* Spruce *auct. non* Mitt. has been applied to New Zealand specimens, however the apparent lack of alternative name and the absence of a comprehensive study of this pantropical species, both support the continued use of the name *L. flava* for New Zealand plants.

9. **Lejeunea gracilipes** (Taylor) Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 213. 1884.

Basionym: *Omphalanthus gracilipes* Taylor, London J. Bot. 5: 385. 1846.

= *Taxilejeunea gracilipes* (Taylor) Steph., Hedwigia 29: 141. 1890.

= *Lejeunea discreta* var. *gracilipes* (Taylor) G.E.Lee & Heinrichs, Phytotaxa 358: 30. 2018.

Original material: Hab. Pacific Isle, Nightingale, Hook. Herb.

Type: Pacific Isles, *T. Nightingale* (FH00079615, G00115757, NY01059499)

Lejeunea gracilipes is an Australasian-Oceanian species that is relatively common in the northern third of the North Island and associated islands, with an outlying occurrence on the Chatham Islands. It is often encountered as an epiphyte on nikau trunks. The combination *Lejeunea gracilipes* (Taylor) Mitt. was published in synonymy of *Lejeunea uvifera* Mont., and is therefore invalid (Art. 36.1). The prior existence of an invalid name does not preclude subsequent valid publication of the same combination, so *Omphalanthus gracilipes* was transferred to *Lejeunea* by Spruce (1884).

While *Lejeunea gracilipes* and *L. discreta* may be closely related, they consistently differ in details of both perianth and lobule morphology, in particular the perianths of *L. gracilipes* are ecarinate with a short rostrum, whereas those of *L. discreta* are pentacarinate with a longer, flared rostrum (see Fig. 189 in Lee (2013)). To reflect these differences, and the presence of only one morphotype of consistent expression in New Zealand, we continue to recognise *L. gracilipes* at species rank, contra Lee *et al.* (2018).

Lejeunea gracilipes is most often confused with *L. flava*, as both share a distinctive whitish green living colour, have granular leaf cell surface ornamentation, and are a similar size. When perianths are present distinguishing these two species is straight forward, *Lejeunea flava* has pentacarinate perianths, while those of *L. gracilipes* are eplicate. However, *L. gracilipes* is often found without perianths, which introduces the possibility for confusion. If a search for old perianths buried within the mass of shoots is fruitless, *Lejeunea gracilipes* and *L. flava* can be distinguished by differences in underleaf and leaf lobe and lobule size and shape. *Lejeunea flava* has more ovate underleaves that may be weakly cordate at the base, and may be contiguous or weakly imbricate and almost completely obscure the relatively small lobules; whereas *L. gracilipes* has more rotund underleaves that are often remote and leave the pyriform lobules visible between sequential underleaves. The leaf lobes of *L. flava* are ovate to elliptic, and longer than wide and so have outlines that tend to curve more toward their apex whereas those of *L. gracilipes* are more rotund and evenly curved around their outline.

10. **Lejeunea helmsiana** (Steph.) Steph., Sp. Hepat. (Stephani) 5: 796. 1915.

Basionym: *Eulejeunea helmsiana* Steph., Hedwigia 35(3): 89. 1896.

Original material: Hab. Nova Zelandia, Northern Island (Colenso) Southern Island (Helms).

Type: New Zealand, Helms, ex herb. Steph. (lectotype designated by Renner (2013a): G-19618)

= *Lejeunea pocsii* R.M.Schust., J. Hattori Bot. Lab. 85: 84. 1998.

Type: New Zealand, North Island, Mamaku Plateau, w. of Lake Rotorua, ca. 400 m, 26.I.1995 *R.M.Schuster 95–230*, hb R.M.Schuster.

Lejeunea helmsiana is endemic to New Zealand, where it occurs from the Auckland region to Southland, and east to Rekohu/Chatham Island. For a full description, illustrations, and details on ecology and recognition see Renner *et al.* (2009b).

11. **Lejeunea hodgsoniana** Grolle ex R.J.Lewington, Bever. & M.A.M.Renner, PhytoKeys 29: 2. 2013.

Type: New Zealand, North Island, Porirua: Titahi Bay, Stuart Park, track to cliff edge at S end of bay: Sounds-Wellington Ecological Region, Wellington Ecological District, on trunk and branches of *Melicytus ramiflorus* in coastal thicket with *Pittosporum crassifolium* and *Coprosma repens*. Bryophyte associates, *Cololejeunea minutissima*, *Frullania monocera*, *F. patula*, *Lejeunea colensoana*, *Rhynchostegium muriculatum*, *Siphonolejeunea nudipes* and *Syntrichia papillosa*, 41°06’33"S, 174°49’43"E, ca. 15m, 19.VII.2012, *P. Beveridge MB-2* (holotype: WELT [WELT H012563]; isotypes: AK, CHR, F, NSW).

Lejeunea hodgsoniana is endemic to New Zealand, where it is widespread in lowland and coastal forest throughout the North Island, and northern South Island, with outlying populations on the Kermadec and Chatham Islands. For a full description, illustrations, and guidance on recognition of this species see Lewington *et al.* (2013).

12. **Lejeunea oracola** M.A.M.Renner Aust. Syst. Bot. 23: 448. 2010.

Type: New Zealand, North Island, Maungataniwha Ecological District, Wainui River catchment, Iwitaua Road, on trunk of *Kunzea aff. ericoides*, 100 m, *M.A.M. Renner 2940*, 5.VII.2007 (holotype: AK299972; isotypes: CHR, F, NSW).

