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A revision of New Zealand *Porella* (Porellaceae: Marchantiophyta) integrating morphological and molecular evidence

Matthew A.M. Renner[1,2] & David S. Glenny[3]

[1]National Herbarium of New South Wales, Botanic Gardens of Sydney,
Australian Botanic Garden, Locked Bag 6002, Mount Annan, NSW 2567, Australia
[2]Herbarium, Auckland War Memorial Museum, Auckland, New Zealand
[3]Manaaki Whenua, P.O. Box 69-040, Lincoln 7640, New Zealand

Correspondence: matthew.renner@botanicgardens.nsw.gov.au

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Abstract

Patterns of morphological variation in New Zealand *Porella* L. are complex. Intra-specific morphological variation has at least five contributing factors, including pronounced sexual dimorphism, substrate contact, hierarchical substructure, allometry and developmental stochasticity. The complexities introduced by these factors are unprecedented, and in part explain previous treatments of New Zealand plants as belonging to a single variable species. Morphological and molecular evidence support the recognition of six *Porella* species in New Zealand, *P. amoena* (Colenso) E.A.Hodgs., *P. atroviridis* Glenny & M.A.M.Renner sp. nov., *P. elegantula* (Mont.) E.A.Hodgs., *P. pacifica* M.A.M.Renner sp. nov., *P. pulcherrima* S.Hatt., and *P. robusta* M.A.M.Renner & Glenny sp. nov. These six species differ in details of leaf, lobule, and underleaf size, shape, and pouch production, patterns of male branch production and male bract form, female bract shape and dentition, and in shoot architecture. Most diagnostic characters can only be accessed by dissection, which is essential for accurate identification. The six species exhibit ecological and geographic differences. *Porella atroviridis* is restricted to the eastern sides of the North and South Islands, and the Chatham Islands, always in association with sites underlain by cation-rich bedrock. *Porella pulcherrima* occurs on the drier eastern side of New Zealand, in association with a wide range of bedrock types, and may grow above the treeline. *Porella elegantula* occurs in cold-temperate, hyper-humid forests and scrubs throughout New Zealand, though it is uncommon in the northern half of the North Island. *Porella amoena* and *P. robusta* are widely distributed in cool and warm temperate rainforests. *Porella pacifica* occurs in the New Zealand Botanical Region only on the Kermadec Islands, but is also in Fiji and may prove more widespread across islands of the South Pacific. Four other species are all endemic to New Zealand. *Porella elegantula* has been reported from Norfolk Island, however, this report is unlikely given the distribution and ecology resolved for *P. elegantula* in New Zealand, and critical re-appraisal of Australian material attributed to *P. elegantula* is warranted.

Introduction

The 80+ currently accepted species of *Porella* L. are all relatively large plants with regularly pinnate to bipinnately branched shoot systems and are typically epiphytic or lithophytic. The genus is easily recognised by the unlobed underleaves, incubously inserted bilobed leaves with ± ligulate lobules having a narrow transverse stem insertion, and perianths that are dorso-ventrally compressed. *Porella* has a centre of diversity in tropical regions but extends to boreal regions in the north, and subantarctic regions in the south. Australasia is surprisingly species-poor, with one species, *P. cranfordii* Steph. currently accepted for Australia, and another, *Porella elegantula* (Mont.) E.A.Hodgs. currently accepted for New Zealand and Norfolk Island (So 2002).

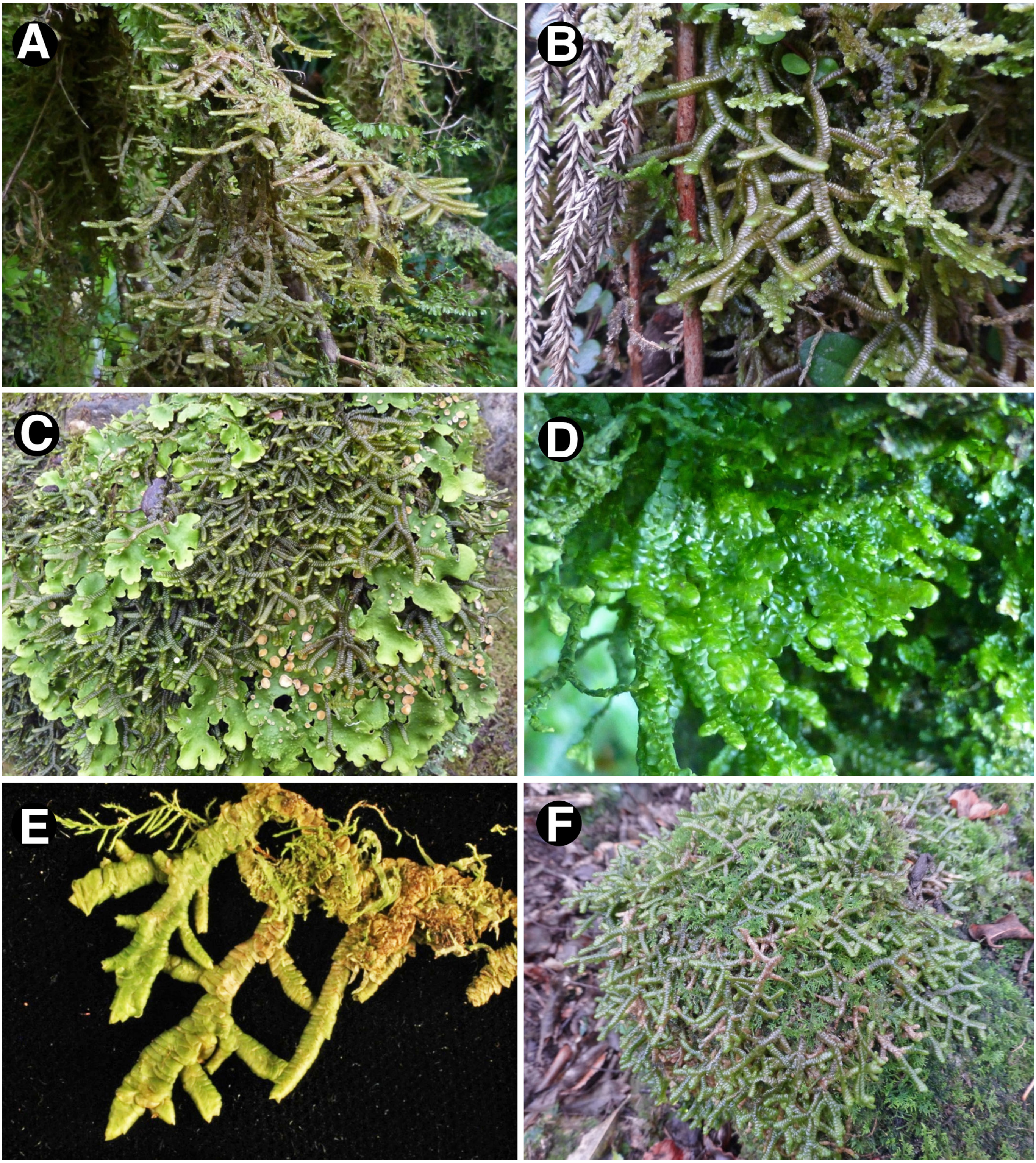

Figure 1. New Zealand *Porella* in situ, illustrating the diversity of growth form previously attributed to a single, variable, species; but re-interpreted in this work as comprising six species, five of which are featured here. A, B: *P. robusta*. C: *P. elegantula* D: *P. pulcherrima* E: *P. amoena.* F: *P. atroviridis.* All photos by David Glenny, not to scale.

Porella elegantula (as *Madotheca* Dumort.) was first reported for New Zealand by Montagne (1843) based on plants collected by Hombron from the Auckland Islands. The following year Hooker and Taylor (1844) published *Jungermannia partita* Hook.f. & Taylor, for plants also from the Auckland Islands collected by Hooker. Forty years later, two more species were described from the Hawkes Bay of the North Island by Colenso (1887), but since 1887 studies of New Zealand *Porella* have been few. Theodor Herzog recognised, but was unfortunately not able to publish, a new species from the South Island. This species was 're-discovered' in herbarium material by Hattori, who concurred with Herzog's assessment and published *P. pulcherrima* Herzog ex S.Hatt. as new in 1971 (Hattori 1971, 1986). The next, and most recent, study of New Zealand *Porella*, which encompassed Australia and the Pacific, was completed by So (2002) who recognised a single species for the Australian mainland, and a single broadly circumscribed species for New Zealand. The three-marker *Porella* phylogeny published by Hentschel *et* *al*. (2007) included no representatives from Australia or New Zealand. All studies of New Zealand *Porella* completed to date have been informed by qualitative appraisal of morphology only.

The genus *Porella* has, like many liverworts, a reputation for high phenotypic plasticity and rather ill-defined species boundaries (Boisselier-Dubayle *et al*. 1998; Bischler *et al*. 2006). Many species exhibit morphological intergradation or overlap that renders morphological circumscription problematic (Hattori 1978). When So (2002) synonymised *P. pulcherrima* with *P. elegantula,* the occurrence of bluntly dentate-angular stem underleaves in several collections, including those by Berggren and the type material of *P. amoena,* and the fact that saccate underleaves were not well-developed in all specimens examined were both cited as evidence supporting the recognition of a single variable species (Figure 1). The conclusion that "from the hundreds of specimens of *P. elegantula* examined, *P. pulcherrima* is conspecific with the former species" (So 2002: 9) followed from this interpretation of character variation. The inference of a single variable *Porella* species in New Zealand is, however, not entirely satisfactory. Two, and even three, morphotypes may co-occur. Among co-occurring morphotypes there are evidently few if any morphological intermediates. Some morphotypes are associated with particular substrates, including cation-rich rock.

In *Porella,* as in many other liverwort genera, molecular techniques have provided valuable insights upon which morphological variation within and among species can be better understood (Boisselier-Dubayle and Bischler 1994; Therrien *et al*. 1998; Bischler *et al*. 2006), and for substantiating the systematic significance of subtle morphological differences when circumscribing phylogenetically distinct species (e.g. Heinrichs *et al*. 2009, Renner *et al*. 2011, 2013; Medina *et al*. 2012). Here, we complete a re-examination of patterns of morphological variation informed by a small molecular data set designed to test the hypothesis that a single variable species of *Porella* is present in New Zealand.

Material and Methods

Study material

Around 1000 specimens held in the herbaria AK, CHR, F, NSW and WELT were examined as part of this study. These were complemented by field-collected material from around New Zealand gathered by the authors and colleagues.

Molecular data collection and analysis

Eighteen specimens representing the range of morphological variation in New Zealand were included in the molecular data set (Table 1). At the time specimens were selected for inclusion in the molecular data collection (July 2012), *Porella pacifica* M.A.M.Renner was not known to the authors and was not present within the suite of specimens then available. From each specimen, clean shoot tips comprising the meristem and immature leaves were excised to obtain 25–50 mm^2 of cleaned material. Total genomic DNA was extracted using the DNeasy Plant Minikit (QIAGEN Pty Ltd, Sydney Australia). Two chloroplast markers were sequenced, (1) the *trn*G G2 intron and the plastid *trn*L-F region including the *trn*LUAA group1 intron and the *trn*L-F intergenic spacer, hereafter *trn*L-F, with primers trnGF (CCCGCATCGTTAGCTTG) and trnGR (GCGGGTATAGTTTAGTGG); and A50272 (ATTTGAACTGGTGACACGAG) and B49317 (CGAAATCGGTAGACGCTACG) (Taberlet *et al*. 1991; Pacak and Szweykowska-Kulinska 2000). Polymerase chain reaction (PCR) was carried out using the following protocols. F For *trn*L-F each 15 µl reaction contained 1.5 µl 10× PCR Buffer, 1.5 µl 20 mM MgCl$_2$, 0.9 µl of each primer at 10 µM concentration, 0.12 µl of 1% BSA, and 0.12 µl of Immolase Taq. For *trn*G each 15 µl reaction contained 1.5 µl 10× PCR Buffer, 0.75 µl 20 mM MgCl$_2$, 0.9 µl of each primer at 10 µM concentration, 0.12 µl of 1% BSA, and 0.08 µl of Immolase Taq. The temperature profile used for sequencing was 95°C for 10 minutes, then 35 cycles of 95°C for 1 min, 1 min at annealing temperature of 53°C then 72°C for 1 min, followed by a final extension step of 72°C for 10 min. The same primers were used for sequencing of cleaned PCR products by Macrogen Inc., South Korea (www.macrogen.com). For both DNA markers, forward (5′–3′) and reverse (3′–5′) sequences were assembled and checked for inaccurate base calling using Geneious v.6 (Drummond *et al*. 2012). Consensus sequences were aligned by MUSCLE (Edgar, 2004) on the CIPRES portal (Miller *et al*. 2010) and manually edited in BioEdit 5.0.9 (Hall 1999) following alignment rules and principals of homology outlined in Kelchner (2000) and Morrison (2006).

Table 1. Voucher details for New Zealand *Porella* specimens utilised in molecular analyses.

Species	Island	Georeference	Date	Collector	Collection	Haplotype	trnG	trnL-F	Voucher
Porella amoena	North Island	34.4086 S 173.0364 E	2011-Sep-21	*P.J. de Lange*	*9976*	A	PZ162980	PV976729	AK327778
Porella amoena	North Island	34.4086 S 173.0364 E	2011-Sep-21	*P.J. de Lange*	*10109*	B	PZ162978	PV976728	AK327941
Porella amoena	South Island	42.6215 S 171.1241 E	2012-Feb-17	*M.A.M. Renner*	*6173*	C	PZ162972	PV976726	NSW895499
Porella amoena	South Island	41.0943 S 172.5688 E	2012-Feb-19	*M.A.M. Renner*	*6257*	C	PZ162973	PV976729	NSW896390
Porella atroviridis	South Island	46.042 S 167.704 E	2010-Dec-06	*D.S. Glenny*	*11064*	D	PZ162979	PV976720	CHR618683
Porella elegantula	South Island	41.2163 S 173.9832 E	2012-Feb-11	*M.A.M. Renner*	*6060*	I	PZ162965	PV976710	NSW895335
Porella elegantula	South Island	41.3141 S 173.5738 E	2012-Feb-12	*M.A.M. Renner*	*6065*	I	PZ162967	PV976711	NSW895340
Porella elegantula	South Island	42.9290 S 171.5561 E	2012-Feb-14	*M.A.M. Renner*	*6096*	I	PZ162969	PV976712	NSW895371

Species	Island	Georeference	Date	Collector	Collection	Haplotype	trnG	trnL-F	Voucher
Porella elegantula	South Island	44.0973 S 169.3587 E	2012-Feb-15	*M.A.M. Renner*	*6116*	H	PZ162970	PV976713	NSW895386
Porella elegantula	South Island	44.0803 S 169.3901 E	2012-Feb-15	*M.A.M. Renner*	*6138*	K	PZ162971	PV976714	NSW895438
Porella elegantula	South Island	40.8482 S 172.8703 E	2012-Feb-20	*M.A.M. Renner*	*6260*	I	PZ162975	PV976714	NSW896395
Porella elegantula	South Island	45.9931 S 167.3836 E	2010-Dec-06	*J. Salter*	*s.n.*	J	PZ162981	PV976725	AK322896
Porella pulcherrima	North Island	39.9324 S 176.2996 E	2012-Feb-21	*M.A.M. Renner*	*6261*	F	PZ162976	PV976722	NSW896399
Porella pulcherrima	North Island	39.9324 S 176.2996 E	2012-Feb-21	*M.A.M. Renner*	*6263*	F	PZ162977	PV976723	NSW896402
Porella pulcherrima	South Island	41.13 S 172.6085 E	2012-Feb-19	*M.A.M. Renner*	*6258*	G	PZ162974	PV976724	NSW896392
Porella robusta	South Island	41.2153 S 173.9801 E	2012-Feb-11	*M.A.M. Renner*	*6061*	E	PZ162966	PV976717	NSW895336
Porella robusta	South Island	41.3144 S 173.5734 E	2012-Feb-12	*M.A.M. Renner*	*6078*	E	PZ162968	PV976718	NSW895353
Porella robusta	South Island	42.0406 S 171.3993 E	2012-Feb-18	*M.A.M. Renner*	*6228*	E	PZ162961	PV976716	NSW895689

These eighteen New Zealand individuals from which both *trn*G and *trn*L-F sequences were obtained were included in haplotype analyses. Sequences were concatenated, and haplotype networks were created using statistical parsimony analysis (Templeton *et al*. 1992) in TCS v.1.3 (Clement *et al*. 2000) based on concatenated data. Separate haplotype networks are expected to comprise single species or a few closely related species groups (Hart and Sunday 2007, Pons *et al*. 2006). Gaps were treated as missing, and networks remained connected if the 95% connection limit was less than 20 steps, otherwise separate networks were reconstructed.

Morphology

We completed an analysis of character variation among guided by the results of analysis of molecular sequence variation. All elements of plant form were included in this analysis, from shoot architecture to spore size and ornamentation. Material was rehydrated for manipulation including slide mounting of shoot systems, dissection of leaves, underleaves, bracts, and other parts; and sectioning of stems and perianths. Illustrations were composed with the aid of a Leitz Wetzlar camera-lucida attached to a Leica Laborlux S compound microscope, which were then inked and shaded freehand.

Results

Molecular variation

The alignment for *trn*L-F was 649 bases long, and *trn*G 1291 bases long, for a combined alignment length of 2002 bases, of which 83 were parsimony informative, including the indels not included in the haplotype analysis. The 18 sampled individuals formed a single network comprising five haplotype groups, each separated by between 12 and 21 inferred sequence changes (Figure 2). Two of these groups contained a single haplotype, the other three comprised two to four haplotypes each separated by one or two steps. Three haplotypes were recovered in the *Porella amoena* samples from the North and South Islands. All three sampled individuals of *P. robusta* were from the South Island and shared the same haplotype. *Porella pulcherrima* yielded two haplotypes, one for the two North Island samples, the other for the South Island individual. *Porella elegantula* exhibited the greatest haplotype diversity, all of which was expressed by individuals from the South Island, no North Island samples being included. Only a single individual of *P. atroviridis* was sampled. Pairs of haplotypes included in the sample were sympatric, including haplotypes E and I at Queen Charolette Sound, and haplotypes G and C at Cobb Valley.

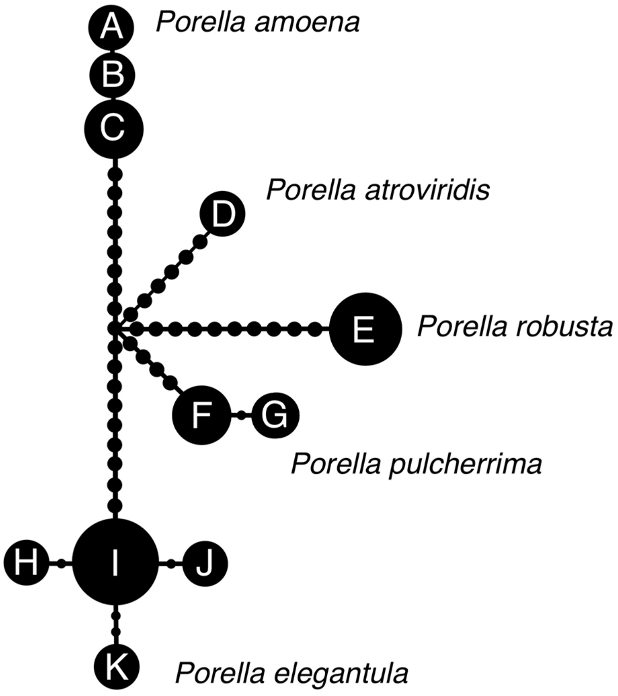

Figure 2. Haplotype network for New Zealand *Porella* estimated from concatenated *trn*G and *trn*L-F sequences. Circle diameter is proportional to the number of a given haplotype within the sample set, haplotypes are separated by branches whose length is proportional to the number of inferred base-pair differences in sequence composition. Inferred, but unobserved, haplotypes linking observed haplotypes are marked by small solid circles. The five clusters of haplotypes correspond with five of the six species present in New Zealand, *Porella pacifica* was not included in this dataset as it does not, so far as is known, occur on mainland New Zealand.

Morphology

Shoot morphology: Shoot width varies from 1.7–6.0 mm, and shoot length varies up to 140 mm, and may be variable within individuals. Branching is regularly 1-pinnate or 2-pinnate in some individuals, and pseudo-dichotomous or irregular in others, but does not vary within individuals.

Leaf-lobes: Shape of leaf lobes varies from rotund to ovate-rectangular. Leaf lobes are always imbricate, though the degree of imbrication exhibits some variability between individuals. Lobe margins are almost always entire, though in some individuals, several small marginal teeth are present on lobes adjacent gynoecia. In some individuals lobe margins are reflexed, mostly at the antical base, by the dorsal end of stem insertion. Some individuals with this feature also produce irregular appendages at the antical base of the lobe margin occasionally, usually on larger lobes. Some individuals have conspicuously scalloped postical lobe margins, formed by pronounced undulations that give the lobe margin a 'curtain'-like appearance. Leaf-lobes may be auriculate at one or both bases, and the degree of auriculation varies between individuals. The leaf lobe apex is typically inrolled, however there is variation in which portion of the lobe margin is inrolled with the apex, and how sharply inrolled the apex is.