Lejeunea oracola is endemic to New Zealand, where it is common in coast and lowland forests of the North Island, usually in situations of high light. For a full description, illustrations and recognition see Renner *et al.* (2010).

13. **Lejeunea perichymidia** M.A.M.Renner sp. nov. Fig. 8.

Diagnosis: *Lejeunea perichymidia* is distinguished by its rotund underleaves with a broad sinus with obtuse to rounded vertex; the ovate leaf-lobes whose apex is rounded; the smooth leaf cell surfaces; the lobules with a keel deeply and nearly continuously curved through 90°, with the lobe-lobule junction situated in a shallow notch, with a first lobule tooth always composed of a single-cell; gynoecia borne on normal leafy shoots, and subtended by a single subfloral innovation of similar stature that continues vegetative growth; and the pentacarinate perianths with a short stipe.

Type: New Zealand, North Island, Auckland Ecological Region, Waitakere Ecological District, Waitakere Ranges, Spraggs Bush, 29.VII.1973, *R.E. Beever & J.E. Beever s.n.* (holo: AK291280)

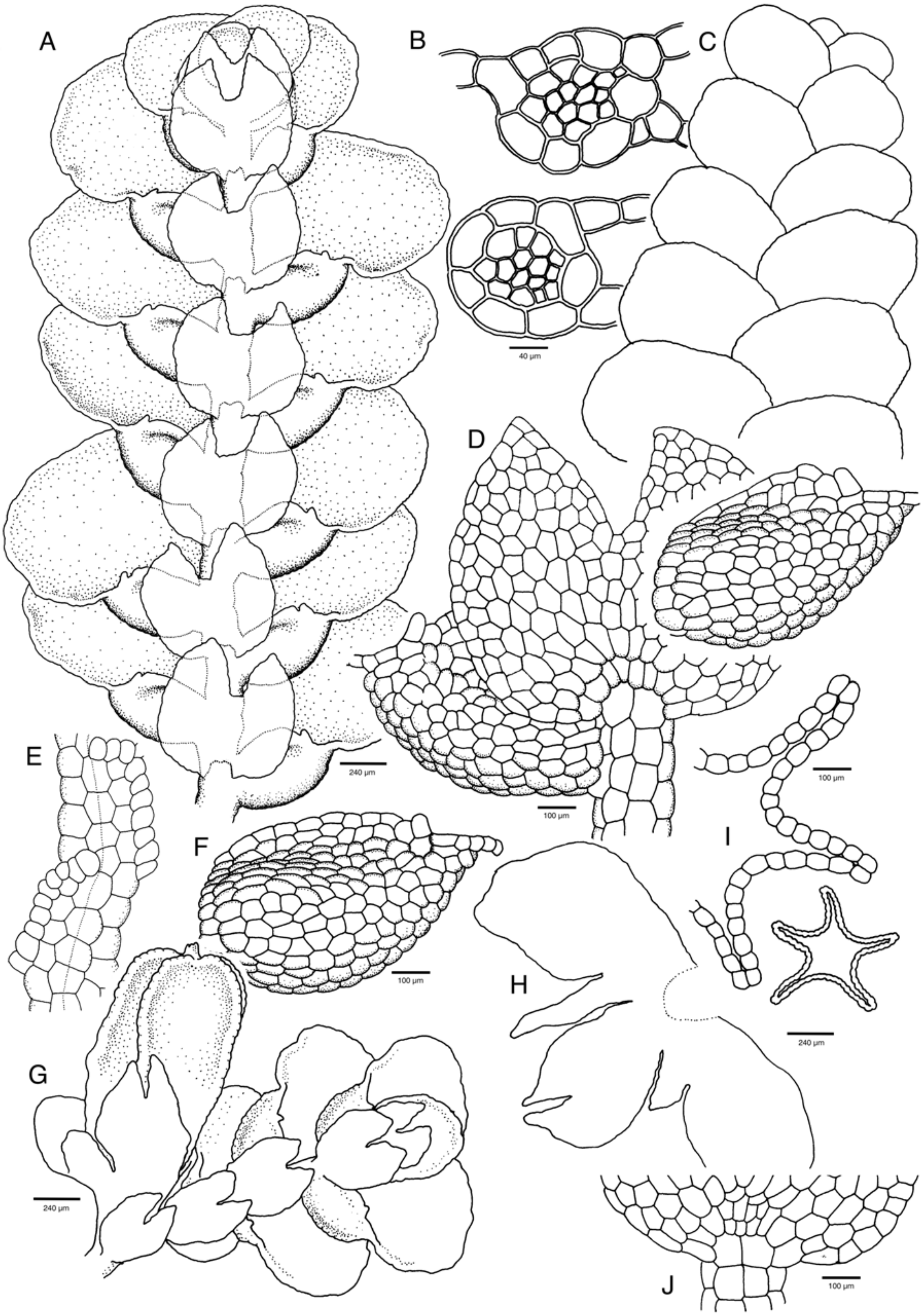

Fig. 8. *Lejeunea perichymidia.* A: Shoot in ventral view. B: Two transverse stem sections. C: Shoot in dorsal view. D: Lobule pair and underleaf comprising a single module, with underleaf partially cut away. E: Dorsal stem surface showing leaf insertion lines, with dorsal stem midline indicated. F: A single lobule. G: A gynoecium bearing shoot showing normal leafy subfloral innovation. H: Gynoecial bracts and bracteole. I: Perianth transverse sections, smaller to same scale as G. J: Underleaf base. A, C, D, J from CHR556174, others from AK291280.