Leaf-lobe cells: Size of leaf-lobe cells varies from 15–40 µm, shape consistently isodiametric. Secondary thickenings are not deposited on medial cell walls, but those at cell wall junctions vary from concave, to triangular, to nodular trigones.

Oil-bodies: Oil-body morphology is invariant across the individuals for which oil-bodes are known, being consistently smooth, homogeneous, colourless, fusiform, small (3–7 µm), and arranged in a submarginal ring (Figure 3). The number of oil-bodies per cell is around 20, and generally increases with distance from the shoot apex, in other words, as cells age they accumulate more oil-bodies.

Leaf-lobules: Shape of leaf-lobules varies from triangular to ovate-lanceolate to oblong. Lobules may be orientated parallel to the shoot axis, so that their apex points toward the shoot tip, or may be inclined to the shoot so their apex points outward, away from the shoot tip. Lobules may be approximately symmetrical, or asymmetrical with margins reflexed to varying degrees, along the basal lobule margins. Flange-, pouch- or sac-like structures may be formed on the lobule margin at the base of the antical insertion. The margins may be entire, irregular, crenulate, or armed margins with broad triangular teeth. In this work we call the 'sacs' at the base of lobule and underleaf margins pouches for two reasons. Firstly, the term associated with sac, 'water-sac' is misleading because the volume of water that may be stored in lobules is a fraction of that stored within the plant matrix and is entirely ineffective at alleviating desiccation. Secondly, 'water sac' has been applied most frequently to *Lejeunea*-type lobules, which enclose the ventral leaf surface, but it has also been applied to *Frullania*-type lobules, wherein the dorsal leaf surface is enclosed. Because the pouches of *Porella* are elaborations of the lobule and underleaf margin, and do not involve invagination of one or the other surface of a lobe in its entirety, they are not homologous to the lobules of Lejeuneaceae, Frullaniaceae, Jubulaceae, Radulaceae, or Goebeliellaceae, and therefore a distinct and different term of reference for them is appropriate. We use pouch because they usually hang from and below 'the belt', the line delimited by the stem insertion. They bring to four the modes employed by Porellales, in the broad sense, to bear 'sacs'. The wide occurrence, and multiple origins by different modes imply a significant function for sacs, one that is, in our opinion, more likely tied to plant nutrition than desiccation resistance.

Underleaves: Underleaf shape varies from ovate-lanceolate to rotund. Underleaves vary in similar fashion to lobules in other features, they may be approximately symmetrical, or asymmetrical; the margins may be entire, irregular, crenulate, and the margins may be reflexed to varying degrees. Flange-like, pouches or pouch-like structures may be formed at the base of the underleaf margin. Where no pouch-like (or similar) structures are formed, underleaf bases may be auriculate, or may form a long decurrent wing running down the lateral stem surface, particularly on asymmetrical underleaves. In some specimens a continuity in lobule base from auriculate to pouched may be observed. The underleaf lamina may be plane or it may be elaborated medially into an outwardly (on the ventral surface, away from the stem) projecting medial 'boss', so-named for its resemblance to the central boss of bronze-age and medieval shields.

Stem anatomy: Stem anatomy is similar in all individuals investigated. The stem of *Porella* has a sharply differentiated cortical layer comprised of 2–4 layers of cells whose walls bear heavy secondary thickenings that constrict the cell lumen. The secondary thickenings are brown pigmented, though the intensity of this pigmentation is greatest in the outermost cortical layer. The transition to medullary walls is abrupt. Medullary cells are larger than cortical cells and have walls that are unthickened and unpigmented bar triangular trigones at cell wall junctions. The number of cortical cell layers, and the number of cortical and medullary cell rows may vary between individuals.

Branching: Branching is exclusively terminal, and always of the *Frullania*-type. Although branch type is invariant between individuals, the shape of appendages associated with *Frullania*-type branches does vary between individuals. In most individuals the branch half leaf is ± identical to the surrounding leaf-lobes, however in a few individuals the branch half leaf is larger and is ovate-triangular rather than ovate as in surrounding lobes. The first branch underleaf is generally similar to surrounding underleaves, though in some individuals it tends to be highly asymmetrical. The first branch underleaf in the lectotype of *Porella viridissima* (Mitt.) Grolle (a tropical species from north-eastern Australia and New Guinea) was fused with the lobule of the preceding leaf, but this feature was not observed in any material from New Zealand.

Asexual reproduction: Most Australasian individuals exhibit no evidence of asexual reproduction. However, a few individuals bear conspicuous evidence that their leaf-lobes erode, the resulting fragments may function as asexual propagules. Even if this is not the case, there is variation in the propensity for leaf lobe fragmentation among individuals.

Androecia: In all *Porella* species androecia are produced on specialised branches. Androecial branches are always determinate, and bear lobes and lobules modified to house antheridia, as is typical of Porellales. Underleaves exhibit varying patterns of fusion to adjacent lobules, in some individuals underleaves are fused on only one side, in others underleaves are fused to both adjacent lobules. Androecial branches are produced either in regular alternate pairs, or as scattered individual branches. The density of androecial branches along shoots varies. The length, and correspondingly the number of antheridial bract pairs per branch is also variable, from one to four pairs of bracts in some, and four to seven and up to eleven in others.

Gynoecia: Gynoecia are borne on short lateral branches that bear only one or two gyres of bracts. The branch half-leaf associated with gynoecial branches is as for vegetative branching. The bracteole, however, is well differentiated from vegetative underleaves, and in all individuals examined is oblong with an obtuse to truncate apex. The bracts are typically asymmetric, the lobules are lanceolate-ovate, the lobes ovate to lanceolate ovate, both may have acute or obtuse apices. The margins of bracts and bracteoles may be entire, or densely spinose-ciliate.

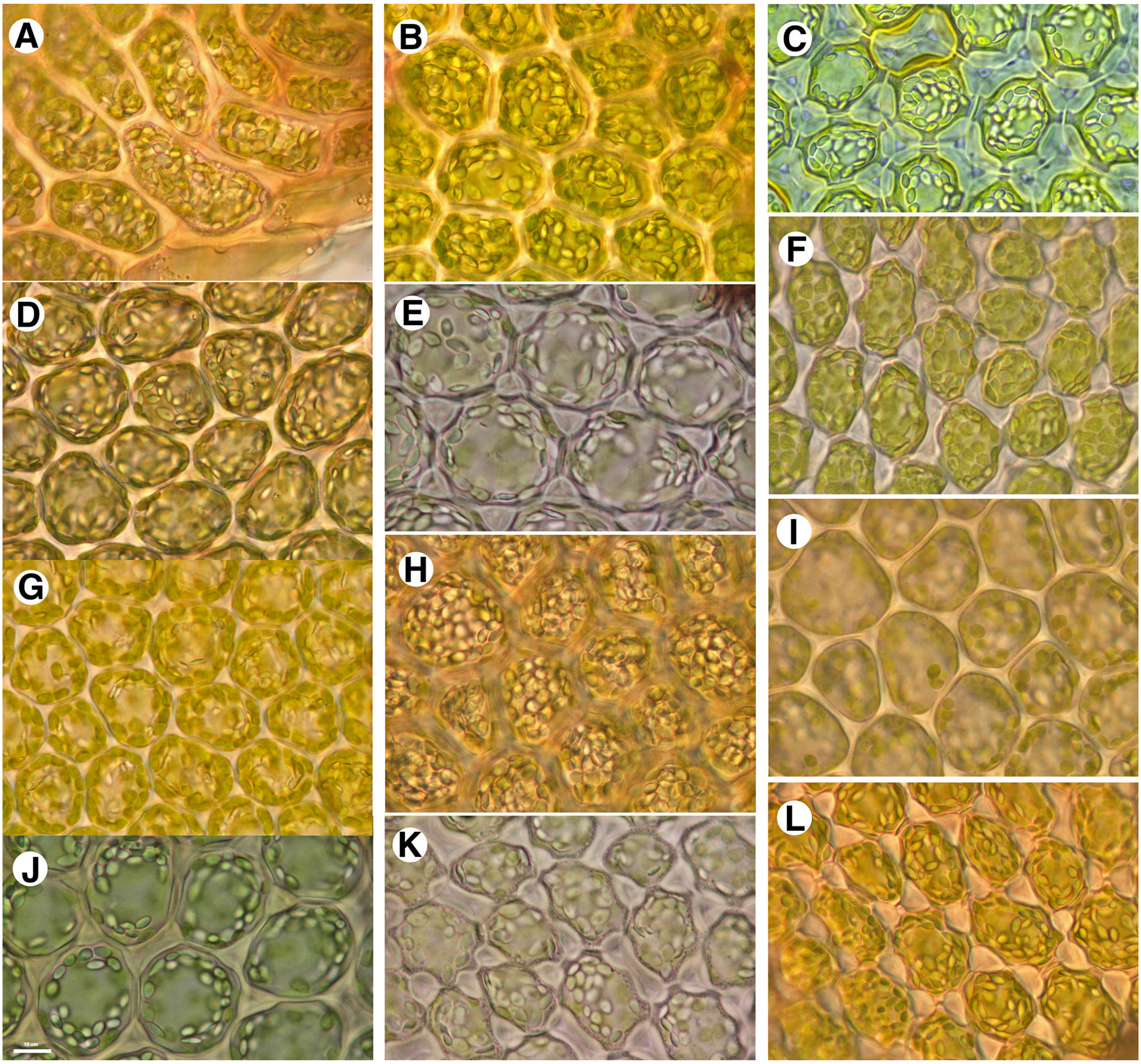

Figure 3. Oil-bodies and medial cell walls of three New Zealand *Porella* species, illustrating the relatively consistent expression of numerous, small, smooth, homogeneous spheroidal to ellipsoidal, colourless oil-bodies in leaf medial and basal cells. Oil-body number varies within individuals and tends to increase with leaf age. A: *P. atroviridis* basal cells, *Glenny 14719,* wherein oil-bodies appear green due to light passing through chloroplasts, homogeneous, broadly ellipsoidal with rounded tips to narrowly ellipsoidal with acute tips, this variation suggests the actual shape is discoid and the disk is 3.9–6.5 um diameter and 1.7 um thick. B: *P. atroviridis* medial cells, *Glenny 14719,* in which the suggestion of discoidal oil-body shape is present but not so pronounced as in the basal cells. C: *P. elegantula* medial cells, *Glenny 14934a*. D: *P. robusta*, *Glenny 14724*. E: *P. robusta*, *Glenny 14459*. F: *P. elegantula* medial cells, *Glenny 14727.* G: *P. robusta*, *Glenny 14666*. H, I: *P. amoena*, *Glenny 14659*. J: *P. pulcherrima* medial cells, *Glenny 14274*. K: *P. elegantula* basal cells, *Glenny 14470*. L: *P. amoena*, *Glenny 14664*. All photos by David Glenny, to same scale, scale bar 10 µm in image J.

Perianths: Perianths in *Porella* are dorso-ventrally compressed and bear little or no evidence of a ventral carina, they are broadly ovate and may approach a nearly rotund shape. Given that trigonous perianths bearing three carinae (two lateral and one ventral) appear to be plesiomorphic within the Porellales, the perianths of *Porella* probably represent an apomorphic state (Renner, unpublished data). In New Zealand, the perianth mouth, as far as is known, is always narrow and heavily spinose ciliate, while Australian species have campanulate perianths with a wide mouth with dentate labia. The perianths of *Porella* have a short stem perigynium at their base. This structure is the result of secondary growth activity at the apex of the gynoecial branch (Schuster 1966) which elevates the margin of the gynoecial branch apex up and around the sporophyte foot. The perianth and calyptra bases are elevated above their original position adjacent the female bracts. The stem perigynium in New Zealand *Porella* is 3- or 4-stratose throughout, and bulbous, the walls are unpigmented and unthickened with the exception of the free outer and inner walls that have heavily brown-pigmented secondary thickenings. The perianth walls in New Zealand *Porella* are bistratose at their base and unistratose above and also bear heavy brown thickenings on their outer and inner free walls. Hattori (1971) noted that he was aware of only three “Asiatic” (Hattori included southern temperate Australasia in his definition of Asiatic) species of *Porella* that possessed perianths with constricted perianth mouths, *P. elegantula, P. pulcherrima* and *P. novoguinensis* S.Hatt.

Sporophytes: In New Zealand *Porella* the sporophyte foot is obconical with a marginal wing. The seta is massive, with a weakly differentiated cortex, of c. 60 cell rows, and a medullar of c. 150 cell rows. Bulging trigones are present at cell wall junctions within the medullar. The capsule is spherical, dehisces nearly to the base into four valves. The valves are three to four stratose, without differentiated regions within strata. The outermost layer bears simple nodular thickenings at cell wall junctions, these are orange-brown pigmented, and distributed haphazardly, in a one- or two- phase pattern.

Discussion

The individuals included in our molecular dataset formed five haplotype groups, each of which corresponded to a different morphotype, this morphotype being shared by all the individuals of the group. Each morphotype was characterised by qualitative and quantitative character states that were unique, either alone or in their combination. That morphological and molecular data delimit the same groups of individuals, with groups separated by unique and distinctive combinations of morphological character states and mutually exclusive molecular sequences is interpreted as evidence against the hypothesis that New Zealand *Porella* comprise a single variable species. Were that the case, we would not expect to observe individuals subdividing into such distinct morphological and molecular subgroups as observed in this study, neither would we expect such perfect correlation between the morphological and molecular subgroups in terms of individual membership. Neither would we expect the observed degree of divergence in qualitative morphological character states. The recovery of five haplotype clusters, each corresponding to a different morphotype, and the existence of a sixth morphotype in herbarium material, support the recognition of six *Porella* species in New Zealand. To accommodate the empirical data gathered by this study, we refine the circumscription of *Porella elegantula* by narrowing its concept. We also reinstate two species, *P. amoena* (Colenso) Martin and *P. pulcherrima* Herzog ex S.Hatt., whose type specimens correspond in form with the morphotype of individuals belonging to two of the haplotype clusters. For the remaining morphotypes, and their corresponding molecular clusters, we describe three new species, *P. atroviridis* Glenny & M.A.M.Renner, *P. pacifica* M.A.M.Renner, and *P. robusta* M.A.M.Renner & Glenny.

Our claim that evidence refutes a broad circumscription is justified within the overarching framework governing the operation and progress of taxonomy and systematics, which is a general comparative method that permits an assessment of the generality of biological phenomena (de Pinna 1991: 371) where the phenomena to be explained include the existence of different kinds of organisms and the similarities and differences between them. These phenomena are in general explained by three major classes of causal biological relationships phylogenetic, tokogenetic, and ontogenetic (Hennig 1966). Explanations in systematics proceed from effects – the observed similarities among members of a group of organisms – to possible explanatory hypotheses via causal relationships (Fitzhugh 2005). These explanatory hypotheses call upon evolutionary theory to achieve their explanation.

From a systematic viewpoint, our task then is to explain the correlated variation in the occurrence of these distinctive features across individuals, it is not to simply explain variation away. In some sense, a species name serves as an answer to specific causal questions regarding observed properties of organisms (Fitzhugh 2005). In New Zealand *Porella*, an example of such a question is ‘why do some individuals have lobule margins invaginated at the base forming a pouch, while other individuals have lobules with plane margins?’ Questions of the same form apply to all other characters exhibiting variable states that may be used to group individuals, including undulate versus plane leaf-lobe margins; entire versus ciliate-spinose female bract margins; nodular versus triangular trigones; rotund versus oblong underleaves; decurrent versus ‘normal’ underleaf insertion; among many others. The inferred explanatory hypotheses (species hypotheses) account for the observed distribution of character states, as products of the origin of novel morphological features in combination with past tokogenetic events in separate groups of organisms (Fitzhugh 2005).

With regards species hypotheses, any character state that may have arisen, propagated, and fixated within a tokogenetic group is potentially informative, because the distribution of character states provides clues as to tokogenetic group membership (Fitzhugh 2005). However, discriminating among intra-specifically variable characters, and inter-specific differences can be challenging *a priori*, especially in quantitative characters. This is part of the reason molecular data is so helpful for resolving challenging species complexes, in liverworts and other plant groups. Distinguishing intra- from inter-specific variation is, of course, a different problem from identifying and quantifying morphological variation in the first instance. Unfortunately, previous studies of New Zealand *Porella* failed to even delimit, let alone resolve, many of the dissimilarities that do exist between the six New Zealand species recognised here. Examples of overlooked character states include the entire female bract margins in *Porella atroviridis*, a state unique to that species in New Zealand; the absence of lobule and underleaf pouches in *P. atroviridis* and *P. pulcherrima*, the recurved underleaf margin in *P. robusta*; the red-brown colouration in some individuals of *P. pulcherrima*. Informative variation also exists in antheridial branches and antheridial bracts. Though these structures are described within the generic description, they are not mentioned in any species description by So (2002), implying invariance among species. New Zealand *Porella* exhibit differences in antheridial branch length and patterns of fusion of antheridial bracts and bracteoles which is informative at species level. Informative variation also exists in underleaf shape; the production and shape of flanges, sacs, or their absence and corresponding presence of long decurrent wings at the underleaf base. Greater logical specificity in character statements implies greater empirical content of those character statements (Magee 1973 cited in de Pinna 1991) and the species hypotheses they are based on. Indeed, the description of character state variation is a good place to seek an explanation for the omission of the diversity of New Zealand *Porella* species documented here from the most recent previous revision (So 2002).

Species names are formal placeholders for species hypotheses and the proposition, and refutation thereof, is more than the expression of opinion, or preference to circumscribe taxa narrowly or broadly, in the sense of the clichéd ‘lumper’ versus ‘splitter’ debate. Taxonomy strives to formulate hypotheses that best explain observational data in a manner compatible with an overarching theory, and this is a matter of evidence, which is why taxonomy is a science. There are also means of deriving testable predictions from established hypotheses, another scientific property. In the case of New Zealand *Porella,* testable predications given the hypothesis that a single species is present in New Zealand are 1) the existence of a single corresponding morphotype with characteristic parameters of morphological variation, such as normally distributed quantitative variables; and 2) the existence of a single genetic cluster, howsoever variable. Observational data obtained by our study are incompatible with these predictions, therefore the hypothesis that there is a single species has failed a reasonably strict, if straightforward, test. That is the essence of refutation defining hypothetico-deductive inference, and why we are at liberty to state this refutation in categorical terms here, and in other unambiguous instances in other plant groups (e.g. Renner *et al*. 2022). This perspective, in its general form, is nothing new (e.g. Cope & Lacy 1992; Pante *et al*. 2015). However, by asserting the falsifiability of species hypotheses, we do not make the claim that falsification implies the necessary condition that taxa must be true or false (Thiele *et al*. 2021). Like all hypotheses, they are explanatory models, compatible with an overarching body of theory, that make predictions about what we might expect to observe *if* they were true. Failure of that predictive capacity identifies falsehood, but no amount of corroboration will lead a taxonomist to truth (Popper 1972).

When liverwort taxonomists claim that species are variable, especially when variation invokes polymorphism in qualitative characters, they implicitly adopt the view that character data is an unreliable indicator of tokogenetic group membership. In other words, they adopt a position of character scepticism in which the distribution of character states among individuals is no longer capable of indicating tokogenetic group membership. In their character scepticism, liverwort taxonomists burden their species hypotheses with untested assumptions derived from outdated, and even erroneous, ways of thinking about the origins and maintenance of morphological variation. These assumptions invoke environmentally induced variation to explain the attribution of different morphotypes to single species in ways that can never be established based on study of herbarium material alone, because every observation of phenotype is confounded by genotype, given every herbarium specimen comprises a different individual. It is little surprise then, that species hypotheses so burdened by such untested assumptions fail so readily and so often in response to critical re-evaluation. This should not be misconstrued to imply that we think species names somehow represent pure factual knowledge obtainable by direct structural observation (see de Pinna 1991; Eldredge and Cracraft 1980: 38). Species inferences are fallible as they represent our current best explanation. Our understanding of any system advances when we are explicit about our uncertainties, and in this study, we think our circumscription of *Porella elegantula*, even in the narrow sense in which that taxon is re-circumscribed here, may be insufficiently resolved. However, delaying publication of this revision until such time as additional samples have been gathered from the Auckland Islands, and additional data has been collected would defer, perhaps indefinitely, the dissemination of the meaningful refinement in our understanding of New Zealand *Porella* diversity yielded by this study.

Informative character systems identified by Bischler *et al*. (2006) included 1) female bract margins, 2) lobule margins, 3) lobe apex, 4) the underleaf base, 5) the degree of fusion between male bracts and bracteoles. Several of these characters, including lobule margin armature and shape of underleaf base had been utilized by Hattori (1986) to circumscribe *P. pulcherrima*. Variation in these features was implicitly equated with infraspecific variation by So (2002), an interpretation at odds with the conclusions reached by Bischler *et al*. (2006). Many of the character systems identified by Bischler *et al*. (2006) for European *Porella* are also informative in New Zealand.