= *Lejeunea epiphylla* Colenso Trans. & Proc. New Zealand Instit. 21: 73. 1889 *nom illeg. non* Mitten J. Proc. Linn. Soc., Bot. 5: 118. 1861 *pro parte.*

Original material: Hab. Epiphytical on *Hymenophyllum* (sps.), woods, Dannevirke, County of Waipawa; 1888, W. C.

Description: Plants yellow brown in herbarium forming untidy mostly pure patches. Medium sized for genus, shoots up to 25 mm long, 1.2–1.4 mm wide, shoots monomorphic, sparingly branched. Stems 250–285 µm diameter, with 7 cortical cell rows and around 13 smaller medullar cell rows, cortical cell walls evenly thickened, medullar cell walls thin, all unpigmented. Lobes ovate, 326–748 (507 ± 94) µm long by 308–878 (544 ± 104) µm wide, imbricate, not falcate, not obliquely spreading, slightly concave, outer margin slightly downrolled. Lobe margins entire, lobe dorsal surface pseudopapillate by virtue of cell bulge. Lobules 326–748 (507 ± 94) µm long by 326–748 (507 ± 94) µm wide, 0.125–0.2 lobe area, naviculiform, carinal region broadly inflated, narrowing and turning with keel toward shoot apex at outer end, keel half lobe width. Antical lobule margin inrolled and hidden along the inner two thirds, less or not inrolled along the outer third so that the primary and secondary teeth are visible in ventral view, keel half width of lobe. Lobule primary tooth single celled, prominent, pointing toward shoot apex, fused with surrounding cells along 1.5 sides, rounded, papilla at base, slightly entally displaced. Lobule margin between primary tooth and lobe-lobule junction forming a bridge over the opening into carinal region which is perpendicular to shoot axis and fused seamlessly with the lobe margin, but for a shallow depression in the lobe surface behind this margin . Lobule secondary tooth obtuse to rounded, usually of a single reniform cell, occasionally two cells, not exceeding the primary tooth except in robust lobules. Lobules dimorphic, reduced lobules 12–16 cells, with prominent apical tooth. Underleaves 326–748 (507 ± 94) µm long by 326–748 (507 ± 94) µm wide, rotund, broadest at midpoint, bifid 0.25–0.33, sinus 326–748 (507 ± 94) µm deep, U-shaped, lobes not divergent, apices obtuse. Attached to 2–3 stem cortical cells, insertion shallowly arched, underleaves scalloped at base, lateral basal cells not markedly inflated. Underleaves equally spaced, remote to contiguous on robust shoots. Oil-bodies numerous, small, fusiform, hyaline, smooth, arranged in a submarginal ring. Asexual reproduction absent.

Paroicous. Gynoecia produced sporadically on normal leafy shoots, subtended by a single lejeuneoid subfloral innovation that continues vegetative growth. Female bracts united to bract underleaf on both sides, the whole bract gyre flexed and reflexed, forming a cradle around the archegonium. Perianths obovate, around 1500 µm long overall, with free perianth c. 1400 µm long, equally 5–carinate, carinae ridged, and extending approximately half way down the perianth sides; rostrum distinct; with short stipe at base c. 150 µm long of two or three tiers of elongated cells.

Distribution and Ecology: *Lejeunea perichymidia* is known from Tasmania and New Zealand.

Lejeunea perichymidia is a facultative epiphyll and, in our experience, exhibits one of the broadest microsite ranges of any Australasian *Lejeunea,* growing on soil, tree trunks, branches, and leaves of both fern and broad-leaved tree and shrub leaves. In all microsites except leaves *L. perichymidia* grows as part of established, low, bryophyte turfs. On leaves it colonises naked leaf surfaces, and may co-occur with another member of the *Lejeunea epiphylla* complex, *L. demissa,* as in the type of *L. epiphylla* Colenso.

Recognition: *Lejeunea perichymidia* is a fairly nondescript *Lejeunea* at first glance, not being endowed with any particularly distinctive features such as unusual lobule shapes, multicellular first lobule teeth, or unusual perianths. Rather it shares with many *Lejeunea* species the overall appearance of vegetative and reproductive parts, meaning it could conceivably be confused with many other *Lejeunea* species, hence identification of *L. perichymidia* is to some extent a matter of elimination. The first check on any suspected individual is to confirm that the leaf-lobe cell surfaces lack ornamentation. In living plants, smooth leaf cell surfaces will co-occur with numerous, small, fusiform, smooth oil-bodies arranged in each cell in a sub-marginal ring. The next check is to confirm that the first lobule tooth is always unicellular, even on the most well developed lobules, and that the perianths, if present, are penta-carinate. The third check is on shoot size, shoots of *L. perichymidia* are 1.2–1.4 mm wide, while a couple of species with which it could be confused, including *L.* sp. (p) have smaller shoots. Another character to confirm is the presence of a continuously rounded leaf-lobe margin, one which lacks a distinct rounded to obtuse apex as occurs in, for example, *L. demissa*. Finally, check the details of the lobule morphology, the second tooth is indistinct and level with the first, the keel should be deeply curved and the lobe-lobule junction is situated in a shallow notch. *Lejeunea perichymidia* may co-occur with *L. demissa*, so the possibility that a collection is mixed should always be considered. For guidance distinguishing *L. perichymidia* from *L. demissa*, see the recognition section of *L. demissa*.

Etymology: from the ancient Greek περι – all around and κῦμα – wave, and ιδια – the diminutive suffix; surrounded by small waves referencing the shape formed by the lobe and lobule at their junction.