Within New Zealand, each species is associated with characteristic distributions and microhabitat preferences. *Porella pulcherrima* occurs on the eastern side of both main islands, but also in Nelson and Marlborough. These regions have lower than national average annual rainfall and typically suffer summer water deficit. *Porella pulcherrima* grows as either an epiphyte or a lithophyte and may occur on rocks well above treeline. *Porella atroviridis* also has an eastern distribution including the central eastern side of the South Island, the Chatham Islands, Campbell Island, and the lower North Island. It appears to be a facultative bascicole occurring primarily as a lithophyte on exposed basalt but also grows epiphytically on tree trunks adjacent the rocks, presumably in response to dust accumulation on bark in the overlaying vegetation. *Porella pacifica* is known in New Zealand only from Raoul Island in the Kermadec Islands group. This is evidently an Oceanian taxon that may have dispersed southward to Raoul Island from island sources to the north and north-east. *Porella amoena, P. elegantula* and *P. robusta* are all epiphytes in forest habitats and may grow together in various combinations. *Porella amoena* is found throughout the North Island and northern two thirds of the South Island, east to the

Chatham Islands, and north to the Kermadec Islands. *Porella robusta* occurs throughout the North and South Islands. *Porella elegantula* is restricted in its distribution on the North Island to higher elevation forests along the main axial ranges and is more common in wetter habitats of the South Island, and subantarctic Islands. It is not known to occur on the Chatham Islands. This distribution pattern suggests that records of *Porella elegantula* from Norfolk Island and Lord Howe Island in Australia are in error, and the plants likely belong to other species whose identity is as-yet unresolved.

Conclusion

The correlated distribution of qualitative character states, some of which are subtle, presents sound morphological grounds for species circumscription and recognition despite considerable overlap in quantitative characters associated with the size and shape of leaf lobes, lobules and underleaves. These are corroborated by patterns molecular sequence diversity. Six *Porella* species are present in New Zealand of which three are undescribed. At least four of the six species are endemic to New Zealand, and further investigation into the presence of *Porella elegantula* outside of the New Zealand Botanical Region is now warranted following the clarification of its circumscription in this study. *Porella* is another cosmopolitan genus with a centre of species richness in tropical regions, and small but distinct southern temperate elements.

Taxonomic Treatment

Key to New Zealand Porella

Dissection of hydrated lobules and underleaves from *primary* shoots **will be necessary** to access many of the features described in the key. There is no way around it, if you wish to identify *Porella* accurately and consistently, you must dissect and slide mount lobules and underleaves. Primary shoots are the main axis of pinnate shoot systems, the one from which the first order branches arise. Some of the diagnostic features mentioned are inconsistent in expression *within individuals*. Several shoots should be examined to confirm the presence or absence of various character states. New Zealand *Porella* may, rarely, form mixed mats or patches containing more than one *Porella* species.

1. Underleaves on primary shoots with pouches developed at the base on either side. Pouch expression in male *Porella amoena* is variable, therefore it is necessary to confirm firstly the sex of the material being identified and, if male, to check thoroughly several *primary* shoots for pouch development. In male *P. amoena* the underleaf base on primary shoots, when pouches are not developed, is plane and without flanges, and is ±symmetrical (compare with the underleaf base in the next couplet, the underleaves are also ± oblong. Lobules on primary shoots with pouches at the base, at least at the antical (proximal) end of the stem insertion line, with or without a second pouch at the base at the end of the postical (distal) end of the stem insertion, however male *P. amoena* lobules may not bear pouches....................................2

1: Underleaves on primary shoots lacking pouches, instead the underleaf base has irregular flanges on either side or is plane. If plane the underleaf is asymmetrical, with the insertion long the side of the stem longer on one side than the other. Lobules with irregular flanges at their base, or plane, never with pouches 5

2. Primary shoots 1.7–1.9 mm wide; stem surface with longitudinal striae (best viewed in transverse stem sections)...*Porella pacifica*

2: Primary shoots (3–)4–6 mm wide; stem surface smooth....................3

3. Underleaves with broadly and continuously rounded antical margin, rotund in the upper half, margin continuously reflexed in upper half; lamina with a prominent central boss. Lobules on primary shoots oblong and weakly falcate, not reflexed inward in upper portion, margins plane ....*Porella robusta*

3: Underleaf tapering to a narrowly rounded or truncate apex, more rhomboid in upper half, margin may be reflexed on either side but not reflexed across the apex; lamina with or without a prominent central boss. Lobules on primary shoots ligulate to ovate-falcate, usually reflexed in upper portion, either along a line oblique to or parallel with the stem, apex turn inward toward the stem in both, margins undulate, irregular or plane...4

4. Underleaves with medial boss. Lobules tapering to a narrowly rounded to obtuse apex. Leaf lobes without a conspicuous curtain formed by undulations on the ventral margin. Shoot systems irregularly or pseudo-dichotomously branched, with branches widely spaced, sometimes from one side of the primary shoot only; displacing the primary shoot to the side; secondary shoots and primary shoots similar in stature. .... *Porella elegantula*

4: Underleaves usually lacking a medial boss. Lobules ligulate, sides ± parallel to the rounded apex. Leaf lobes with a conspicuous curtain formed by undulations on the ventral margin. Shoot systems pinnately branched, branches regularly produced, from opposing sides of the shoot in alternation, not only slightly displacing the primary shoot to the side; secondary shoots smaller in stature than primary shoots. ....*Porella amoena*

5. Female bract margins entire. Underleaves rotund. Lobules triangular falcate. Plants vibrant green, lacking red pigmentation. Antheridial branches bearing 3–6(–7) pairs of antheridial bracts, with one or two pairs of sterile and ± normal vegetative leaves at the branch base; antheridial bracteole at base of male branch free on both sides, all others fused with the bract lobule on one side only ....*Porella atroviridis*

5: Female bract margins spinose-ciliate. Underleaves ovate, usually asymmetrical at base with the insertion longer down the stem on one side. Lobules triangular-ovate, not conspicuously falcate. Plants bronze-green, with or without red-brown pigmentation. Antheridial branches bearing (3–)5–8(–11) pairs of antheridial bracts, without sterile leaves at the base; antheridial bracteole at base of male branch fused with bract lobule on one side only, second from base the same, all others fused with both bract lobules...*Porella pulcherrima*

Porella amoena (Colenso) W.Martin, *Transactions and Proceedings of the New Zealand Institute* 77: 273. 1949. *Madotheca amoena* Colenso, *Transactions and Proceedings of the New Zealand Institute* 19: 296. 1887.

Original material: Hab. On trunks of trees, hilly forests, Glenross, County of Hawke's Bay; 1886: *Mr. D.P. Balfour.*

Type: New Zealand: Glenross, Hawkes Bay, on branches of trees, hilly forest, 1886, *Colenso* a 1369, ex herb. E.A. Hodgs. No. 14106 (lectotype: MPN28434!, designated by So (2002: 8); isolectotypes: ex herb Steph. G 00282363 (18260)! NY 01021228!d).

Madotheca latifolia Colenso, *Transactions and Proceedings of the New Zealand Institute* 19: 295. 1887. *syn. nov.*

Original material: Hab. on branches of trees, slightly adhering to their bark, and foliaceous lichens, and to its own under-branches; Seventy-mile Bush, County of Waipawa; 1882–86; *W.C*[*olenso*]. Forest near Palmerston, County of Manawatu; 1886: *Mr. A. Hamilton*.

Type: New Zealand: Forest near Palmerston, County of Manawatu, 1886, *Mr. A. Hamilton s.n.* (lectotype: WELT-H007723!d), designated by So (2002: 8).

Description: Forming extensive pure mats of overlapping pinnately to bipinnately branched shoots, creeping, descending, or pendulous, typically attached to substrate and mat at base of shoot and free at least around the apex, which arches outward away from the shoot toward the horizontal; shoots typically mid-green, occasionally with brown or golden brown pigments on older shoot sectors, never with reddish pigments, lobe margins not becoming hyaline in herbarium. Male and female plants sexually dimorphic, male plants smaller in stature, with less frequently branched shoot systems, antheridial branches extending slightly beyond lobe margins, plants irregularly to regularly pinnately branched, one- or two-pinnate. In female plants shoot systems 40–100 mm long, 20–30 mm across; primary shoots 3–5 mm wide. Rhizoids brown, in dense tuft from underleaf base. Leaf lobes oblong, slightly falcate, 2300–3400 µm long, 1750–2500 µm wide on primary shoots, smaller on secondary shoots; apex broadly rounded, incurved, margins entire, interior part of antical margin not scalloped or undulate, never with an irregular appendage though it may be reflexed for a short distance above the stem insertion but, when dry dorsal margin not reflexed; postical margin weakly reflexed to strongly undulate for most of its length, giving the postical margin a curtain-like appearance; antical margin incurved. Lobe medial cells isodiametric, 22–35 µm long, 19–28 µm wide, walls thin or with weak medial thickenings, between large triangular to bulging trigones, basal cells oblong 35–60 µm long, 22–35 µm wide, medial walls without thickening, trigones strong, bulging; cell wall pigments absent. Oil-bodies 12–35 per cell, ellipsoidal, 3.0–7.0 × 1.9–4.0 µm. colourless, homogeneous, and smooth, arranged in a loose spheroid around the middle of the cell around half way between the cell centre and the cell walls. Lobules broadly elliptic to oblong or slightly obovate, weakly falcate or not, 1400–2100 µm long, 700–975 µm wide on primary shoots, outer portion usually reflexed toward the shoot, especially in dry material; apex emarginate, rounded or rounded-truncate; margins entire to irregular, plane or, more usually with one or more broad undulations along the postical margin and reflexed or with a small undulation on the antical margin; pouch expression variable, with or without a pouch at the base of the antical margin, usually without a pouch at the base of the postical margin although robust shoots may bear lobules having two pouches, one at the base of each margin, pouches ovoid, lobule margins at the stem insertion may be reflexed or plane; lobule bases not auriculate. Mid-basal cells of lobules forming an indistinct zone of larger cells. Underleaves oblong to broadly ligulate, 1100–1900 µm long, 900–1450 µm wide on primary shoot, apex broadly rounded to truncate, lamina plane with central boss absent to weak, margins plane, except at base where inrolled and dilated to form a pouch adjacent to the stem insertion, one pouch on either side. Branching exclusively terminal, of the *Frullania*-type. Branch half-leaf not differentiated from adjacent leaf-lobes, or slightly smaller than adjacent leaf lobes but of like shape. Branch underleaf asymmetrically ovate to obovate, margins and apex often irregularly reflexed, with one or both margins bearing pouches at stem insertion, antical stem insertion. Stems 350–450 µm wide diameter on primary shoots, oval in transverse section, cortex c. 130 cell rows in three layers, walls heavily thickened constricting cell lumen, thickening brown pigmented, intensity decreasing from outer to inner layers, transition to medullar cells abrupt, medullary cells in c. 80 rows, walls unpigmented and unthickened except for triangular trigones at cell wall angles. Asexual reproduction absent, though the specimen from Raoul Island has fragmenting leaves and underleaves, leaving shoot sectors devoid of leaves and underleaves.

Antheridia on short, spicate, lateral, antheridial branches; branch production varying from scattered along shoots to regularly paired, by *Frullania*-type branching, 900–1500 µm long, bearing 3–5 pairs of antheridial bracts, each containing a single antheridium; antheridial stalk two cell columns, side by side. Bracteoles ligulate, apex truncate, reflexed, free from bract lobules on both sides. Antheridial bract lobes deeply concave, imbricate, apices plane, entire. Bract underleaves connote with lobules on both sides three or four cells above their respective stem insertions. Gynoecial branches produced in pairs, sometimes sequential and appearing alternate, nearly sessile comprising first branch underleaf and single ‘gyre’ of female bracts and bracteole only. Bracteole and lobules of female bracts not fused. Bracteole 750–1440 by 430–790 µm, heavily spinose-ciliate toothed on margins of upper half, lower half less so and typically bearing scattered hyaline papillae. Female bracts asymmetric, the larger with lobe 1260–2410 by 650–1280 µm, the smaller with lobe 940–1380 by 400–580 µm, ovate with obtuse apex, both heavily spinose-ciliate toothed on all margins except the basal quarter, which typically bears scattered hyaline papillae. Female bract lobules similar size in both bracts, 869–1478 µm long, 333–608 µm wide in larger, 753–1376 µm long, 405–565 µm wide in smaller, heavily spinose-ciliate toothed on all margins except the basal quarter. Perianth broadly elliptic to orbicular, 2500–3000 µm long, 2100–2500 µm wide, dorsal surface plane, ventral surface convex, sometimes with pronounced medial ridge, apex strongly recurved, mouth broad, labia free from slightly above mid-point of perianth length on either side, labia margins spinose-ciliate, perianth walls unistratose except for base where bistratose, outer walls of bistratose portion bearing heavy brown secondary thickening. Calyptra unistratose throughout, calyptral perigynium absent. Stem perigynium present, bulbous, 4- or 5- stratose throughout, enclosing sporophyte foot. Female bracts and perianth wall both attached to the top of the stem perigynium, apparently having been elevated away from the first branch underleaf by growth of the stem perigynium. Outer and inner free walls of the stem bearing heavy brown secondary thickening.

Sporophyte foot conical. Seta massive, with c. 60 cortical and c. 150 medullary cell rows, cortical cells slightly smaller than those in the medulla, both with nodular trigones at cell angles. Capsule spherical, splitting into four valves, valves polystratose, cells of outer most layer quadrate to short-rectangular, bearing weak nodular thickenings on all longitudinal walls, in a typical one-phase pattern. Spores 35-50 µm diameter, with primary ornamentation of barbed echinae. Figures 4, 5.

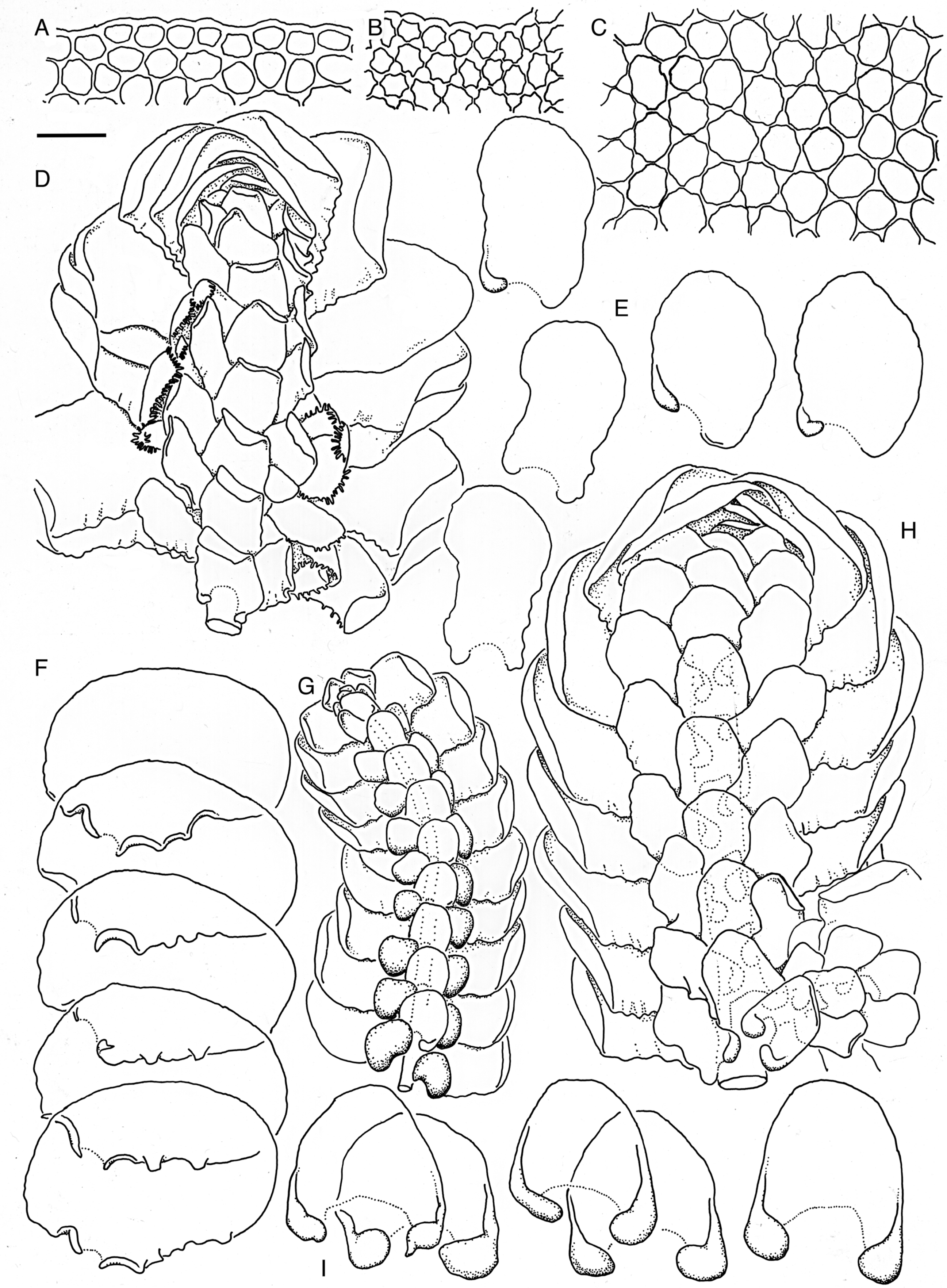

Figure 4. *Porella amoena* (Colenso) W.Martin. A. Cells of the dorsal leaf lobe margin AK324718. B. Cells of the ventral leaf lobe margin AL324718. C. Cells of the medial leaf lobe AK324718. D. Secondary shoot of female plant bearing gynoecia on determinate lateral branches CHR305106. E. Five lobules from primary shoots AKU69432. F. Five leaf lobes from primary shoots AKU69432. G. Shoot morphotype found adherent to naked bark in exposed situations AK357803. H. Primary shoot from pendulous shoot system hanging free of substrate AK324718. I. Five underleaves from primary shoots AKU69432. Scale bar: A, B, C: 40 µm; D, F, G, H: 800 µm; E, I: 500 µm.

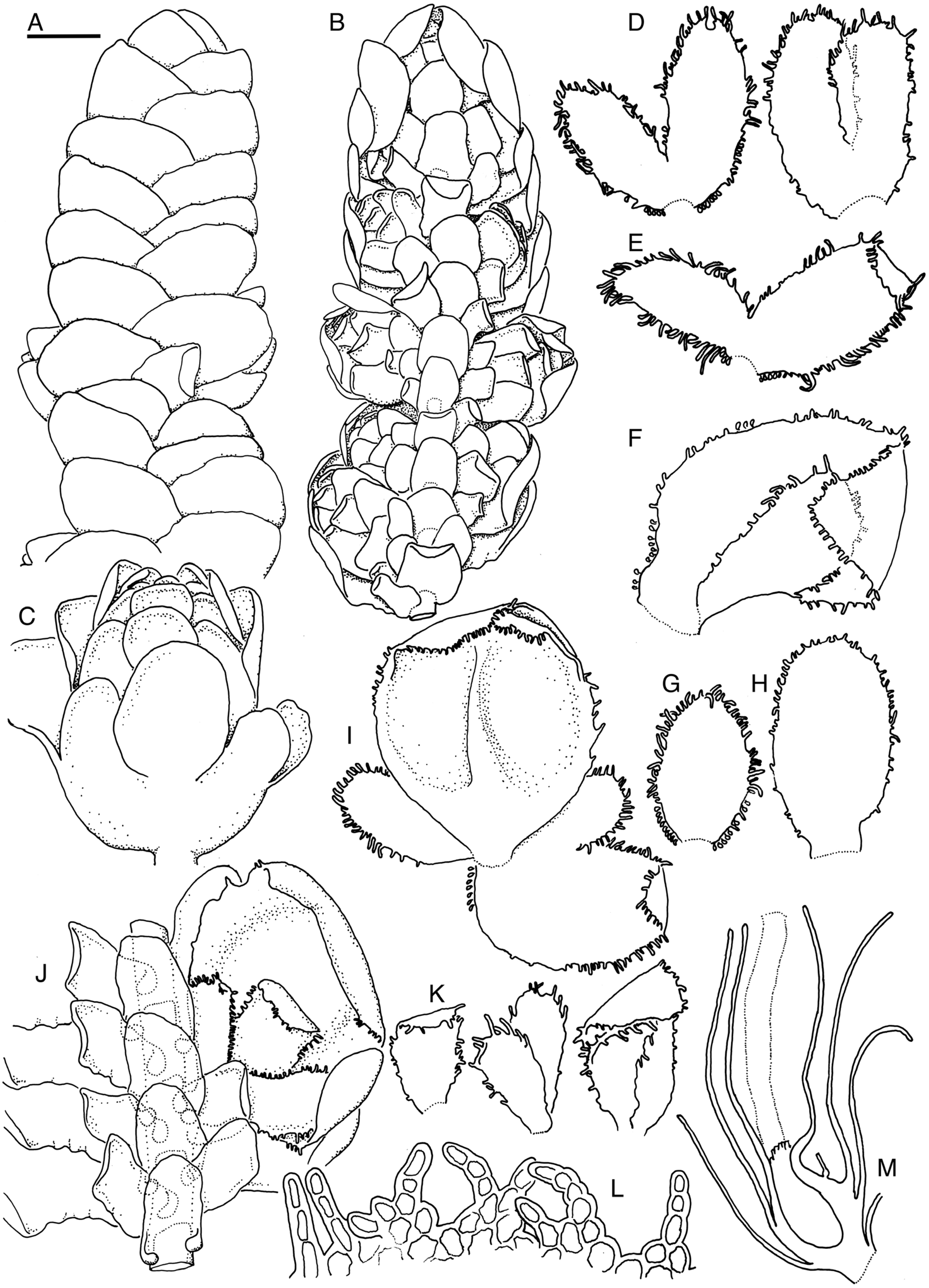

Figure 5. *Porella amoena* (Colenso) W.Martin. A. Dorsal view of primary shoot of male plant AKU068349. B. Ventral view of primary shoot of male plant bearing closely set lateral antheridial branches AKU068349. C. Antheridial branch AKU67124. D, E: Female bracts AK305106. F. Female bract CHR350998. G Female bracteole AK305106 H. Female bracteole CHR350998. I. Perianth with female bracts, note the width of the perianth mouth AKU064935. J. Perianth, bracts and bracteole on lateral branch arising from a secondary shoot AK324718. K. Female bracts and bracteole from syntype material of *P. amoena* (MPN). L. Detail of perianth mouth AKU064935. M. Longitudinal section of mature perianth with sporophyte emergent from calyptra, with the bulbous stem perigynium to which perianth wall and female bract are inserted, and on which archegonia are elevated above the original gynoecial disc level with the female bracts AKU064935. Scale bar: A,B, I, J: 800 μm; C, D, E, F, G, H, I, K, M: 500 μm; L: 40 μm.