Conservation: *Lejeunea perichymidia* was listed in de Lange *et al.* (2020) as *Lejeunea* aff. *flava* (a) (AK 291280; Waitakere), where it was assessed as Not Threatened using the criteria of Townsend *et al.* (2008). We regard that assessment as appropriate, to which may be appended the qualifier ?SO to reflect its Tasmanian occurrences.

Specimens examined: NEW ZEALAND, North Island, Wellington, west side of Hutt Valley, 18.V.1969, *B.G. Hamlin 1195* (WELT-H000645); Wadestown, Otari Reserve, 13.IV.1969, *B.G.*

Hamlin 1056 (WELT-H000471); ibid, *B.G. Hamlin 1062* (WELT-H000477); Australia: Tasmania: Cartwright Creek, 42° 56'S 147° 21'E, 25.I.1980, *A.V. Ratkowsky H1063* (HO303361).

Representative misidentified specimens:

Lejeunea flava

New Zealand, North Island: Wellington, Kaitoke, Pakuratahi Forks, 41°3.5'S 175°11.6'E, 200 m, *D. Glenny 5357* (WELT H010243); Wellington, Hutt Valley, Percy Reserve, 41°31.1'S 174°52.7'E, 30 m, 11.V.1994, *D. Glenny 5305* (WELT H-010151);

South Island, Nelson, York Valley, matai track, 41°18.1'S 173°16.5'E, 200 m, 15.V.1994, *W. Malcolm* (WELT H-010237)

Lejeunea helmsiana

New Zealand, North Island, South Auckland, near Whakatane, c. 7 km SSE of Taneatua on SH2, Waimana Gorge Scenic Reserve, 38°6.43'S 177°2.43'E, 60 m, 1.XII.2011, *P. Beveridge LU-5* (WELT-H012460); Volcanic Plateau, c. 27 km SW of Tauranga on SH29, Kaimai Summit, Loop track 37°52.42'S 175°55.70'E, 460 m, 30.XI.2014, *P. Beveridge NW-41* (WELT H-013463)

14. **Lejeunea primordialis** (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, Syn. Hepat. 375. 1845.

Basionym: *Jungermannia primordialis* Hook.f. & Taylor, London J. Bot. 4: 92. 1845.

Original material: Lord Auckland's group, on *Sticta flava,* Tayl.

Type: Auckland Islands: Lord Auckland's Group J. D. Hooker 1840 (lectotype designated by Grolle (1982): FH00079614; isolectotypes: S, W)

= *Microlejeunea primordialis* (Hook.f. & Taylor) Steph., Hedwigia 29(2): 84. 1890 (see Söderström *et al.,* 2015).

Lejeunea primordialis is endemic to southern temperate Australasia including Tasmania and New Zealand, and the subantarctic Auckland Islands. It is a distinctive species that can be recognised by the relatively small shoot width, the tendency to form near pure bright yellow-green turfs on branches and twigs, the ovate-triangular leaves, which taper to a distinct rounded or even obtuse apex, the production of microphyllous cladia, which are often fairly long and which dislocate from normal leafy shoots at their base, and the remote, rather squat underleaves. *Lejeunea primordialis* is usually found in higher-elevation forest and scrub as an epiphyte in well-lit situations.

15. **Lejeunea rhigophila** M.A.M.Renner, Aust. Syst. Bot. 23: 453. 2010.

Type: New Zealand, North Island, Pureora Ecological District, Waihaha Stream catchment, on *Coprosma propinqua*, 480 m, 8.VII.2007, *M.A.M. Renner 2993* (holotype: AK300148; isotypes: CHR, F, NSW).

Lejeunea rhigophila is endemic to New Zealand, where it is common in montane forests of the interior of the North Island, usually in situations of high light. For a full description, illustrations and recognition see Renner *et al.* (2010).

16. **Lejeunea schusteri** Grolle, Haussknechtia 8: 60. 2001.

Replaced synonym: *Rectolejeunea denudata* R.M. Schust., J. Hattori Bot. Lab. 89: 143. 2000, *non Lejeunea denudata* (Pearson) J.J.Engel, Bryologist 78: 361. 1975.

Type: New Zealand, North Island, Northland, lowland coastal forest near Portland, *R.M. Schuster 95-141* (holotype: F ex herb. R.M. Schuster).

Lejeunea schusteri is known from northern New Zealand, the Chatham Islands, the Kermadec Islands, and the Cook Islands (Renner & de Lange, 2011). It is distinctive in its small size, brownish colour, and leaf lobes that dislocate from the stem.

17. **Lejeunea sp.** (p) (AK286681; Mangere)

This tag-named entity is found in the upper North Island, often growing as an epiphyte on puuriri (*Vitex lucens*). It is similar in stature to *L. primordialis*, but differs by its rotund leaves (rather than ovate with a slightly obtuse apex), the absence of cladia (rather than frequent), and the ovate underleaves that are contiguous along the shoot (rather than rotund, remote underleaves). The two species are not known to overlap in distribution, *L. primordialis* occurs in montane to subalpine forests and shrublands, whereas *L.* sp. (p) (AK286681; Mangere) occurs in lowland forests. The format of this tag-name follows that applied to informally recognised species in New Zealand, where AK286681 is the herbarium voucher substantiating the tag-name.

18. **Lejeunea sp.** (s) (AK306857; Surville Cliffs)

This tag-named entity of unresolved status is known, within the New Zealand Botanical Region, only from North Cape. The plants are distinct among New Zealand species in having a distinctly crenulate leaf-lobe margin, a feature imparted by the bulging marginal cells.

19. **Lejeunea subelobata** Carrington & Pearson, Proc. Linn. Soc. of New South Wales, ser. 2 2: 1039. 1888.