Variation: *Porella amoena* is capable of considerable morphological variation, even within single patches. This morphological variation has at least four dimensions. Firstly, there is allometric variation within shoots as occurs in all liverworts, secondly there is variation among shoots of different order, thirdly variation associated with whether shoots are adherent to substrate or free-hanging, and fourth sexual dimorphism.

The free-hanging shoot systems of *P. amoena* are pinnate, and primary and secondary shoots have lobules of different stature. Patches may comprise typical, free-hanging shoots expressing a normal phenotype ± compliant with the description above, or they may comprise mixtures of two or more different shoot types whose gross morphology appears quite different, to the extent that single patches may appear to comprise mixtures of two different species. Often, patches comprise a mixture of free-hanging shoots and adherent shoots, and while these appear quite different, these extremes comprise different sectors of the same shoot systems.

Adherent shoots differ from free-hanging shoots in several ways. The leaf lobes tend to be more rounded than oblong-falcate and are shorter for their width, so adherent shoots may be slightly narrower than typical shoots. This narrowness contributes to the lobules appearing considerably wider relative to the shoot width than on free-hanging shoots, to the extent that on adherent shoots the largest lobules may spread, on either side of the stem, nearly the entire width of the shoot. The leaf lobes may still express the undulation along the postical margin that is characteristic of *P. amoena*. Lobule shape also differs among free-hanging and adherent shoots. In adherent shoots the largest lobules are totally different from those which occur on typical shoots, they are broadly triangular, with a distinct obtuse apex and broadly rounded outer margin and have a broad line of fusion with the lobe, and the interior margin may be weakly auriculate above the stem insertion. Indeed, their shape is more reminiscent of *Porella atroviridis* than *P. amoena*. Even this extreme lobule morph, however, expresses features that serve as clues regarding affinities of the plant bearing them, in that the outer portion of the lobule is sometimes reflexed, and the lobule margin may be undulate. Underleaves on adherent shoots also tend to be plane, without reflexed or undulate margins, and so appear to have a different shape from those on typical shoots. However, they retain the central boss above the stem insertion and typically have pouches at the base of either lateral margin. Adherent shoots are usually found to be part of shoots systems that include free-hanging shoots of more typical morphology, though this is not always the case.

In *Porella amoena* the shoots of male plants are smaller than female plants, and are typically less openly branched, the secondary shoots bring short, spicate, male branches that do not continue vegetative growth. This combination of smaller stature, and closely spaced, loosely adherent shoot systems means male plants have a completely different field aspect than female plants, and look more like an oversized *Frullania*, such that though they may grow alongside or even intermingled with each other, the two sexes may not immediately be recognised as belonging to the same species, or even the same genus.

The production of pouches on the underleaves and lobules is constant in female plants, in that almost all underleaves and lobules in female free-hanging shoots have them, but is variable in male plants, in that many, or even most of the underleaves and lobules in male plants may not produce pouches.

Recognition: As the variation section above suggests, the identification of *Porella amoena* may be challenging. The diagnostic features of *Porella amoena* are 1) the undulate postical margin of the leaf lobe, 2) the oblong to broadly ligulate underleaves lacking a conspicuous central boss, 3) the ligulate-falcate lobules whose outer margin may bear one or more undulations and whose apex is often swept inward and downward toward the shoot mid-line along a line parallel with the main axis of the shoot; and 4) the female bracts having spinose-ciliate margins. These features will all be found in free-hanging shoots, which are predominantly female. In large size of the free hanging shoots, with their oblong leaf-lobes bearing a distinctive 'curtain' of undulations along the postical margin, the outer margin inrolled and forward-swept, with the lobules and underleaves occupying a relatively narrow band along the shoot mid-line, in that they are narrower than the space between the inrolled leaf-lobes on either side of the shoot in ventral view, impart a characteristic aspect to free-hanging shoots. Fortunately, free-hanging female shoots of *Porella amoena* are among the largest and most conspicuous of the epiphytic bryophytes in the New Zealand flora, and are the morph most frequently encountered.

Adherent shoots have quite different facies, and may be confusing, especially when they comprise the entire specimen. Small stature adherent shoots may produce pouch-like lobules (Fig. 4G), which are globose, and without conspicuous free margins in ventral view. *Porella amoena* is the only New Zealand species to produce lobules of this form, and this is therefore a useful character by which smaller, more isolated shoots adherent to otherwise naked bark may be identified. These saccate lobules transition to normal plane lobules as size increases, so that larger-stature adherent shoots have the plane lobules typical of most *Porella* species, however in these shoots the lobules are often much broader than those on free-hanging shoots, and large adherent shoots appear quite different from free-hanging shoots. In adherent shoots the lobules are broader than in free-hanging shoots, oblong-ovate to triangular-ovate usually with a rounded apex, which may be narrow or broad, and continuously curved exterior margin that is ampliate at its base, and the interior margin may be concave, straight or concave. Despite these broad underleaves, adherent shoots have several features that indicate the plant at hand belongs to *P. amoena*, including the broad-ligulate to oblong underleaves whose margins and lamina are ± plane, but may express to greater or lesser degree the characteristic 'boss'. The curtain of undulations at the base of the postical margin of the leaf-lobe is usually evident in at least some of the lobes along a shoot, and several shoots may need to be inspected to assess the presence of this feature.

Male plants can be recognised as belonging to *Porella amoena* by their broad-ligulate to oblong underleaves whose margins and lamina are plane, and by the presence of undulations on the postical margin of the leaf lobe, though the frequency of this character's expression in male plants may be low, and several shoots may need to be inspected as part of assessing this features' occurrence. The combination of small stature, abundant production of lateral spicate androecial branches, oblong underleaves whose margins and lamina are plane, and whose bases lack pouches, flanges, or decurrencies, is usually characteristic of male *P. amoena*.

Porella amoena may be confused with *Porella elegantula*, and indeed the two species may grow in mixed wefts, a situation that only serves to reinforce the impression that a single variable species is at hand. Differentiating *Porella amoena* and *P. elegantula* is achieved by paying careful attention to shoot architecture in the first instance, and lobule and underleaf morphology in the second. Free-hanging shoot systems of *Porella amoena* are regularly pinnate or bipinnate, whereas those of *P. elegantula* approach a pseudo-dichotomous pattern, wherein single secondary shoots arise in alternating sequence along the length of the shoot system, separated by long lengths of unbranched primary shoot. The secondary shoots are similar in stature to the primary shoots that produce them, and they displace their parent slightly, which imparts the pseudo-dichotomous like pattern. The difference is quite distinctive once recognised and constitutes an excellent field character for *Porella elegantula*. The underleaves of *P. amoena* have plane margins and lamina, while the underleaves of *P. elegantula* have lateral margins that are reflexed slightly to form a shallow channel between the margin and the central boss, the inflated region immediately above the middle of the stem insertion, whose presence is also characteristic of *P. elegantula*. The lobules of *P. amoena* are weakly falcate and narrower for their length than in *P. elegantula*, as such there is usually more space between the lobules and the lobe margins in shoots of *P. amoena* than in shoots of *P. elegantula*, in which the lobules and lobes are usually imbricate due to the strongly down-swept lobes.

Distribution and ecology: *Porella amoena* is endemic to New Zealand, where it occurs from Auckland Island, in the subantarctic, and from Rakiura-Stewart Island north to North Cape at the top of the North Island, north east to the Kermadec Islands, and east to the Chatham Islands. It is the most widespread and common *Porella* species in New Zealand and may be found in forest and scrub from sea level to more than 1100 m asl. Across this geographic and elevational range, *Porella amoena* occupies all the major forest types that occur in New Zealand, including kauri-, kauri-broadleaf-, broadleaf-, podocarp-broadleaf-, podocarp- dominated forests, and beech forest, on both sides of the main axial ranges of both main islands. It occurs in mature phase and all successional stages of these various forest types. It has also taken to suburban and agricultural landscapes, in which it colonises isolated specimen trees in landscapes whose associated climate supports luxuriant bryophyte growth. *Porella amoena* is epiphytic on tree trunks, large branches, small branches, and twigs. It does not appear to have any particular preference for where on trees or shrubs it grows, nor does it exhibit any preference for what species of tree it grows on, any suitably well-lit and hydrated bark will do, and as such *Porella amoena* can be found on almost all indigenous and exotic tree species that support luxuriant epiphytic bryophyte communities, exotic hosts include species of *Acer, Alnus, Casuarina, Juglans,* and *Ulex*.

The details of three collections illustrate the ecological diversity and preference of *Porella amoena*. At North Cape, it is common on gabbro boulders strewn across forest floor in dense *Metrosideros excelsa-Corynocarpus laevigatus-Vitex lucens-Kunzea linearis* forest. In Northland, in a setting within regenerating forest, corticolous on *Cordyline australis* trunk in *Kunzea linearis* forest, associated with *Pseudocyphellaria aurata, P. carpoloma*, *Heterodermia japonica, Frullania, Collema, Leptogium, Macromitrium gracile, Leptostomum inclinans* and *Weymouthia cochlearifolia*. On the west coast of the South Island, in another successional community on a flat alluvial plain, on the trunk of *Carpodetus serratus* in riparian secondary forest with *Coriaria arborea*, *Fuchsia excorticata, Aristotelia serrata, Carpodetus serratus, Melicytus ramiflorus* and *Cyathea smithii*, with *Blechnum novae-zelandiae* and *Asplenium bulbiferum* on forest floor.

Representative specimens examined: New Zealand: Kermadec Islands: Raoul Island, Moumoukai Track, 8 May 2009, *P.J. de Lange 283 & D. Havell* (AK305106). North Island: Te Paki, North Cape, North Cape Scenic Reserve, 'Wasp Sting Bush', 34°24′31″S, 173°2′11″E, 140 m, 21 Sep 2011, *P.J. de Lange 10109 & M.A.M. Renner* (AK327941, NSW904726); Te Paki, Pandora Road, 34°28′46″S, 173°51′00″E, 40 m, 19 Sep 2011, *P.J. de Lange 9976 & M.A.M. Renner* (AK327778, NSW900012); Northland, Mangonui County, s.d., *H.B. Matthews 254* (AK18801); Omahuta Forest, north of Kaikohe, 160 m, 22 Oct 1980, *J.E. Braggins s.n.* (AKU063090); Hen and Chickens Islands, Mauitahi Island, 2 Jan 1982, *A.E. Wright* (AKU67221); Rangitoto Island, along track at base of cone, 21 Jul 1984, *J.E. Braggins 84/313a* (AKU69439); North Auckland Province, Waitakere, 37°7′S, 174°32′E, c. 130 m, 10 Jul 1973, *J. Child H2239* (F1033826); Waitakere Ranges, along Dam access road, 7 Aug 1984, *J.E. Braggins 84/312* (AKU69438); Auckland Ecological Region, Manukau Ecological District, Manukau City, Otara Creek catchment, Murphys Road, Murphys Bush, 14 May 2004, *J. Salter & M.A.M. Renner 672a* (AK286674); Auckland Ecological Region, Hunua Ecological District, near Whitford, small Island in Turanga Creek estuary, 4 Feb 1988, *A.E. Wright 7975* (AK179296); Coromandel Ecological Region, Colville Ecological District, Te Moehau, May 1950, *T.C. Chambers* (AK58674 *p.p.*); Te Kouma Peninsula, Coromandel Harbour, at end of road, 25 Jan 1973, *J.E. Braggins s.n.* (AKU063096); Tainui Ecological Region, Kawhia Ecological District, Te Kauri Park Scenic Reserve, on SH31, east of Kawhia Harbour, 23 Jul 1988, *J.E. Braggins 88/036* (AK258536); Auckland, 1895, *T.F. Cheeseman*, ex herb Levier 20 as *M. stangeri* (G); Coromandel Ecological Region, Colville Ecological District, Moturamarama Island, southern slope, 23 Feb 2005, *E.K. Cameron 12831* (AK289656); North Island, Auckland Ecological Region, Rodney Ecological District, Ti Point, 2 Nov 1986, *J.E. Braggins 86/268C* (AK258807); Anderson's track, Te Kauri Park, Kawhia, Aug. 1970, *P. Parkinson* (AKU063098); South Auckland Province, Ngongotaha, Rotorua, near western shore of Lake Rotorua, 38°5′S, 176°13′E, 300 m, 11 Jul 1969, *J. Child H32* (F1033819); Rotorua, buried village site, 6 Jul 1984, *J.E. Braggins 84/306*, (F1105673, AKU69432); Te Whaiti, Urewera, Jan 1920, *H.B. Matthews & D. Petrie s.n.* (AK18843); Waipapa Ecological Area, Pureora Forest, 26 Jan 1982, *J.E. Braggins et al.* (AKU65753); West Taupo, Pureora Totara Walk, 24 May 1982, *G.M. Taylor* (AKU66813); Tongariro National Park, Whakapapanui track, near Chateau, 27 May 1981, *J.E. Braggins s.n.* (F1105666, AKU064935); Central Plateau, Taurewa, 25 Sep 1982, *J.E. Braggins s.n.* (AKU66825); Wairarapa Plains Ecological Region and District, Wairarapa lake shore scenic reserve, parking area on lake side of road, 23 Nov 2001, *J.E. Braggins 01/605* (AK287797); Eastern Wairarapa, Big Hill, Range Road, 1 Oct 1967, *J.E. Braggins s.n.* (AKU063095); Wellington, Eastbourne, Kowhai Street Track, Nov 1981, *T. Moss*, (AKU67124); On branches of trees, slightly adhering to their bark, and to foliaceous lichens etc. Seventh mile bush, county of Waipawa, 1886, *Colenso a1370* (MPN28435); near Whitford, on small island in Turanga Creek estuary, 4 Feb 1988, *A.E. Wright 7975* (AK). South Island: Marlborough, Pelorus, Circle track, 29 Sep 1983, *J.E. Braggins s.n.* (AKU067963); Pelorus Bridge, Trig track, 2 Oct 1983, *J.E. Braggins s.n.* (AKU068349); Marlborough, Mt. Stokes, 750 m, 31 Jan 1938, *A.J. Healy* (F1027333); Richmond Ecological Region, Pelorus Ecological District, Brown River Reserve on SH6 North of Rai Valley township, 28 Oct 2004, *J.E. Braggins 04/058B* (AK290997); North West Nelson, Kahurangi National Park, Cobb Valley, 41°05′39.6″S, 172°34′7.8″E, 885 m, 19 Feb 2012, *M.A.M. Renner 6257* (NSW896390); Westland, Chesterfield, Kapitea Creek, 42°37′18″S, 171°07′27″E, 35 m, 17 Feb 2012, *M.A.M. Renner 6173* (NSW895499); Westland Province, Camp Creek, west of Alexander Range, 42°42′S, 171°33′E, 470 m, Dec 1982, *A. Reif C284A* (F1062598); Westland Province, Franz Josef Glacier, 43°25′S, 170°30′E, 22 Aug 1970, *J. Child H353* (F1033813); Westland Province, Haast, 6 miles north of bridge, 43°49′S, 169°6′E, 20 m, 4 Mar 1972, *J. Child H512* (F1033814); Otago Province, Ross Creek, Dunedin, 45°51′S 170°30′E, 200 m, 21 Feb 1972, *J. Child H715* (F1033307); Otago Province, Catlins River area, near Purakanui, NE of Maclennan, 46°30′S, 169°30′E, 170 m, 18 Feb 1972, *J. Child H803* (F1033458); Fiordland, Te Anau, Boundary Creek, 28 Nov 1970, *G.M. Taylor s.n.* (AKU71467). Rakiura-Stewart Island: Paterson Inlet, Ulva Island, 19 Feb 1935, *R.E. Hatcher 1597* (F); Half Moon Bay, near Oban, 20 Feb 1955, *R.E. Hatcher 1621* (F). Chatham Islands: Chathams Ecological Region and District, Rekohu (Chatham) Island, Tuku-a-Tamatea Nature Reserve, Abyssian Stream, 26 Feb 1996, *P.J. de Lange & G.M. Crowcroft CH145* (AK227375).

Porella atroviridis Glenny & M.A.M.Renner, *sp. nov.*

Type: New Zealand: Canterbury, Banks Peninsula, Port Hills, Cass Peak, 43.634587°S, 172.624482°E, 480 m, *Melicytus ramiflorus* – *Pseudopanax arboreus* / *Polystichum vestitum* – *Lecanopteris pustulata* forest on ridge, on boulders, mixed with *Lecanopteris pustulata* and *Echinodium hispidum*, 1 Jun 2025, *D. Glenny 15922* (holotype: CHR 700599; isotypes: AK, F, G, HO, NSW, OTA, WELT).

Diagnosis: *Porella atroviridis* is distinguished by its falcate, ovate-triangular lobules, reniform to rotund underleaves whose lateral bases bear irregular flanges of tissues, but no pouches, and entire female bracts.

Description: Plants forming extensive pure colonies of regularly pinnately branched overlapping shoots, descending, usually attached only at the base and descending free of the substrate, shoots vibrant green when fresh, lustrous, leaves eroding on older shoot sectors. When dry becoming pale yellow green. Shoots regularly 1-pinnate, infrequently 2-pinnate, pinnae alternate, 10–14 mm long, c. 6–20 pinnae per shoot system. Shoot systems 35–70 mm long, 2.8–4.1 mm wide. Rhizoids brown, in a dense tuft from underleaf base. Stem c. 450 µm diameter, c. 17 cell rows across, cortex c. 150 cell rows in two or three layers, walls heavily thickened constricting cell lumen, thickening brown pigmented, intensity decreasing from outer to inner layers, medullary cells in c. 100 rows, walls unpigmented, and unthickened except for triangular trigones at cell angles. Leaf lobes imbricate, 1.5–2.0 mm long from attachment to apex, 1.8–2.45 mm wide, 1.1–1.5× as long as wide, oval to rounded-oblong, slightly wider at base, margins entire but slightly uneven, ventral base very shortly decurrent, dorsal base auriculate, overlapping stem to mid-line or to the opposite side of stem, the insertion line forming an inverted J, plane but slightly recurved at the apex when fresh, a little more when dry. Cells at mid-lobe 20–37 × 17–30 µm, mostly hexagonal, almost isodiametric, walls thin, secondary thickenings absent, trigones indistinct, small and concave. Mid-basal leaf cells not forming a distinct zone and hardly elongated, 40–54 × 22–33 µm, 1.8–1.9× longer than wide. Oil-bodies (11–)20–28 per cell, ellipsoidal to discoidal, when ellipsoidal 3.0–5.3 × 2.5–3.3 µm, when discoidal the disc 3.9–6.5 µm diameter and 1.7 µm thick, 3.0–6.5 × 2.0–4.5 µm, homogeneous, smooth, colourless (though may appear green due to light refracted from chloroplasts), arranged in a submarginal ring. Lobule triangular, falcate, apex rounded to obtuse, 391–855 µm wide, 580–1188 µm long, typically remote, but contiguous to imbricate with increasing stature, asymmetrically ovate, apex truncate to rounded-acute, margins irregularly weakly crenate, rarely a broad triangular to oblong tooth present on postical margin near stem insertion, plane except for irregular flange at antical base, never bearing pouches, auriculate at one or both basal margins, usually antical margin only, almost free of lobe; apices pointing outward from shoot apex by 30-45°, not closely overlapping with underleaves. Underleaf reniform to rotund, squat, widest at extreme base, as wide or wider than long, 0.48–0.68 mm long, 0.86–1.0 mm wide, usually weakly asymmetrical due to longer stem insertion on one side which is weakly decurrent, apex broadly and continuously rounded to truncate, occasionally deflexed, margins irregular, sometimes with one or two small undulations, otherwise typically plane except for weakly reflexed outer margins in some lobules, and the basal margin which is reflexed into a broad, irregular flange, pouches never present, and underleaf bases never decurrent in a wing down the stem side. Cells at mid-underleaf base neither elongated nor enlarged, not forming a distinct zone of larger cells. Branch half-leaf triangular-ovate, symmetrical to slightly asymmetrical, bases auriculate; first branch underleaf ovate, insertion asymmetrical, weakly decurrent on one side otherwise similar to normal underleaves. Asexual reproduction apparently by leaf fragments.