Original material: hab. – On wet rocks, George's River, Botany Bay, Janry., 1885 (47); George's River, Botany Bay, Janry., 1885 (42).

Type: Australia, New South Wales, near Sydney, Ball's Head Bay, Jun.1885, leg. Whitelegge no. 47 (lectotype designated by Grolle (1982): BM – 3 packets; isolectotypes: JE, G-19832, MANCH).

Lejeunea subelobata occurs in Tasmania and along the east Australian coast at least as far north as Sydney, where it is a frequent lithophyte on damp rock, usually in association with waterways. In New Zealand *L. subelobata* is also most frequently encountered as a lithophyte within waterways, but may also grow on rotting wood. The species was accepted as distinct from *L. drummondii* Taylor by Renner (2013b) on the basis of morphological evidence. The molecular evidence cited from Renner *et al.* (2011) is based on a mis-labelled sample of what was actually *L. gracilipes*. This makes the relationships resolved for *'L. subelobata*' more sensical, given that *L. subelobata* has smooth leaf lobe cell surfaces and numerous small fusiform oil-bodies arranged in a submarginal ring, suggesting it is a member the other major lineage within *Lejeunea* evidently circumscribed by these characters. The major lineage to which *L. gracilipes* belongs is circumscribed by a granular leaf lobe cell surface, and 4–7 larger granular oil-bodies per cell as in, for example, *L. gracilipes* and *L. flava*. This has no significant impact on the inference of separate species status for *L. drummondii* and *L. subelobata*, which remains supported by the morphological differences described in Renner (2013b). *Lejeunea subelobata* is distinctive in the dark green colour, and the lobules which are almost exclusively explanate, in addition to the occurrence in association with waterways in New Zealand.

20. **Lejeunea thalassoides** M.A.M.Renner & Glenny sp. nov. Figs. 9, 10.

Diagnosis: *Lejeunea thallassoides* is distinguished by its ovate underleaves with a broad U-shaped sinus with obtuse to rounded vertex; the ovate leaf-lobes whose apex is obtuse; the smooth leaf cell surfaces; the lobules with a straight keel, with a first lobule tooth composed of a single-cell or rarely of two or more cells; the dimorphic shoot systems with branches smaller in stature than the primary shoot; gynoecia borne on short lateral branches subtended by a single subfloral innovation that is small-statured and does not continue vegetative growth; and the perianths with a long stipe.

Type: New Zealand, North Island, Hawkes Bay Ecological Region, Heretaunga Ecological District, Tangarewai Stream catchment, Monckton Scenic Reserve, 39° 57.816'S 176° 16.906'E, 290 m, 16.X.2009, *M.A.M. Renner 4407* (holotype: AK314727).

Description: Plants forming extensive pure mats lithophytic or terrestrial on limestone and other cation-rich substrates, including cation-rich greywacke and calcareous mudstone. Shoots large for genus, procumbent, sparingly branched, exclusively lateral-intercalary with a basal collar, up to 35 mm long, 1.2–2.5 mm wide. Stems 87–155 µm diameter, with 7 cortical cell rows, but up to 10 in vicinity of leaf insertion lines, and 11–31 medulla cell rows; cortical cell walls evenly and continuously thickened, medulla cell walls unthickened, hyaline. Leaves imbricate, insertion attaining dorsal stem midline, and interlocking across the dorsal cortical cell row, dorsal leaf-free strip absent; lobes ovate-triangular, 348–1067 (643 ± 135) µm long by 378–1021 (657 ± 123) µm wide, plane or concave along the postical margin, obliquely spreading and weakly dorsally assurgent, postical margin straight or weakly curved from keel to apex, extending away from stem at 45–60° to shoot axis, apex obtuse to acute, antical margin weakly curved then lobe broadly rounded and auriculate to top of stem insertion, lobe medial cells with small triangular trigones, and 1–2 small medial wall thickenings occasionally developed on each wall, lobe cell surface with fine granular ornamentation; lobules approximately one sixteenth the lobe area, 57–304 (184 ± 48) µm long by 56–283 (187 ± 45) µm wide, trapezoid, keel and stem insertion approximately equal lengths, free external margin shorter than free antical margin; carinal region rounded, maximally inflated at keel-stem junction, contoured and rounded outward from this point, inflation weak, carinal region indistinct; keel straight to slightly arched, running cleanly into lobe postical margin; first lobule tooth one or two celled, with cell long axis pointing slightly outward away from shoot apex, single celled tooth with cell fused along its base with one or two cells, usually slightly larger than the tooth cell, and fused along its interior margin with one or two cells for 0.5 to 0.8 of its length; two-celled first lobule teeth usually have cells one atop the other, rarely side by side, the two-celled teeth are hooked inward from their base, but still have their apex pointing outward away from the shoot apex; first lobule tooth separated from second tooth by one or two cells, one of which may be larger than surrounding cells; lobule second tooth indistinct, developed on lobules on robust shoots, broadly rounded, apex with two elongated cells whose long axis is parallel with margin; lobule margin interior of second tooth shallowly curved, marginal cells similar in size and shape to adjacent cells, sometimes down-rolled and obscured in ventral view, but usually visible its entire length. Underleaves contiguous to imbricate, typically obscuring stem and lobules in ventral view, ovate, broadest near base, 201–835 (450 ± 121) µm long by 204–691 (423 ± 96) µm wide, bifid to 0.3, sinus U-shaped, vertex obtuse to rounded, 61–264 (147 ± 45) µm deep, lobes acute, insertion strongly arched, underleaf base slightly cordate, lateral basal cells not inflated. Oil-bodies small, homogeneous, spherical to fusiform, in mature leaves near the shoot apex 16–35 per cell arranged in a submarginal ring. Asexual reproduction absent.

Paroicous. Antheridia on highly abbreviated determinate branches, either produced in pairs from adjacent-opposite leaf bases, or scattered, not extending beyond shoot margin, hidden in dorsal view, bearing 2 or 3 pairs of hyaline antheridial bracts, each containing two antheridia, bract stature decreasing dramatically from branch base, sterile bract and underleaf at branch base, underleaves otherwise absent. Gynoecia on short lateral branches, either lacking subfloral innovations, or with one, rarely two Lejeuneoid innovations of reduced stature that grow a short distance before terminating growth. Female bracts united to bracteole on both sides, lobe, lobule, and bracteole more or less equal length, bract lobules lanceolate, sinus between bract lobe and lobule sometimes reflexed. Perianths around 3000 µm long overall, with free perianth c. 2000 µm long, equally pentacarinate, carinae extending around half way down perianth, unfertilized perianths sessile, fertilized perianths with a hyaline basal stipe 900–1010 µm long, of leptodermous cells. Sporophytes not seen.

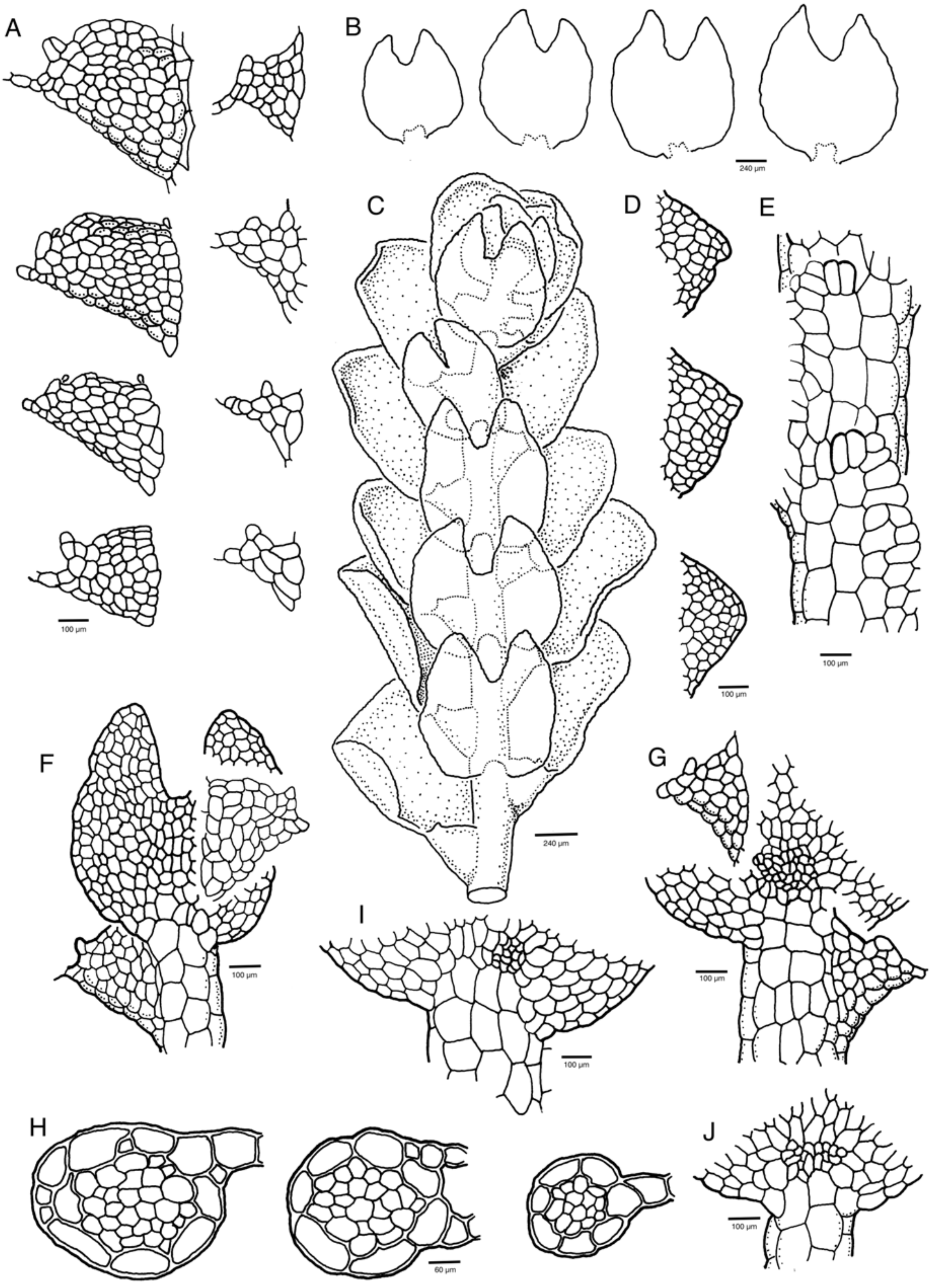

Fig. 9. *Lejeunea thalassoides* A: Eight lobules showing variation from fully developed with first lobule tooth of two cells through to few-celled explanate lobules. B: Four underleaves showing variation in size. C: Shoot in ventral view. D: Three lobe apices. E: Dorsal stem surface showing leaf insertion lines that interlock over the dorsal stem midline. F, G: Lobule pair and underleaf comprising single modules, with underleaf partially cut away. H: Three stem transverse sections showing variation in stature. I, J: Underleaf bases showing variation in stem attachment from two to four stem cells. A, B, F, J CHR571529; D, E, G, I, H, WELT-H10386; C, CHR424338.