Dioicous. Antheridial branches produced in regular opposite pairs, determinate, 1500–2500 µm long, often with one or two pairs of sterile leaves at their base, then bearing 3–6(–7) pairs of antheridial bracts, each containing a single antheridium, with the exception of the basal pair of bracts, one or both of which are sterile; basal bracteole free on both sides, all others fused with the bract lobule on one side only; antheridial bract lobes 700–1000 µm long, 400–750 µm wide, bract lobules 480–610 µm long, 230–350 µm wide, apices plane, entire. Gynoecial branches scattered, nearly sessile comprising first branch underleaf and one or typically two gyres of female bracts and bracteoles, the lower pair of bracts symmetrical, the upper pair typically asymmetrical; bracteole and lobules of female bracts not fused; bracteole 950–1000 × 630–720 µm, margins entire, without teeth or with a few small teeth at apex only, with scattered hyaline papillae on lower margins; lobes of upper female bracts asymmetrical, larger lobe 1460–1610 × 980–1180 µm, smaller lobe 1140–1570 × 450–1280 µm, ovate with obtuse apex, margins entire, without teeth; female bract lobules similar size in both bracts, with lobule 960–1600 × 460–770 µm, lanceolate, margins entire. Perianth broadly ovate to orbicular, 2500–3000 µm long, 1800–2100 µm wide, inflated, shrivelling to appearing sub-trigonous when dry, contracted to a narrow plane mouth either entire or bearing scattered spinose-ciliate teeth; perianth walls unistratose except for base where bistratose, outer walls of bistratose portion bearing heavy brown secondary thickening; calyptra unistratose throughout, calyptral perigynium absent; stem perigynium present, bulbous, 4- or 5-stratose throughout, enclosing sporophyte foot, female bracts and perianth wall both attached to the top of the stem perigynium, outer and inner free walls of the stem bearing heavy brown secondary thickening. Sporophyte foot conical; seta massive, with c. 60 cortical and c. 150 medullary cell rows, cortical cells slightly smaller than medullary, both with nodular trigones at cell angles; capsule spherical, to 1.5 mm diameter, splitting into four valves, valves polystratose, bearing weak nodular thickenings in outer most cell layer, distributed in one-phase pattern. Spores not seen. Figures 6, 7.

Variation: Morphology of plants from Banks Peninsula is fairly uniform, the leaf lobes are ovate-rectangular and contiguous to weakly imbricate, the lobules triangular-falcate, widely remote, and deflexed outward from shoot axis. Specimens from the Chatham Islands, Otago, North-west Nelson, and the Hawkes Bay are more variable in lobe imbrication and lobule size. Lobules may be larger and imbricate, and lobes may be closely imbricated and dry to an obliquely patent orientation. Larger lobules in these specimens tend to be similar in shape to those found in more typical individuals, having the slightly falcate triangular-ovate shape, but their larger size and greater degree of overlap with adjacent lobules imparts a different facie to the plants. In these northern and eastern plants, underleaves and lobules may have strongly recurved margins, and so have a totally different appearance to dry plants. Male plants seem to exhibit this morphology more than females, but in the latter the reflexed margins of the lobule and underleaf may still be pronounced, as in specimens of *P. atroviridis* from North West Nelson (e.g. AK286193).

Recognition: *Porella atroviridis* is distinguished from other New Zealand *Porella* by the combination of 1) falcate ovate-triangular lobules, 2) the broad triangular tooth present on the acroscopic or basiscopic margins of some lobules (Fig. 6N, lowermost lobule), 3) the reniform to rotund underleaves, 4) the presence of irregular flanges at the base of underleaf and lobule margins in place of pouches, pouches being entirely absent, 5) the female bracts with entire margins.

The absence of pouches is one of the distinctive features of *Porella atroviridis*, and in combination with the falcate triangular ovate underleaves makes plants of the species relatively easy to identify. *Porella pulcherrima* is the only other New Zealand *Porella* that does not produce sacs, but *P. atroviridis* and *P. pulcherrima* differ in characters of sufficient number and conspicuousness that confusion between these two species should not be possible. Plant colour provides the first clues to identification, in life plants of *Porella atroviridis* the plants are usually a glossy dark green colour, whereas those of *P. pulcherrima* are often a golden-brown and may have reddish hues. The underleaves also provide useful characters, in *P. atroviridis* the underleaves are reniform to rotund, the stem insertion is nearly symmetrical, and the insertion on either side of the stem is the same length. In contrast, the underleaves of *P. pulcherrima* are more triangular ovate, with a broad truncate apex, and an insertion that is oblique across the stem and asymmetrical on either side, extending as a long decurrent wing on one side.

Distribution and ecology: Endemic to New Zealand, where known from Campbell Island, the Chatham Islands, the eastern side of the southern and central South Island, north west Nelson in the north of the South Island, and the Hawkes Bay in the North Island. The current known northern limit is at Whakamahia near Wairoa in the Hawkes Bay, where a gathering was made by G.O.K. Sainsbury in the late 1920's. These are the only known North Island gathering and whether *P. atroviridis* persists at this locality is unknown.

In the South Island *Porella atroviridis* ranges from West Whanganui Inlet in northwest Nelson south to the Otago District. *Porella atroviridis* is widely distributed within the Canterbury Ecological Province, including Motunau Ecological District (Mt Cass), Port Hills ED (Mt Cavendish, Sugarloaf, Ahuriri Scenic Reserve, Otahuna), Herbert ED (Prices Valley, Kaituna Valley, Okains Bay), Akaroa ED (Hinewai), and is also known from Christchurch Botanical Gardens (c. 10 m) on basalt boulders immediately next to a spring-fed stream under planted native forest, and was probably transported on the basalt boulders from the Port Hills as the site of the gardens was originally a swampy alluvial plain. *Porella atroviridis* also occurs in hills around Dunedin. On the Chatham Islands *P. atroviridis* is known from Rekohu (Chatham Island), and Rangiauria (Pitt Island), where it is a common saxicol on limestone and epiphyte on forest margins, particularly *Myrsine chathamica,* where these grow on limestone. A single collection is known from Campbell Island.

Porella atroviridis is an obligate basicole and is typically found on steep to vertical basic rock faces, particularly limestone and basalt, under forest and may also be found on decaying logs or as an epiphyte on surrounding trees, within the zone of influence of dust from eroding bedrock. *Porella atroviridis* forms large pure colonies and is often associated with *Lembophyllum divulsum, Camptochaete angustata, Leptogium denticulatum, Metzgeria furcata, Pseudocyphellaria dissimilis, Racopilum convolutaceum, Syntrichia princeps* and *Siphonolejeunea* spp. On Banks Peninsula *Porella atroviridis* occurs mainly on steep to vertical basalt rock faces or basalt boulders under forest or epiphytic. When on rock and boulders forming large pure colonies and associated with *Lembophyllum divulsum, Camptochaete angustata, Leptogium denticulatum, Metzgeria furcata, Pseudocyphellaria dissimilis, Racopilum convolutaceum,* and *Syntrichia princeps*. On Banks Peninsula commonly epiphytic, on the lower trunks and roots of *Melicytus ramiflorus*, *Coprosma linariifolia*, *Hoheria angustifolia*, there associated with *Lembophyllum divulsum, Camptochaete angustata*, *Siphonolejeunea lanceolata*, and *Frullania patula*. In both epiphytic and rock under lowland forest c. 10–12 m high of *Fuchsia excorticata, Hoheria angustifolia, Kunzea ericoides, Melicytus ramiflorus, Pittosporum eugenioides* with shrubs of *Urtica ferox, Pseudowintera colorata,* and *Helichrysum lanceolatum* common.

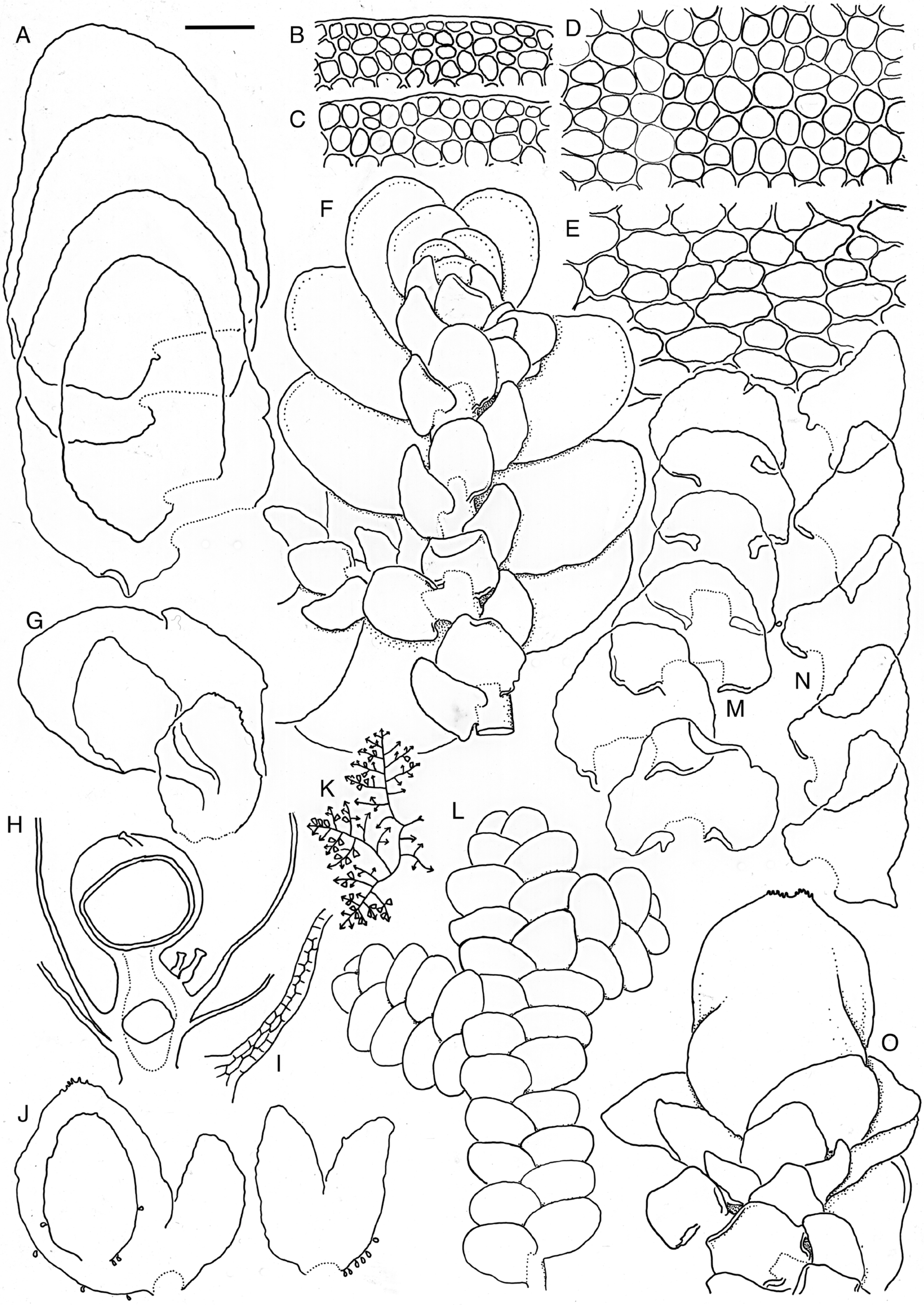

Figure 6. *Porella atroviridis* Glenny & M.A.M.Renner. A. Five leaf lobes from primary shoot of female plant CHR603069. B. Cells of the dorsal leaf lobe margin AK295337. C. Cells of the ventral leaf lobe margin AK295337. D. Medial leaf lobe cells AK295337. E. basal leaf lobe cells AK295337. F. Primary shoot of female plant, ventral view CHR603069. G. Female bract and bracteole CHR602649. H. Longitudinal section of mature perianth with sporophyte emergent from calyptra, with the bulbous stem perigynium to which perianth wall and female bract are inserted, and on which archegonia are elevated above the original gynoecial disc level with the female bracts CHR602649. I. Perianth wall, bistratose basal portion CHR602649. J. Female bracts and bracteole CHR603069. K. Cladogram of female shoot system AJK295337. L. Primary shoot of female plant in dorsal view CHR603069. M. Six underleaves from primary shoot CHR603069. N. Five lobules from primary shoot CHR603609. O. Perianth, bracts and bracteole on a lateral branch arising from a secondary shoot CHR631083. Scale bar: K: 50 mm; L: 3 mm; F, O: 800 µm; A, G, H, J, M, N: 500 µm; I: 250 µm; B, C, D, E: 40 µm.

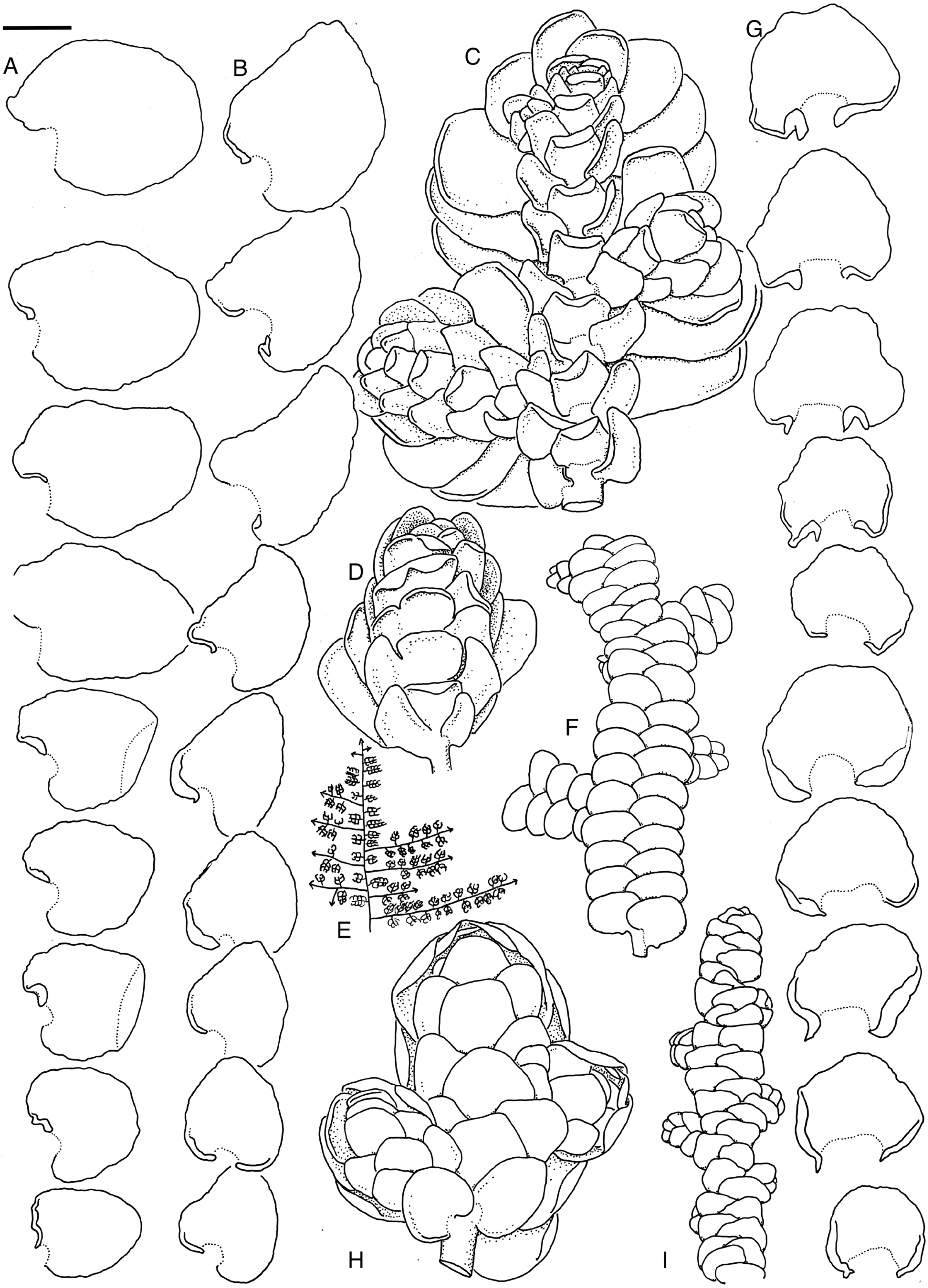

Figure 7. *Porella atroviridis* Glenny & M.A.M.Renner. A. Nine leaf lobes from primary shoots, arranged to illustrate the range of variation in size and shape, upper four from CHR40049, lower five from CHR523835. B. Nine lobules from primary shoots, arranged to illustrate the range of variation in size and shape, top four from CHR40049, lower five from CHR523835. C. Primary shoot of male plant, with androecia on lateral branches that bear a pair of sterile leaves at their base AK303487. D. Androecial branch, with sterile leaf pair at base AK302629. E. Cladograph of male shoot system AK302629. F. Dorsal view of primary shoot of male plant CHR523835. G. Ten underleaves from primary shoot arranged to show variation in size and shape, upper five from CHR40049, lower five from CHR523835. H. Primary shoot of male plant with androecia on lateral branches CHR523835. I. Dorsal view of primary shoot of male plant CHR523835. Scale bar: E: 50 mm; F, I: 3 mm; C, D, H: 800 µm; A, B, G: 500 µm; I: 250 µm.

Porella atroviridis occurs on limestone bedrock or boulders at other locations including the Chatham Islands, Whanganui Inlet, Waima River, Clarence River, Blue Duck Reserve, Mt Cass, Craigmore, Kelsey's Bush, Trotters Gorge, and Clifden. It may be found on bones under forest at Oaro. At these locations sometimes also found as a trunk epiphyte, on *Carpodetus serratus, Plagianthus regius*, On Mt Cass *P. atroviridis* grew on a calcareous boulder, and on Chatham Island on a limestone bluff, while on Campbell Island the species was apparently collected from peat soil. On Banks Peninsula *P. atroviridis* is commonly encountered as an epiphyte on the lower trunks and roots of *Melicytus ramiflorus, Coprosma linariifolia*, and *Hoheria angustifolia* growing in steep gullies containing exposed basal bedrock and boulders. There it is associated with *Lembophyllum divulsum, Camptochaete angustata*, and *Frullania patula*. In both epiphytic and lithophytic situations *P. atroviridis* is found under lowland forest c. 10–12 m tall dominated by *Hoheria angustifolia, Kunzea ericoides, Melicytus ramiflorus, Pittosporum eugenioides*, and *Sophora microphylla*; with shrubs of *Urtica ferox, Pseudowintera colorata,* and *Helichrysum lanceolatum* common. All known sites are mostly in shady valley bottoms or shaded gullies and gully heads, often close to streams, from 10–460 or 600 m asl.

The Campbell Island specimen grew on the surface of deep peat soil in *Poa litorosa* maritime tussock grassland on a 25º slope, an atypical substrate and habitat for this species.

Specimens examined: New Zealand: 'New Zealand', comm. Brotherus, ex herb bryol. C. Alb. Tärnlund and ex herb Delessert as *M. stangeri* (G). North Island: Whakamahia, near Wairoa, Hawkes Bay, on bark, 21 July 1929, *G.O.K. Sainsbury s.n.* ex herb E.A.Hodgs. No. 128, as *Porella elegantula* det. K.W. Allison (CHR 523835); South Island: North-west Nelson Ecological Region, West Whanganui Ecological District, West Whanganui Inlet, Hillside above swamp east of bridge at Paturau, 40°38′44″S, 172°26′14″E, 20 m, 30 Nov 1995, *J.E. Braggins 95/700A* (AK286193); West Whanganui Inlet, South Headland, Te Hapu property, track to Gilberts Beach, 40°36.309′S, 172°30.432′E, 50 m, 19 Feb 2011, *G. Pritchard* (CHR 616088); Marlborough, Waima River, Isolated Creek, 41.880°S, 173.987°E, 155 m, trunk of *Podocarpus totara* under *Podocarpus totara / Dodonaea viscosa – Coriaria arborea* forest, 15 Oct 2015, *D. Glenny 13069* (CHR 638492); Marlborough, Clarence River, near Matai Flat, 42.017°S, 173.898°E, 136 m, calcareous sandstone bedrock under mahoe forest, 7 Nov 2021, *D. Glenny 15140* (CHR 682503); Marlborough, Blue Duck Scientific Reserve, 42.229°S, 173.789°E, 264 m, 14 Oct 2015, *D. Glenny 13093* (CHR 638513); Canterbury, Waipara, Mt Cass, 900 feet [270 m], on calcareous boulder under broadleaf forest. 14 Oct 1978, *B.H. Macmillan 78/132* (CHR 267994); Christchurch, Christchurch Botanical Garden, Leonard Cockayne Garden, 10 m, on basalt boulders next to stream. 6 Sept 2008, *D. Glenny 10248 & M.A.M. Renner* (CHR); Banks Peninsula, Sugar Loaf, 6 Sept 1974, *J. Lewinsky 74-468* (CHR 240525); Banks Peninsula, east side of Sugarloaf, 310 m, 19 Sept 1983, *H.D. Wilson* (CHR 528937); Port Hills, Otahuna Bush, 200 m, 18 Nov 2005, *B.H. Macmillan 05/32* (CHR 607122); Port Hills, Otahuna valley north of Gibraltar Rock, 200 m, 6 Sept 2008, *D. Glenny 10253 & M.A.M. Renner* (CHR); Port Hills, Mt Cavendish, south side, 43°35.41′S, 172°43.09′E, 340 m, 19 Oct 2008, *D. Glenny 10273* (CHR 603083); Port Hills, Sign of the Bellbird, 460 m, 1 Mar 2009, *D. Glenny 10602* (CHR 606632); Banks Peninsula, Red Bay, Fishermans Bay Farm, 13 Nov 2009, *B.H. Macmillan 09/9* (CHR610807); Banks Peninsula, March 1849, *D.L. [D. Lyall ?]* (BM). Canterbury Province, Banks Peninsula, Kaituna Valley, 28 Sep 1954, *R.E. Hatcher 106*, (F); ibid, *R.E. Hatcher 120* (F); ibid, *R.E. Hatcher 170* (F); Banks Peninsula, Montgomery Residence (near hill top) Summit Road, 43°45′S, 172°52′E, Jan 1975, *J.E. Braggins 75/26* (AK314152); Banks Peninsula, Upper Kaituna Valley, 9 Sept 1962, *B.H. Macmillan* (CHR 163129); Banks Peninsula, Prices Valley, 200 feet [60 m], on rock, 13 Oct 1977, *B.H. Macmillan 77/205A* (CHR 240834); Banks Peninsula, Okains Bay, Northwest Bay, 30 m, 27 Dec 2009, *D. Glenny 10700* (CHR); Orton Bradley Park, 60 m, on basalt boulder, 6 Mar 2010, *D. Glenny 10860* (CHR); Herbert Scenic Reserve, 370 m, basalt boulder on stream bank, 28 Mar 2010, *D. Glenny 10926* (CHR); Kelseys Bush, 44.703°S, 170.967°E, 239 m, face of large limestone boulder, 12 Oct 2015, *D. Glenny 13055* (CHR 638479); Canterbury Province, Peel Forest, 43°53′S, 171°14′E, 500 ft, Apr 1973, *J. Child H2087* (F1033816); Otago Province, Leith Valley near Dunedin, Tyson's Stone Wall, 1 m from George Street, 45°50′S, 170°30′E, 100 m, 20 Jun 1969, *J. Child H16* (F1033837); Otago Province, Morrisons Creek north of Dunedin, 45°51′S, 170°30′E, 160 m, 9 Aug 1981, *J. Child H3441* (F1086923); Otago Province, Akatore 20 miles SW of Dunedin, 46°07′S, 170°10′E, 15 Jun 1969, *J. Child 11* (F1033839); ibid, *J. Child 13* (F1033838); Otago Province, Weston, Oamaru, 45°05′S, 170°56′E, 300 ft, 23 May 1976, *J. Child H3012* (F1033846); Otago Province, 20 miles SW of Dunedin, Akatore, 46°7′S, 170°10′E, 15 Jun 1969, *J. Child 11* (F1033839); ibid, *J. Child 13* (F1033838); Otago Province, Blue Mountains, Horse Range, 45°17′S, 170°33′E or 45°24′S, 170°42′E, 3 Apr 1970, *J. Child 232* (F1033821); Trotters Gorge, 45.40°S, 170.77°E, 100 m, 4 Jan 2011, *A. Fife 13193* (CHR 624855); Southland, Clifden, limestone bluff behind gold course, 46.042°S, 167.704°E, 50 m, on limestone bedrock under forest of *Schefflera digitata*, 6 Dec 2010, *D. Glenny 11064* (CHR 618683). Chatham Islands: Chatham Island, Tuku-a-Tamatea Nature Reserve, Abyssinian Stream, 100 m, 26 Feb 1996, *P.J. de Lange CHR145 & G.M. Crowcroft* (CHR 515365); Chatham Island, Maipito Road Swamp Forest, upper Wairarapa Creek, 31 May 2008, *P.J. de Lange & P.B. Heenan CH1829* (CHR 602743); Chathams Ecological Region and District, Rekohu (Chatham) Island, Southern Tablelands, Sweetwater Covenant, 44°5′S, 176°18′W, 247 m, 12 Feb 2006, *P.J. de Lange CH701* (AK297849); Rekohu (Chatham) Island, southern Tableland, just east of Rangaika Scenic Reserve, 44°3′40″S, 176°26′0″W, 240 m, 6 Jan 2007, *E.K. Cameron 14221f* (AK298921); Rekohu (Chatham) Island, Nikau Bush Scenic Reserve, 43°46′S, 176°34′W, 60 m, 28 Jun 2007, *P.J. de Lange CH1034* (AK301098); Rangiauria (Pitt) Island, Waipaua Scenic Reserve, 80 m, 16 Feb 2006, *M.A.M. Renner 2287 & D.J. Clarke* (AK295337); Rangiauria (Pitt) Island, North Head, "Orchard Bush", 40 m, 44°16′S, 176°10′W, 15 Sep 2007, *P.J. de Lange CH1187 & P.B. Heenan* (AK302613); Rangiauria (Pitt) Island, North Head, "Caravan Bush", 30 m, 44°17′S, 176°10′W, 15 Sep 2007, *P.J. de Lange CH1201 & P.B. Heenan* (AK302629); Rangiauria (Pitt) Island, Waipaua Scenic Reserve, 44°17′S, 176°10′W, 95 m, 30 May 2008, *P.J. de Lange CH1737 & P.B. Heenan* (AK303524); Rangiauria (Pitt) Island, North Head, "Gravel Pit Bush", 30 m, 44°17′S, 176°10′W, 15 Sep 2007, *P.J. de Lange CH1392 & P.B. Heenan* (AK302896); Pitt Island, Allison Elizabeth Preece Reserve ('Caravan Bush'), 50 m, 44°17′10″S, 176°11′20″W, 9 Jan 2007, *E.K. Cameron 14273c* (AK299159). Campbell Island: Campbell Island, W central St Col ridge, 152 m, 8 Jan 1981, *C. Meurk* (CHR).

Porella elegantula (Mont.) E.A.Hodgs., *Svensk Botanisk Tidskrift* 42: 277. 1948. *Madotheca elegantula* Mont. *Annales des Sciences Naturelles; Botanique*, sér. 2, 19: 255. 1843. *Madotheca stangeri* var. *γ elegantula* (Mont.) Lindenb. & Gottsche, *Synopsis Hepaticarum* 280. 1845, *nom. illeg*. *Jungermannia elegantula* (Mont.) Hook.f. & Taylor, *Botany of the Antarctic Voyage 1. Flora Antarctica* 1: 163. 1845.

Original material: Hab. in insulis Auckland ad terram, ad cortices et ad Stictam Richardi Nob. parasitantem invenit cl. Hombron.

Type: New Zealand: Auckland Islands, *Hombron* (lectotype: ex herb Bischerelle, G00124223!, designated by So (2002: 8, as ‘holotype’); isolectotypes: ex herb. Montage PC0103351; BM! FH!).

Madotheca stangeri Lindenb. & Gottsche, *Synopsis Hepaticarum* 280. 1845, *nom. illeg*. (Art. 52.2). *Porella stangeri* Trevis., *Memorie del Reale Istituto Lombardo di Scienze e Lettere, Serie 3, Classe di Scienze Matematiche e Naturali* 4: 407. 1877. *Bellincinia stangeri* Kuntze, *Revisio Generum Plantarum* 2: 833. 1891.

Original material: Habitat in Nova Zeelandia *α* et *β* (Dr. Stanger in Hb. Gourlie. et Gottsche), ad portum Dusky Bay legit formam *α* Menzies (Hb. Hk., L. et Lg.), var *γ* in Insulis Auckland atdterram et in cortice (Hombron).

Type: New Zealand: *Dr Stanger s.n.* (syntypes: HB, E, W-5791).

Jungermannia partita Hook.f. & Taylor, *London Journal of Botany* 3: 392. 1844. *Madotheca partita* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, *Synopsis Hepaticarum* (fasc. 2): 279. 1845. *Porella partita* (Hook.f. & Taylor) Trevis., *Memorie del Reale Istituto Lombardo di Scienze e Lettere, Serie 3, Classe di Scienze Matematiche e Naturali* 4: 407. 1877. *Bellincinia partita* (Hook.f. & Taylor) Kuntze, *Revisio Generum Plantarum* 2: 833. 1891.

Original material: Hab. Lord Auckland’s group.

Type: Lord Auckland’s Group, Nov 1840, *J.D. Hooker*, c. per, c. sporo. (lectotype (here designated): herb. Taylor FH!; isolecto: ex herb. Taylor, NY01021269).

Description: Forming mats or wefts of overlapping irregularly to pseudo-dichotomously branched shoots, branches alternating along shoot length, widely spaced, secondary shoots usually displacing the parent primary shoot slightly; descending to pendulous, typically attached to substrate and mat at base of shoot and free at least around the apex, which arches outward away from the shoot toward the horizontal; shoots typically bronze-green, occasionally with or without golden brown pigments on older shoot sectors, never with reddish pigments, lobe margins not becoming hyaline in herbarium. Male and female plants similar in stature and branching. Rhizoids brown, in dense tuft from underleaf base. Lobes oblong-elliptic, 2200–2500 μm long, 1800–2000 μm wide on primary shoots; apex broadly rounded, reflexed, tightly hugging the lobules in dehydrated state, margins entire and ± plane, more frequently on primary shoots, sometimes with a recurved appendage; postical margin straight, weakly reflexed near the stem insertion, usually plane but occasionally reflexed or undulate along part of its length beyond the stem insertion; antical margin straight, incurved toward the broadly curved interior margin. Lobe medial cells isodiametric, 15–32 μm long, 12–18 μm wide, medial walls thin or with weak medial thickenings, between large bulging trigones, basal cells elliptic, 30–50 μm long, 16–31 μm wide, with bulging trigones occasionally confluent, medial wall thickenings absent; marginal cells oblong on dorsal margin, rectangular on postical margin, evenly thick walled between bulging trigones; cell wall pigments absent. Oil-bodies 7–21 per cell, ellipsoidal, 3.0–5.0 × 1.5–3.0 μm, colourless, homogeneous, and smooth, arranged in a loose spheroid around the middle of the cell around half way between the cell centre and the cell walls. Lobules asymmetrically elliptic-oblong, weakly falcate or not, 1200–1500 μm long, 650–800 μm wide on primary shoots, outer portion usually reflexed toward the shoot, especially in dry material; apex rounded, broadly obtuse, or weakly emarginate; margins irregular, plane, outer margin curved, inner margin nearly straight; pouch expression variable, with or without a pouch at the base of the antical margin, without a pouch at the base of the postical margin, lobules in some shoots may lack pouches, pouches ovoid, often continuous with reflexed lobule margin, lobule margins at the stem insertion in the absence of pouches may be reflexed or plane; lobule bases not auriculate. Mid-basal cells of lobules forming an indistinct zone of larger cells. Underleaves broadly elliptic to oblong, 1200–1700 μm long, 950–1150 μm wide on primary shoots, with outer margins inrolled along the lower half forming two channels either side of a central boss, while toward the apex the line of reflexed arcs across the underleaf toward the apex and the incurved margins cause the underleaf outline to appear ligulate, with a broadly and shallowly rounded apex that is narrower than the transverse portion of the stem insertion line; underleaf basal not forming a decurrent wing, typically with sacs on both sides, occasionally one only, occasionally sacs absent entirely; mid-basal cells of underleaves forming a zone of larger cells, often associated with a bulging ‘boss’ immediately above the stem insertion line; stem insertion U-shaped, truncate, slightly oblique across the stem. Branching exclusively terminal, of the *Frullania*-type; branch half-leaf larger than adjacent leaf-lobes; branch underleaf asymmetrically ovate, margins and apex often irregularly undulate to reflexed, with one or both margins bearing pouches at stem insertion. Stems 275–425 μm diameter, oval in transverse section, cortex c. 130 cell rows in three layers, walls heavily thickened constricting cell lumen, thickening brown pigmented, intensity decreasing from outer to inner layers, transition to medullar cells abrupt, medullary cells in c. 80 rows, walls unpigmented and unthickened except for triangular trigones at cell wall angles. Asexual reproduction absent.

Antheridial branches widely scattered and isolated, determinate, 1300–1800 μm long, bearing 3–5 pairs of antheridial bracts, each containing a single antheridium; antheridial stalk two cell columns, side by side. Bracteoles ligulate, apex truncate and reflexed, margins free from bract lobules on both sides to their base. Antheridial bract lobes 700–975 μm long, 500–600 μm wide, bract lobules 550–800 μm long, 300–500 μm wide, apices recurved, entire. Gynoecial branches produced singly, widely spaced, ± where vegetative branches would be expected, nearly sessile comprising first branch underleaf and single 'gyre' of the female bracts and bracteole only. Bracteole and lobules of female bracts not fused; bracteole 900–1000 µm long, 430–790 µm, spinose-ciliate on margins of upper half, lower half less so and typically bearing scattered hyaline papillae. Female bract lobes slightly asymmetrical, the smaller having a narrower lobule, lobes elliptic to broad elliptic, 1200–1375 µm long, 600–900 µm wide, apex rounded to obtuse, both spinose-ciliate on all margins except the basal quarter, which typically bears scattered hyaline papillae. Female bract lobules similar size in both bracts, 1000–1150 µm long, 450–550 µm wide, elliptic-ovate, spinose-ciliate on all margins.

Perianth broadly elliptic to orbicular, 3450–4000 µm long, 2300–2775 µm wide, slightly concave in ventral view, with narrowly inflated margins, lateral margins entire, folded downward in the upper quarter, mouth truncate, narrow, occupying a quarter of the perianth width or less across the perianth apex, spinose-ciliate, intact only in perianths with enclosed sporophytes, perianth walls either side of mouth rupturing with sporophyte emergence; perianth walls unistratose except for base where bistratose, outer walls of bistratose portion bearing heavy brown secondary thickening. Calyptra unistratose throughout, calyptral perigynium absent. Stem perigynium present, bulbous, 4- or 5- stratose throughout, enclosing sporophyte foot. Female bracts and perianth wall both attached to the top of the stem perigynium, apparently having been elevated away from the first branch underleaf by growth of the stem perigynium. Outer and inner free walls of the stem bearing heavy brown secondary thickening. Sporophyte not seen. Figures 8, 9.

Variation: Of all New Zealand *Porella, P. elegantula* is the most consistent in its morphology. As usual, there is some variation within shoots, and more particularly among primary and secondary shoots when these are smaller in stature, and the size of their respective lobes, lobules and underleaves. There is also variation among individuals in their overall stature, and in the degree to which underleaves are impressed with a central boss and reflexed margins or are nearly wholly plane. However, despite these differences, in *Porella elegantula*, we have not observed the considerable differences seen among free-hanging and adherent shoots, or among individuals from different regions, or among individuals of different sex, that is observed in other species such as *Porella amoena* and *P. atroviridis*.

Recognition: *Porella elegantula* can be recognized by 1) the irregular, and often pseudo-dichotomous, shoot systems whose branches are widely spaced; 2) the concave leaf-lobes that are tightly inrolled and wrapped around and obscure the lobules when dry; 3) the ovate lobules nearly equal to the underleaves in size; 4) the ligulate underleaves with a distinct but not necessarily pronounced central boss and lateral margins that are weakly reflexed, and 5) pouches on the basal underleaf margin on one or both sides.

Porella elegantula may be confused with *Porella amoena*, especially those morphs having plane or nearly plane underleaves. The widely spaced, slightly pseudo-dichotomous branching pattern in shoot systems of *P. elegantula* serves to place morphs with plane underleaves in this species, rather than in *P. amoena*. For more detail on other characters differentiating *P. amoena* from *P. elegantula* see the recognition section of *Porella amoena* above.

Porella elegantula may be confused with *P. robusta*, as both share lobules and underleaves that bear sacs on the basal margins of underleaves and lobules, have underleaves with a central boss and margins at least partly reflexed, and lobules that are at least contiguous with the reflexed outer portion of the leaf lobe. However, *P. elegantula* is a smaller plant than *P. robusta*, and has shoot systems that are irregularly or pseudo-dichotomously branched, with secondary shoots widely spaced on alternating sides of the parent primary shoot.

Distribution and ecology: *Porella elegantula* is endemic to New Zealand, where it is widely distributed, from the subantarctic Auckland and Campbell Islands in the south, east to the Chatham Islands, and through Stewart Island, the South Island, and the southern two thirds of the North Island in cold to cool temperate forest and scrub. *Porella elegantula* is more restricted in the upper half of the North Island, in conjunction with the upward elevational contraction of cool temperate rainforest toward the tops of isolated ranges and mountains. The species northern limit appears to be in the Auckland Region, on Te Moehau in the Coromandel Range, the most northerly peak exceeding 900 m elevation. *Porella elegantula* may occur on other high points further north.

Porella elegantula is typically an epiphyte and occurs in all forest types from tall lowland podocarp broad-leaf forest to montane beech forest and subalpine scrub, on ridges, faces and in gullies. *Porella elegantula* grows within forests, and along forests edges and riparian margins, colonising bark of many different tree species, including podocarps such as *Dacrydium cupressinum*, southern beech including *Nothofagus fusca, N. solandri* and *N. menziesii*, broadleaf canopy species including *Pterophylla racemosa*, and many subcanopy and shrub species including *Carpodetus serratus, Dracophyllum*. On trees, *P. elegantula* occupies all microsites from trunk bole to twig tip, and is occasionally epiphyllous, though this may be the result of incidental colonisation from fallen fragments. *Porella elegantula* is often associated with other common weft and mat formers, including *Weymouthia cochlearifolia*, *Macromitrium* spp., *Leptostomum* spp., *Radula* spp., *Frullania* spp., and may co-occur with one or more other *Porella* species including *P. amoena*, *P. atroviridis*, and *P. robusta*.

Notes: A specimen ex herb. Stephani in G was identified as the holotype of *Madotheca elegantula* by So (2002). Though this specimen is part of the original material cited by Montagne (1843), it is not a holotype as no single specimen was identified as such by Montagne, rather the gathering(s) by Hombron on Auckland Island were cited as original material, all specimens derived from which are syntypes, (Art. 9.6). The incorrect attribution of holotype status to specimens is one of the three most common typification errors in bryophytes (see Renner 2021 for a review of typification practice), and So's (2002) holotype citation is to be corrected to lectotype (Art. 9.10).