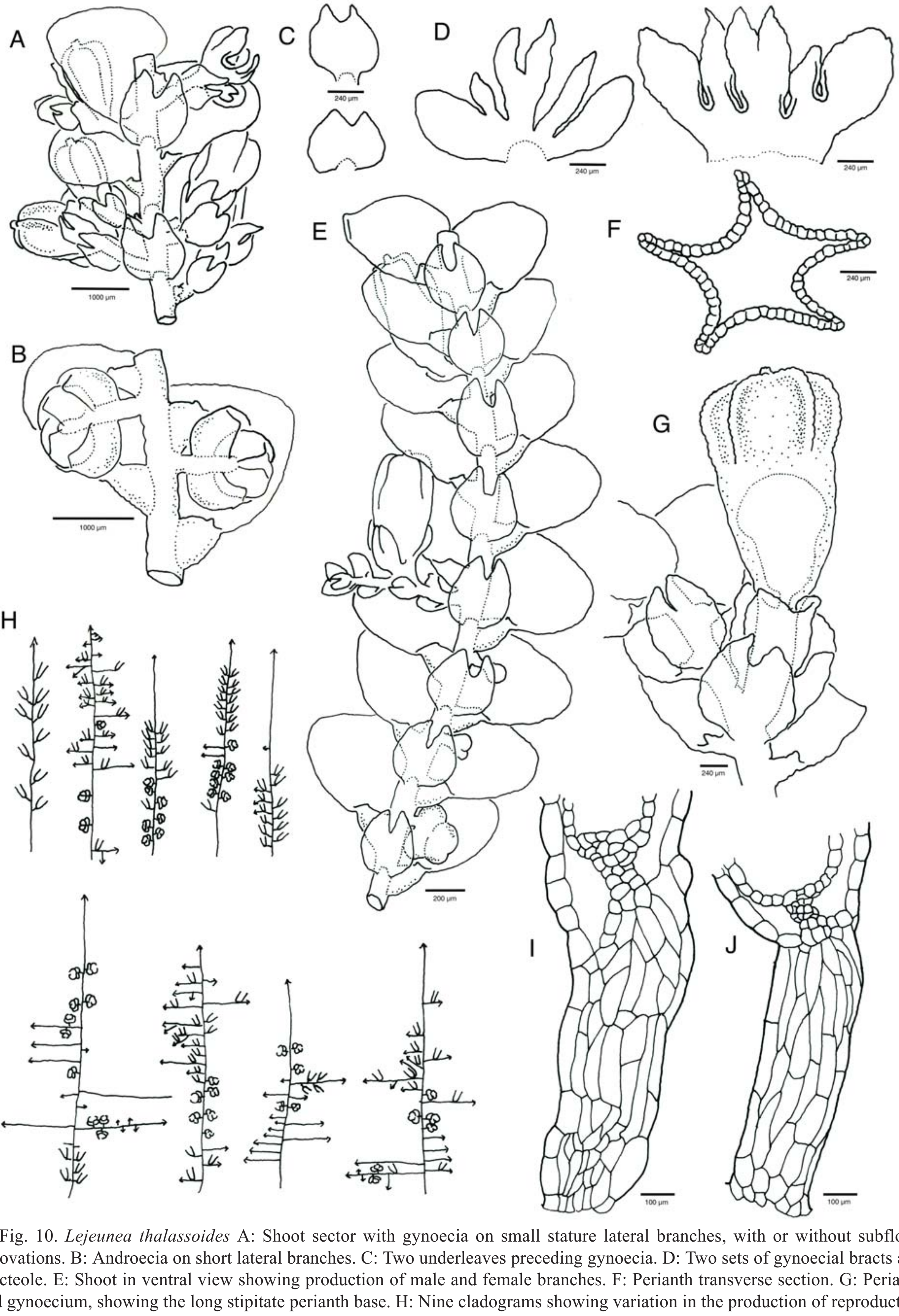

Fig. 10. *Lejeunea thalassoides* A: Shoot sector with gynoecia on small stature lateral branches, with or without subfloral innovations. B: Androecia on short lateral branches. C: Two underleaves preceding gynoecia. D: Two sets of gynoecial bracts and bracteole. E: Shoot in ventral view showing production of male and female branches. F: Perianth transverse section. G: Perianth and gynoecium, showing the long stipitate perianth base. H: Nine cladograms showing variation in the production of reproductive structures among shoots. I, J: Two longitudinal sections of perianth base showing free perianth wall above long stipitate perianth base, note also the multiseriate calyptra stalk. A, B, I, H (upper 5) CHR424338; C, D(left) WELT-H10386; E CHR638295; D(right), F, G, H (lower 4), J CHR571529.