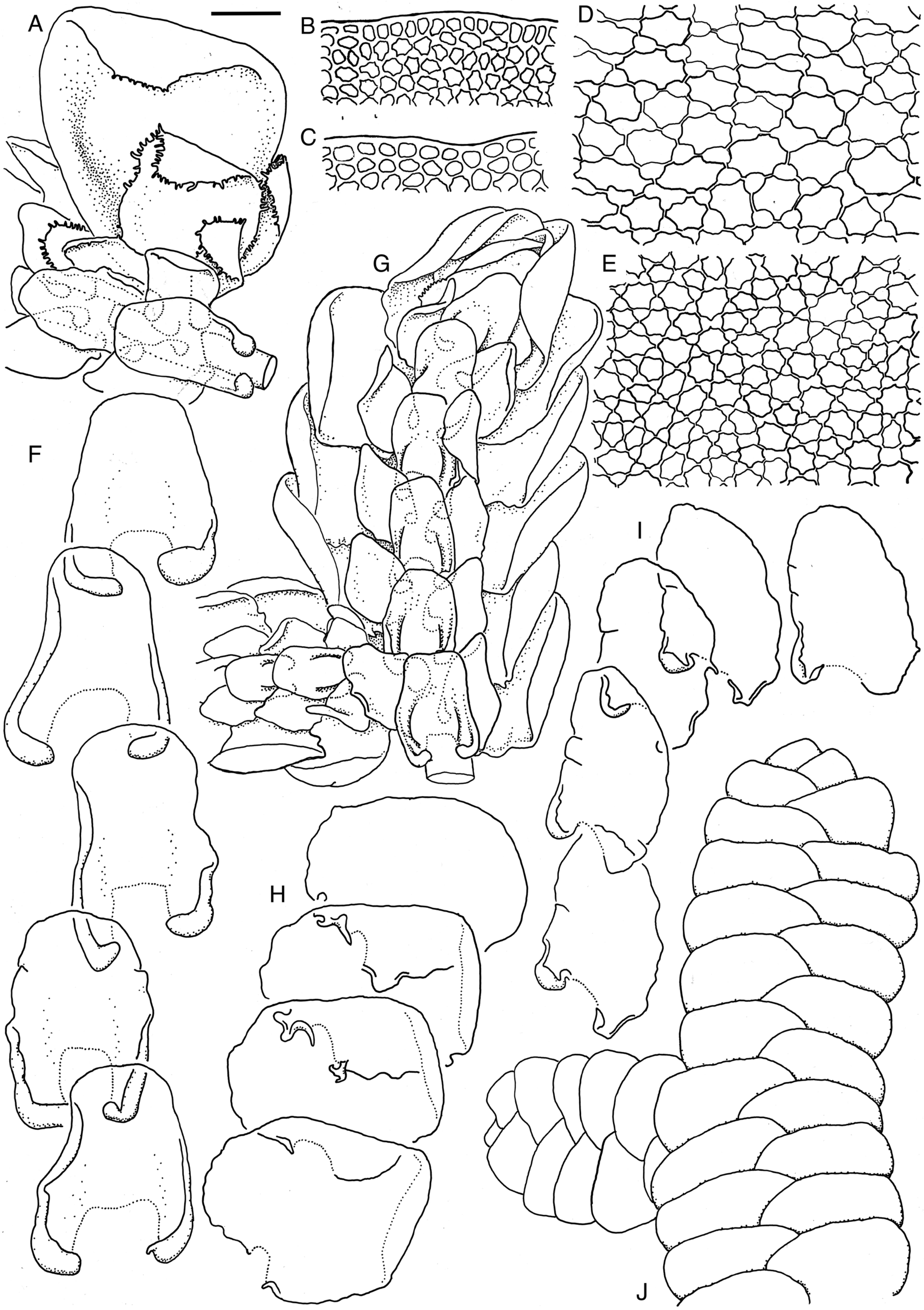

Figure 8. *Porella elegantula* (Mont.) E.A.Hodgs. A. Perianth, bracts and bracteole on lateral branch arising from a secondary shoot AKU71931. B. Cells of the dorsal leaf lobe margin AKU71931. C. Cells of the ventral leaf lobe margin AKU71931. D. Basal leaf lobe cells AKU71931. E. Medial leaf lobe cells AKU71931. F. Five underleaves from primary shoot AKU71931. G. Primary shoot in ventral view AKU71931. H. Four leaf lobes from primary shoot AKU71931. I. Five lobules from primary shoots AKU71931. J. Dorsal view of primary shoot with secondary shoot arising, note slight offset in primary shoot axis induced by branch production AK351053. Scale bar: A, G, H, J: 800 µm; F, I: 500 µm; B, C, D, E: 40 µm.

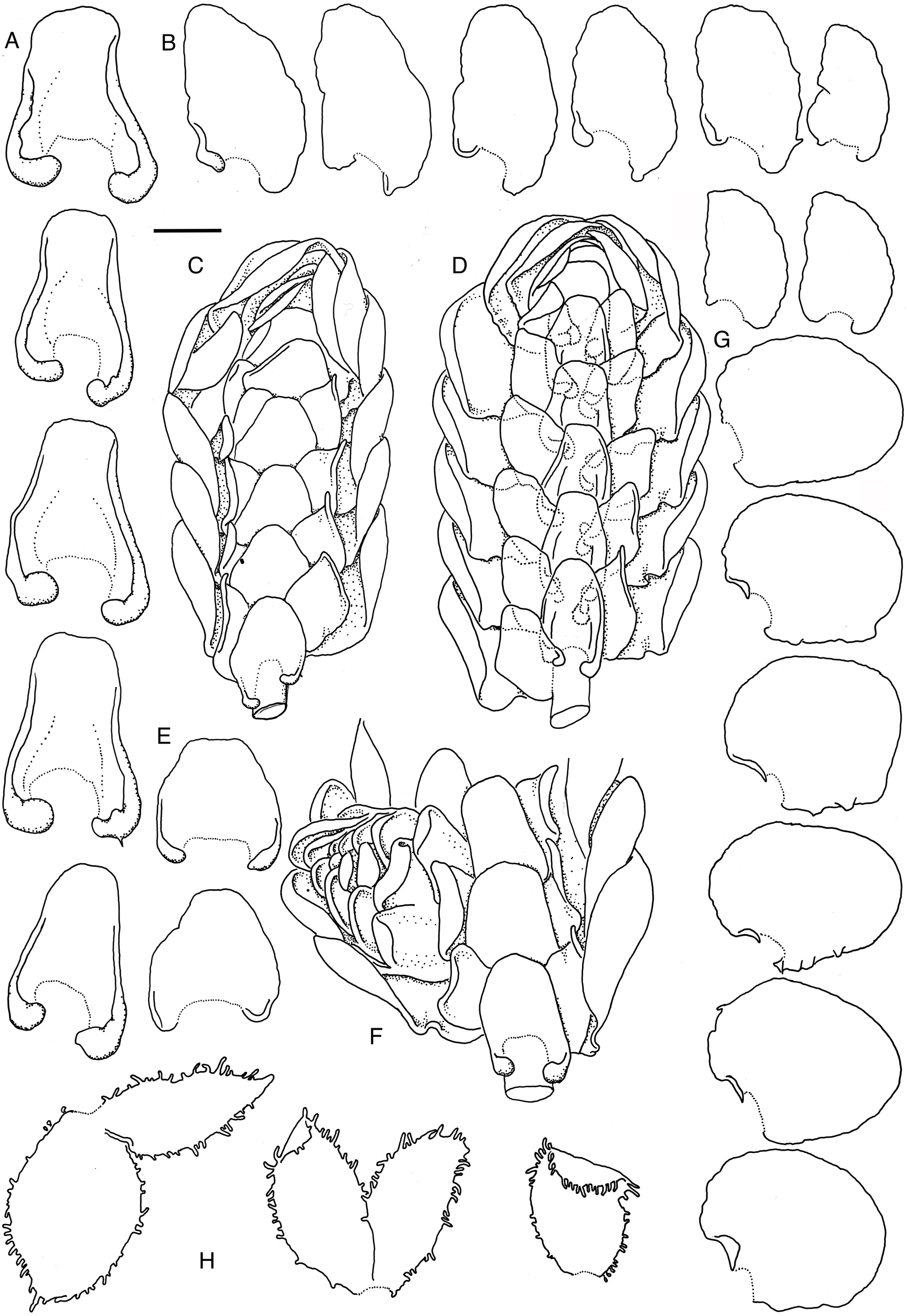

Figure 9. *Porella elegantula (*Mont.) E.A.Hodgs. A. Five underleaves from secondary shoots of female plants AKU71931. B. Eight lobules from secondary shoots, five at left from AKU71931, right top and two bottom from CHR242242. C. Ventral view of male shoot from CHR242242. D. Ventral view of female secondary shoot from AKU71931. E. Two underleaves from male shoot of CHR242242. F. Androecial branch arising from primary shoot AKU065588. G. Six leaf lobes from primary shoots of male plants. H. Female bracts and bracteole CHR242242. Scale bar: C, D, F, G: 800 µm; A, B, E, H: 500 µm.

The protologue of *Jungermannia partita* describes a plant whose shoots branch dichotomously, the branches are short and patent and bear perianths of varying ages, including those with enclosed and emerged sporophytes whose capsules have in some cases dehisced. There are five specimens of *Jungermannia partita* in herb. Taylor, three from the Auckland Islands, and one from Campbells Island. The fifth was collected by Powell. Only one of these specimens bears perianths as described in the protologue, we select this perianth-bearing specimen as lectotype.

Madotheca stangeri, as proposed by Lindenberg and Gottsche (1845), comprised three varieties, *α* alpha, *β* beta and *γ* gamma. For variety *α* Alpha, Lindenberg and Gottsche cited gatherings by Dr Stanger in New Zealand and by Menzies at Dusky Bay. For variety *β* beta '*ramosa*', gathering(s) by Stanger in New Zealand and for variety *γ* gamma '*elegantula*' they cited gathering(s) by Hombron 'in Insulis Auckland ad terram et in cortice'. In their reference to the specimens of variety *γ* gamma '*elegantula*' Lindenberg and Gottsche quote nearly word for word the citation of original material provided by Montagne, by implication including all syntypes of *Madotheca elegantula* within their new species. Lindenberg and Gottsche also cited *Madotheca elegantula* Mont, with a full and direct reference to the protologue, as a synonym of their variety *γ* gamma, *Madotheca stangeri* is therefore illegitimate (Art 52.1, 52.2, Turland *et al*. 2018). The names *Bellincinia stangeri* and *Porella stangeri* should therefore be regarded as replacement names, rather than as combinations based on *Madotheca stangeri,* which was not available to serve as the basionym for either name.

Representative specimens examined: NEW ZEALAND: North Island: Coromandel Ecological Region, Colville Ecological District, Te Moehau, May 1950, *T.C. Chambers* (AK58674, *p.p.*); Coromandel Ecological Region, Tairua Ecological District, Kaitarakihi Track, 31 Jan 1987, *J.E. Braggins 87/023* (AK259079); South of Raglan, Mt. Karioi, 2 Feb 1986, *F.J. Taylor s.n.* (AK291976); Mt Pirongia, Wharauroa Track, 37°59′29″S, 175°07′55″E, 613 m, 19 Apr 2012, *P.J. de Lange 10976* (AK332165, CHR, WELT, NSW); Kaimai Range, 850 m, Jun 1977, *J.K. Bartlett* (CHR 266060); Gisborne, Huiarau Range, Tauranga River, 38°33′44.49″S, 177°09′17.43″E, 900 m, 17 May 2014, *S. Forder* (CHR 599491); Gisborne, Hikurangi, 1067 m, 28 Mar 1932, *L.B. Moore H149* (CHR 555660); Gisborne, Urewera, Maungapohatu, 610–850 m, 9 Jan 1946, *G.O.K. Sainsbury* (CHR 523833); Gisborne, Waikaremoana, track to Ngamoko, 29 Jun 1961, *J. Taylor* (CHR 555524); Urewera Ecological Region, Waikaremoana Ecological District, bush at Lake Waikaremoana, Jan 1958, *E.A. Hodgson s.n.* (AK101482); Waikaremoana, in bush by Lake Waikare-iti, 1000 m, Dec 1936, *E.A. Hodgson* (F1104002); Northern Volcanic Plateau Ecological Region, Rotorua Ecological District, Lake Tikitapu (Blue Lake) track from lake NW to Tarawera Road, 22 Nov 1996, *J.E. Braggins 96/136D* (AK256997); Volcanic Plateau, Mt Hauhangatahi, Jan 1932, *G.O.K. Sainsbury* (CHR 523826); Egmont Ecological Region and District, Taranaki (Mount Egmont), Enchanted walk, 10 Nov 1951, *H.E. Powell s.n.* (AK58226); Taranaki, Pukeiti Rhododendron Trust, track from Hanler Station to Pukeiti Trig, 7 Dec 1981, *G.M. Taylor* (AKU065588); Tararua Range, Te Matawai, 3 Jun 1932, *V.D. Zotov* (CHR 6673); Tararua Range, Ruamahanga River, 3 Dec 1933, *V.D. Zotov* (CHR 9240); Tararua Range, Mt Holdsworth, 23 Jan 1967, *B. Wormald* (CHR 523838). South Island: Marlorough, Kenepuru Sound, Queen Charolette Track, Onahau Lookout, 41°12′58.6″S, 173°58′59.6″E, 11 Feb 2012, *M.A.M. Renner 6060* (NSW895335); Marlborough, Mt Robertson, 975 m, 10 Feb 1983, *J. Child H4401* (CHR 427163); Marlborough Province, Mt Robertson, SES of Picton, 41°22′S, 174°2′E, 1100 m, 10 Feb 1983, *J. Child H4401* (F1086668); Marlborough, Pelorus River catchment, head of Elvy Stream, 41°18′51″S, 173°34′26″E, 285 m, 12 Feb 2012, *M.A.M. Renner 6065* (NSW895340); Western Nelson, Mt Arthur, Jan 1941, *J.M. Dingley* (CHR 555666); North-West Nelson Ecological Region, Wakamarama Ecological District, Mt Burnett, west of and below track to south summit, *J.E. Braggins 95/695G*, 30 Nov 1995 (AK286015); North West Nelson, near Growler Creek, 3 Feb 1988, *E.A. Brown 88/61d* (AKU71931); North-West Nelson, Golden Bay, Pohara, The Grove Scenic Reserve, 40°50′53.4″S, 172°52′12.9″E, 55 m, 20 Feb 2012, *M.A.M. Renner 6260* (NSW896395); Nelson Province, Abel Tasman National Park, Porters Rock Track, 40°56′S, 172°57′E, 1000 m, 26 Jan 1982, *J. Child H4690* (F1088024); Nelson Province, Mt Duppa, 41°44′S, 173°30′E, 1000 m, 1 Feb 1981, *J. Child H3387* (F1086727); North Westland Ecological Region, Punakaiki Ecological District, 4 Mile (Tiropahi) River track south of Charleston, 24 Nov 1995, *J.E. Braggins 95/628A* (AK285635); Western Nelson, Heaphy River, Gouland Creek, 40°56′34.93″S, 172°21′34.48″E, 1030 m, 19 May 2014, *D. Soper* (CHR 597739); Westport, Te Kuha Ridge, 41°48′45.10″S, 171°41′18.80″E, 652 m, 4 Nov 2015, *D. Glenny 13159 & K. Frogley* (CHR 638575); Westland, Haupiri River, Brian O'Lyn, 42°37′26.17″S, 171°44′51.23″E, 590 m, 23 Feb 2020, *D. Glenny 14727* (CHR 658027, F); Westland, Buller River, Husband Creek, 41°44′05.32″S, 172°15′19.51″E, 710 m, 31 Oct 2018, *A. McRae* (CHR 661609); Greymouth, 1886, *R. Helms*, ex herb Jack as *M. stangeri* (G); Westland, Diedrich Range, 1090 m, 13 Mar 2002, *C. Newell* (CHR 583606); Westland, Victoria Range, 42°01′21.50″S, 172°09′23.71″E, 620 m, 11 Dec 2019, *R. Long* (CHR 652731); Westland Province, Camp Creek, west of Alexander Range, 42°42′S, 171°33′E, 840 m, Dec 1982, *A. Reif C160B* (F1062604); Westland Province, South bank of Taramakau River near confluence with Wainihinihi River, track to head of Griffin Creek, 42°47′S, 171°20′E, 300 m, Nov 1982, *A. Reif T5H* (F1136601); Westland Province, Punakaiki, lower gorge of the Pororari River, near 'Big Bridge', 15 Dec 1982, *A.J. Fife 4917* (F1096202); Westland, Lake Rotoroa, Sabine River, 27 Oct 1961, *J. Taylor* (CHR 135022); Insula meridionalis, Kelly's Range, 4 Feb 1903, *T.W.N. Beckett*, ex herb Levier 4321 as *M. stangeri* (G); Westland, Copland Range, Architect Creek, Chlorite Creek, 43°35′23.54″S, 169°53′44.11″E, 760 m, 25 Nov 2018, *R. Hindmarsh-Walls* (CHR 653471); Westland, Lake Harris, 4 Jan 1936, *V.D. Zotov* (CHR 17079); Arthurs Pass, McGrath Stream, above road bridge, 42°55′44″S, 171°33′22″E, 810 m, 14 Feb 2012, *M.A.M. Renner 6096* (NSW895371); Canterbury, Woodstock, 550 m, 6 Oct 1973, *B.H. Macmillan 73/559* (CHR 242442); Canterbury, Cass, Woolshed Hill, 15 Nov 1960, *L. Visch* (CHR 631084); South Canterbury, Waimate, Studholm Bush, Apr 1892, *T.W.N. Beckett*, ex herb Levier 400 as *M. stangeri* (G); Westland Province, Kellys Creek, 42°48′S, 171°34′E, 160 m, 21 Aug 1970, *J. Child H342* (F1033824); Westland Province, near Haast Pass, 47°7′S, 169°21′E, 600 m, 23 Dec 1983, *J. Child H4825* (F); South Westland, Haast Pass, Cross Creek, 44°05′50.4″S, 169°21′31.3″E, 560 m, 15 Feb 2012, *M.A.M. Renner 6116* (NSW895386); South Westland, Haast Pass, track to Brewster Hut, 44°04′49.0″S, 169°23′24.2″E, 660 m, *M.A.M. Renner 6138* (NSW895438); Otago Province, Blue Mountains, Black Gully near Tapanui, 45°53′S, 169°22′E, 300 m, 6 Jul 1969, *J. Child 23*

(F1033843); Otago Province, tributary of Siberia Stream WNW of Makarora, 44°13′S, 169°3′E, 1000 m, 17 Jan 1976, *J. Child H2994* (F1033845); Otago, Hunter Valley, Long Flat Creek, 27 Dec 1960, *R. Mason 7957* (CHR 105898); French Pass, Dec 1896, *H. Schauinsland* (G); Otago Province, Morrisons Creek, N of Dunedin, 45°51′S, 170°30′E, 700 ft, 18 Nov 1972, *J. Child H1659* (F0133457); Fiordland, Lake Te Anau, Dome Island, 6 Feb 1962, *I. Morice & J. Taylor* (CHR 13527); Fiordland, Cascade Creek, 27 Feb 1972, *W. Martin* (CHR); Fiordland, Martins Bay, 44.368°S, 168.015°E, 26 Jan 1955, *R.E. Hatcher 748* (CHR 687905); Fiordland, Cliff Cove, 40°57′30.13″S, 178°05′28.49″E, 436 m, 18 Apr 2002, *M. Renner* (CHR 581086); Fiordland National Park, Caswell Sound, 45°02′S 167°18′E, 27 Mar 1948, *V.D. Zotov*, New Zealand-American Fiordland Expedition 1949 (G145089, CHR206005); Otago Province, Tributary of Siberia Stream, WNW of Makarora, 44°13′S, 169°03′E, 3,000 ft, 17 Jan 1976, *J. Child H2994* (F1033845); Southland Province, Waikaia, Heriot Road, 45°44′S 168°51′E, 600 m, 6 Dec 1981, *J. Child H3915;* Southland, Lake Hauroko, end of Lillburn Valley Road, 45°59′35.0″S 167°23′01.0″E, 6 Dec 2010, *J. Salter s.n.* (AK322896); Southland, Lake Hauroko, C45 750537, 160 m, 6 Dec 2010, *D. Glenny 11061* (CHR 618680). STEWART ISLAND: Patterson Inlet, Ogles Creek, 240 m, 25 Mar 2018, *P. Gillette* (CHR 661631); SOLANDER ISLAND: 330 m, 12 Nov 1973, *P.N. Johnson* (CHR 242806); AUCKLAND ISLAND: Magnetic Survey Bay, 1944, *E.G. Turbott* (CHR 105069).

Porella pacifica M.A.M.Renner, *sp. nov.*

Type: New Zealand: Kermadec Ecological Region and District, Kermadec Islands Nature Reserve, Kermadec Islands northern group, Raoul Island, Mahoe-Prospect track junction with Sunshine Valley track, 29°16′S, 177°56′W, 470 m, 15 May 2011, *P.J. de Lange K732* (holo: AK325688; iso: G, NSW900225).

Diagnosis: *Porella pacifica* is distinguished by its small size, with primary shoots 1.7-1.9 mm wide, the longitudinal striae on the stem dorsal surface, the ligulate to trapeziform underleaves whose margins are reflexed and whose lateral bases bear a large spheroidal pouch; and the spinose-ciliate female bracts whose marginal processes often branch.