Distribution and Ecology: *Lejeunea thalassoides* is endemic to New Zealand, where it occurs in the lower two-thirds of the North Island and throughout the South Island, including in subalpine regions. *Lejeunea thalassoides* usually grows as a lithophyte or on soil in association with cation rich bedrock such as limestone or calcareous mudstone, but it has been observed as an epiphyll and epimuscicol as well. At Hawkes Bay *L. thalassoides* was observed forming extensive yellow-green mats of procumbent shoots on calcareous mudstone exposed by a track cutting. At Takaka Hill *L. thalssoides* overgrew *Echinodium hispidum* (Hook.f. & Wilson) Jur. on karst under *Nothofagus menziesii* forest. At Matukituki Valley on the fronds of *Polystichum vestitum*, again in *Nothofagus menziesii* forest. In the vicinity of Ootepoti/Dunedin *L. thalassoides* appears to be widely distributed and common, as most herbarium specimens came from here, many collected by John Child, at Frazers Gully on shaded rock wall at 100 m elevation; at Peel Forest *L. thalassoides* was an epiphyll on *Austroblechnum lanceolatum* (R.Br.) Gasper & V.A.O.Dittrich at the edge of a waterfall; at Flagstaff Hill on an earth bank at stream side in partial shade; at Bethune's Gully on an earth bank; at Otari in suburban Whanganui-a-Tara/Wellimgton terrestrial on a clay bank in forest; and on the Old Man Range growing amongst *Heteroscyphus coalitus* alongside a small stream within *Nothofagus* forest.

Recognition: *Lejeunea thalassoides* is a distinctive species that, in most instances, should provide little difficulty in identifying. The microhabitat occupied by this species is a good first clue to identity, as the species is almost always associated with cation rich substrates, be they rock or soils derived from them. Not many other *Lejeunea* species in New Zealand occur as lithophytes or terrestrials on limestone or calcareous mudstone, on which *L. thalassoides* is found. The combination of characters from the leaf lobe, lobule, and gynoecium will serve to confirm *L. thalassoides* is at hand. The leaf lobes have a distinct apex, which is often obtuse but may appear acute in the field. The leaf lobe apex shape is best confirmed by dissecting and slide mounting flattened leaves so that their outline is unambiguous. The lobules have a straight keel, are trapeziform in outline and have a first tooth that may be multicellular, often it is composed of two cells sitting side by side, or is a triangular tooth composed of two or three cells. Thirdly, female plants have gynoecia subtended by small-statured subfloral innovations that terminate growth after a few gyres, and do not continue vegetative growth, occasionally gynoecia are not subtended by a subfloral innovation, which is an unusual circumstance within *Lejeunea* from Australasia.

The long basal stipe on the perianth is shared with *L. amphinephea*, and the two species are the most likely to be confused with each other in the New Zealand flora, for further guidance on differentiating *L. thalassoides* from *L. amphinephea*, particularly when small statured plants expressing a high percentage of explanate lobules are at hand, see the recognition section of *L. amphinephea.*

Etymology: from the ancient Greek θαλασσοειδής, a descriptor of a light sea-green, such as that which occurs in near-shore coastal waters under an overcast sky, in reference to the luminescent green colour of the living plants, and the cation-rich rocks they are associated with.

Conservation: Listed in de Lange *et al.* (2020) as *Lejeunea* (a) (WELT H10386; Waitomo). *Lejeunea thalassoides* is currently known from two localities in the North Island but is more widely distributed in South Island. Often, but not always, *L. thalassoides* occurs in association with basicolous substrates including basalt and limestone. We suggest that the current listing (de Lange *et al.,* 2020) of Naturally Uncommon (Range Restricted) is appropriate.

Specimens examined: New Zealand: New Zealand, North Island, Hawkes Bay Ecological Region, Heretaunga Ecological District, Tangarewai Stream catchment, Monckton Scenic Reserve, 39°57.816'S 176° 16.906'E, 290 m, 16.X.2009, *M.A.M. Renner 4408* (AK314735); South Island: North West Nelson, Takaka Hill, Harwoods Hole track, 740 m, 30.X.2004, *D. Glenny 9235* (CHR 571826); Cass-Canterbury, Woolshed Hill, XI.1960, *L. Visch* (CHR 631269); Pareora Ecological Region, Orari Ecological District, Peel Forest Scenic Reserve, Rata Falls track, 10.X.2015, *D. Glenny 13030b* (CHR 638295); Canterbury, Waimate, in forest, V.1901, T.W. N. Beckett, ex herb Levier 2746 (G-19642); Otago, Matukituki Valley near East and West Branches junction, 360 m, 30.XI.2002, *D. Glenny 8759* (CHR 571529); Dunedin, Fraser's Gully, 6 Apr 1973, *J. Child* (WELT-H011266); Dunedin, base of Flagstaff Hill, 27.X.1949, *K.W. Allison H4673* (CHR 556139); Dunedin, Bethune's Gully, 14.XI.1949, *K.W. Allison H4932* (CHR 556178); Dunedin, Fraser's Gully, 6 Apr 1973, *J. Child* (CHR 424338); Southland, Bluff-Invercargill-Winton, June-July 1874, *S. Berggren* (CHR 263554); Old Man Range, I.1961, *L. Visch* (CHR 631270); Dunedin, Apr 1874, *S. Berggren* (G-19654);

21. **Lejeunea tumida** Mitt., Fl. Nov.-Zel. 2: 157. 1854.

Original material: Hab. Northern Island: on trees, Auckland, Sinclair. Amongst mosses, in ravines near Wellington, Stephenson. Tehawera, etc., Colenso.

Type: New Zealand, Auckland, Dr Sinclair, ex herb W. Mitten (Lectotype designated by Grolle (1982): NY; isolectotypes: MPN, Hb. Hodgson 13029 WELT H003394!).

Lejeunea tumida is endemic to New Zealand, where it is common in lowland forests in the North Island. Reports of this species from Australia and Tasmania are based on misidentifications of other species, mostly *Lejeunea gracilipes*, which also has an eplicate perianth. For description, illustration and details of ecology and distribution see Renner *et al.* (2010).

INCERTAE SEDIS

Two other entities from the Surville cliffs of North Cape (*de Lange 10087, 10112)* are not accommodated within the synopsis above; their status and relationships require further investigation.

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