Description (based on AK325688 and AK315553): Forming mats of overlapping pinnately to bipinnately branched shoots, pendulous, typically attached to substrate and mat at base of shoot and free at least around the apex, which arches outward away from the shoot toward the horizontal; shoots golden-green in herbarium, never with reddish pigments. Male and female plants ± isomorphic, male and female plants equivalent in stature, primary shoots 1.7–1.9 mm wide, males usually at the narrower end of that range and females at the wider, males with more tendency to reflex lobule apices and irregular lobule margins, particularly on the postical half of the outer margin, in females lobules have evenly rounded outlines and recurved margins but are not reflexed at their apex; shoot systems 40–70 mm long. Rhizoids brown, in dense clusters from the underleaf base. Stems on primary shoots 300–340 µm diameter, with differentiated cortical layer of three cell tiers with heavily thickened, brown-pigmented, outer layer cell lumen constricted, small and isolated within a near solid mass of secondary thickening, secondary thickening decreasing in thickness from outer to inner cortical cell layer, inner most cortical cell layer with continuously thickened walls, inner most walls thinnest; cortical cells on dorsal stem surface protruding, forming corrugations along the dorsal stem surface. Medullar cells larger than outer two tiers of cortical cells, even in the absence of the latter's thickening, approximately the same size as the innermost tier of cortical cells; cell walls uniformly thin walled and hyaline. Lobes on primary shoots broadly elliptic-oblong, 1000–1420 µm long, 820–1050 µm wide; apex broadly rounded, margin recurved, dorsal and exterior margins entire, postical margin slightly irregular, antical margin weakly auriculate at base, which may be elaborated into a small reflexed flange in female plants, with indistinct, low, short accessory lamellae present adjacent the stem insertion, these obscured by the auricle, occasionally with small, widely spaced accessory teeth on the interior margin; postical margin usually straight but with an irregular outline, but plane and not undulate. Lobe basal cells oblong-hexagonal, 30–53 µm long, 22–29 µm wide, walls thin between bulging trigones, cell length decreasing from base to middle of leaf lobe, medial cells isodiametric to shortly elliptic 18–26 µm long, 14–22 µm wide, walls thin between bulging trigones; cells on antical margin oblong, with long axis parallel to lobe margin, walls continuously thickened between bulging trigones, external wall differentially thickened medially, where bulging into the cell lumen and externally bulging to form indistinct crenulations; cells on postical margin oblong with long axis perpendicular to lobe margin, with walls evenly thickened between bulging trigones, external wall ± evenly thickened; yellow-brown cell wall pigments present, strongest in basal cell walls. Oil-bodies not observed.

Lobules on primary shoots in male plants broadly oblong-elliptic to slightly obovate, weakly falcate, 750–880 µm long, 575–725 µm wide; stem insertion short, slightly curved, lobule base variable in expression of flanges and pouches, at least a single poorly formed, and usually a well-developed pouch present at the antical base, this with a bulbous base extending over the stem insertion, then tapered to a narrow reflexed zone extending up the antical margin, pouches variable from spherical to pyriform; postical base usually auriculate only, weakly reflexed but with neither flange nor pouch, but occasionally, in less than around one in 20 lobules, a second pouch is present; exterior margin variable from continuously curved from base to apex, to indented above the basal auricle, to irregular, sometimes dilated in upper half, in situ antical margin inrolled around the lobule apex and lobule often reflexed in the upper half along a line oblique across the lobule intersecting the margin close to the apex, giving male shoots an untidy, irregular appearance in ventral view; margins entire; apex rounded sometimes with a shallow notch; interior margin straight or irregular; lobules on secondary shoots similar but smaller in stature and squatter, 525–620 µm long, 400–580 µm wide, usually without sacs or flanges at their base. Lobules in female plants oblong, 700–955 µm long, 620–720 µm wide, stem insertion short and slightly curved, in situ antical margin gently reflexed but lobule ± plane, not often reflexed, giving female shoots a tidy appearance in ventral view; margins entire except in lobules preceding gynoecia which bear spines-cilia to varying degrees; apex rounded, interior margin shallowly arched to straight to shallowly curved; lobules on secondary shoots smaller, 640–710 µm long, 400–540 µm wide pouch at antical base, usually no pouch or flange at postical base, often reflexed at the very apex along a line oblique to the stem, otherwise similar to primary shoot lobules. Medial-basal lobule cells forming a zone of larger cells.

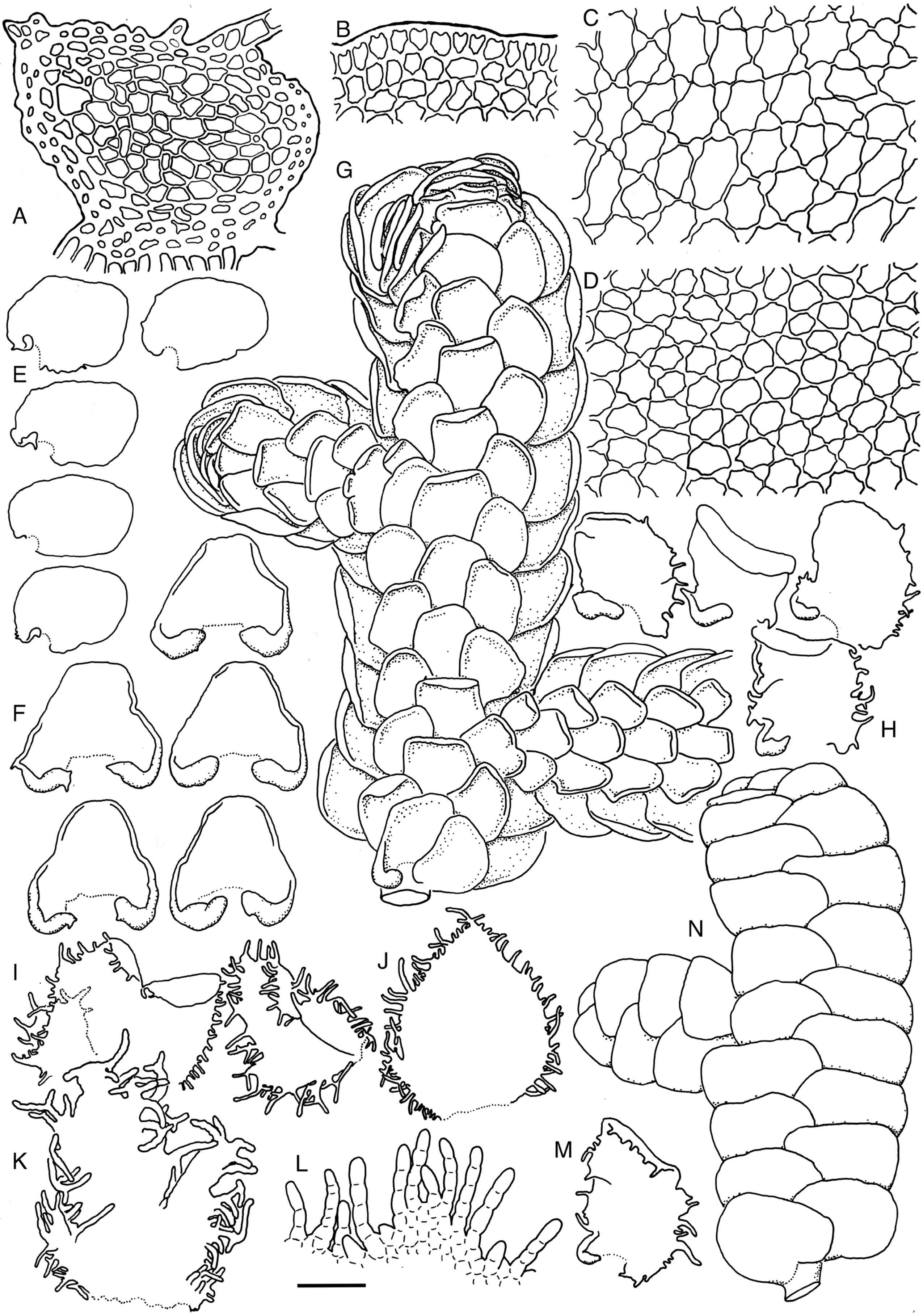

Figure 10. *Porella pacifica* M.A.M.Renner. Female plant. A. Transverse section of primary stem. B. Cells of ventral leaf lobe margin. C. Basal leaf lobe cells. D. Medial leaf lobe cells. E. Five leaf lobes from primary shoots. F. Five underleaves from primary shoots. G. Primary shoot in ventral view. H. Four lobules from primary shoot bearing gynoecia with expression of accessory marginal cilia, as occurs on female bracts. I. Female bracts. J. Bracteole. K. Female bract. L. Perianth mouth. M. Lobule from primary shoot. K. Primary shoot in dorsal view. All from AK315553. Scale bar: G, N: 800 µm; E, F, H, I, J, K, M: 500 µm. L: 100 µm A, B, C, D: 40 µm.

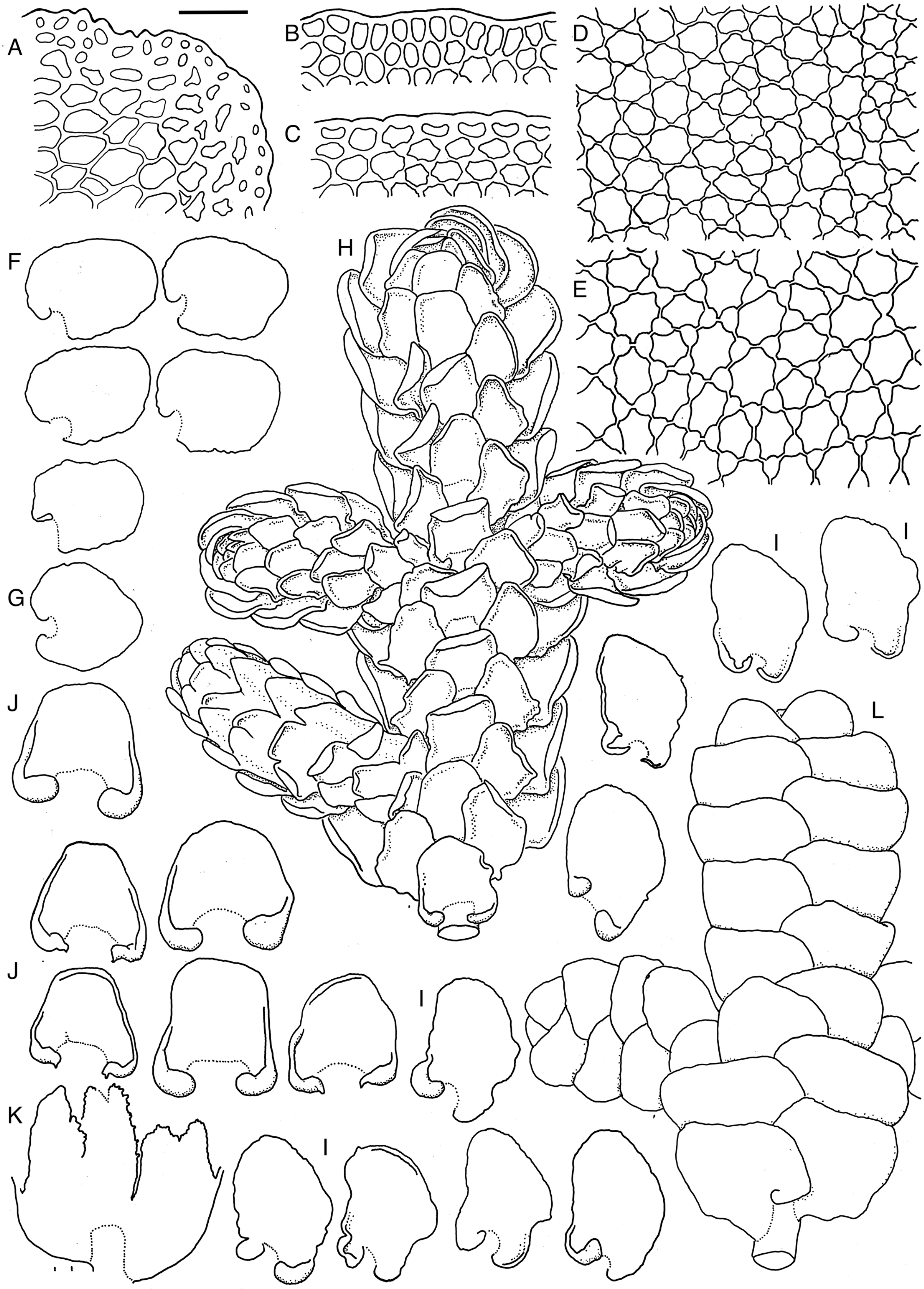

Figure 11. *Porella pacifica* M.A.M.Renner. Male plant. A. Transverse section of primary stem. B. Cells of ventral leaf lobe margin. C. Cells of dorsal leaf lobe margin. D. Medial leaf lobe cells. E. Basal leaf lobe cells. F. Five leaf lobes from primary shoots. G. Branch half leaf from primary shoot. H. Primary shoot in ventral view with androecia on determinate secondary shoots. I. Six underleaves from primary shoots. J. Nine lobules from primary shoots. K. One gyre of androecial bracts with bracteole fused to bracts on both sides. L. Primary shoot in dorsal view. All from AK325688. Scale bar: H, L: 800 µm; F, G, I, J, K: 500 µm. L: 100 µm A, B, C, D, E: 40 µm.

Underleaves on male plant primary shoots trapeziform to ligulate, 810–890 µm long overall, 730–820 µm wide, broadest across the base, with outer margins inrolled, continuous with the spheroidal to short oblate ellipsoidal pouch at the underleaf base on each side, apex broadly rounded to truncate, often also inrolled; margins entire; stem insertion transverse or slightly oblique across the stem ventral surface; underleaf basal not forming a decurrent wing, always with pouches on both sides, mid-basal cells of underleaves forming a zone of larger cells, lamina plane, medial 'boss' not developed; on male secondary shoots underleaves 585–700 µm long overall, 590–760 µm wide, similar to primary shoot underleaves but with apex plane, only the lateral margins reflexed and with oblate spheroidal pouches that are the same size as those on primary shoots, so appearing on secondary shoots much larger in proportion to the underleaf lamina. Underleaves on female primary shoots 820–910 µm long overall, 820–920 µm wide, similar to male primary shoot underleaves but slightly wider for their length and with a narrower truncate apex and longer oblate spheroidal to short cylindrical pouches; on female secondary shoots underleaves similar but smaller in stature. Branching exclusively terminal, *Frullania*-type; branch half-leaf shorter and broader than leaves, auriculate at antical and postical bases, rotund to ovate; branch underleaf oblong, margins plane, apex shallowly bilobed with reflexed margins both margins bearing oblate spheroidal sacs at stem insertion. Asexual reproduction absent.

Antheridial branches scattered, determinate, around 3 mm long, bearing 6 or more pairs of antheridial bracts, each containing a single antheridium; antheridial stalk two cell columns, side by side. Bracteoles narrowly ligulate, apex truncate, plane or reflexed, margins mamillose and with single projecting cells and papillae, fused with bract lobules on both sides, on fusion on downstream side low, around a sixth the bracteole length, fusion on upstream side longer, half the bracteole length or more. Antheridial bract lobes 950 µm long, 680 µm wide, bract lobules around 850 µm long, 480 µm wide, apices plane, entire. Gynoecial branches scattered, nearly sessile comprising first branch underleaf and single 'gyre' of female bracts and bracteole only. Bracteole and lobules of female bracts not fused. Bracteole ovate, around 1000 µm long, 850 µm wide, apex acute, margins spinose-ciliate. Female bract lobes asymmetrical, 890 µm long, 480–860 µm wide, ovate with apex obtuse to acute, both margins spinose-ciliate; female bract lobules similar size in both bracts, around 490 µm long, 350 µm wide, margins spinose-ciliate. Gynoecium bearing 25 or more archegonia 90 µm tall whose neck comprises four tiers of cells that complete a quarter turn from the top of the venter to the mouth. Perianth not seen, except for immature protoperianths surrounding gynoecial discs, unknown except for mouth which is spinose-ciliate. Sporophyte and spores not observed. Figures 10, 11.

Variation: *Porella pacifica* is known by two gatherings only, which limits the extent to which patterns of variation may be inferred. Nevertheless, the two gatherings, one male and one admixed male and female plants suggest that the species is weakly sexually dimorphic, with male plants being slightly smaller overall, and in their underleaf and lobule sizes, than female plants. In addition to size differences, the presentation of lobules on male and female plants differs, with those on male plants tending toward greater degree and frequency of reflexed margins, which imparts a distinctly ragged appearance to male shoots. The consistency of these apparent sex-based differences should be confirmed against observation of additional material.

Recognition: *Porella pacifica* can be recognised by 1) ligulate to trapeziform underleaves with reflexed margins but an otherwise plane lamina and a large oblate spheroidal pouch at the base on each side; 2) lobules on primary shoots having a pouch on the antical base; 3) the shallowly bifid first branch underleaf; 4) the antheridial bracteoles fused to the bract lobules on both sides, with the downstream fusion being half the bracteole length or more; 5) the spinose-ciliate female bracts; 6) the leaf lobes often with a weakly auricle at the antical base, which may be elaborated into a small reflexed flange in female plants, and 7) the indistinct, low, short accessory lamellae present adjacent the leaf lobe stem insertion.

The relatively small stature of *Porella pacifica*, whose primary shoots are 1.7–1.9 mm wide, is distinctive enough to preclude confusion with the larger of New Zealand's other *Porella* species. *Porella pulcherrima,* whose primary shoots are 2.3–2.9 mm wide, comes closest in size to *P. pacifica*. *Porella pacifica* can be distinguished from *P. pulcherrima* by its underleaves, which consistently bear a basal pouch on each side, and whose insertion is symmetrical on either side of the ± transverse insertion line. In *P. pulcherrima* the underleaves never bear pouches, and the insertion line is asymmetrical either side of an oblique insertion line, with a decurrent wing of underleaf lamina often running down the stem on one side.

Distribution and ecology: *Porella pacifica* is currently known by two gatherings, one from Raoul Island in the Kermadec Islands group, the other from Viti Levu in Fiji. These occurrences suggest *P. pacifica* could be more widely distributed across the southern Pacific, and its presence in other island groups having botanical links with the Kermadec Islands, including the Cook Islands, and Norfolk Island, should be anticipated. The two known gatherings provide limited basis for adequate description of the ecology of *P. pacifica*, however, together the gatherings suggest the species may have relatively broad ecological tolerance. At Nadarivatu, Viti Levu, *P. pacifica* was common on rocks and tree trunks alongside a walking track. On Raoul Island *P. pacifica* was corticolous on *Rhopalostylis baueri* trunks in dense *Rhopalostylis-Melicytus ramiflorus* forest with scattered *Metrosideros kermadecensis*. The Viti Levu specimen comprised an admixture of male and female shoots, the Kermadec Island gathering was male only. Specimens consistent with *P. pacifica* are known from the Cook Islands (e.g. AK317743), but these have not been examined critically as part of this study.

Additional specimen examined: Fiji, Viti Levu, Nadarivatu, track to swimming pool, 18 Jan 1974, *J.E. Braggins* (AK315553).

Porella pulcherrima Herz. & Hattori, *Bulletin of the National Science Museum, Tokyo, Series B*. 12: 34. 1986.

Type: New Zealand: Lake Manipouri [sic], South Island, 14 Mar 1927, *W.A. & C.B. Setchell s.n.* (holotype: JE; isotype: NICH *n.v.*).

Description: Forming extensive pure mats of overlapping shoots on rock and trees, creeping or descending, typically attached to substrate and mat along most of shoot, primary shoots 2.3–3.0 mm wide, shoots typically warm golden brown, occasionally mid-green, rarely with reddish pigments, lobe margins may become hyaline in herbarium. Male plants appearing regularly pinnate due to regular production of antheridial branches that extend beyond lobe margins, female plants irregularly pinnately branched; shoot systems 40–70 mm long. Rhizoids brown, in dense tuft from underleaf base. Lobes ovate, apex rounded, incurved, 1139–2116 µm long, 930–1720 µm wide; margins entire, interior part of antical margin scalloped, undulate and reflexed, sometimes with irregular appendage, when dry dorsal margin typically reflexed; postical margin plane, or weakly scalloped or reflexed at stem insertion; reflexed in outer and postical margin. Medial lobe cells isodiametric to elliptic, 16–28 µm long, 15–19 µm wide, secondary thickening present as strong nodular trigones throughout, warm golden brown pigments present in secondary thickenings; basal cells ovate-oblong, 30–46 µm long, 19–26 µm wide, medial thickenings rare, bulging, trigones coarse, bulging, not confluent; cells on dorsal lobe margin nearly quadrate, on ventral margin rectangular. Oil-bodies 12–21 in medial lobe cells, oblate spheroidal to ellipsoidal, colourless, smooth, homogeneous, arranged in a submarginal ring. Lobules ovate-lanceolate to oblong, 580–1188 µm long, 390–855 µm wide, with apex rounded to obtuse, rarely acute, margins irregularly crenulate, plane or undulate, occasionally with reflexed basal margins that may form a narrow flange, never bearing pouches, interior margin straight or slightly arched, exterior margin curved, with or without a small and narrow to large and broad triangular tooth at the base of the exterior margin, weakly auriculate at antical and postical stem insertions; closely overlapping underleaves, apices pointing toward shoot apex. Mid-basal cells of lobules forming a distinct zone of larger cells. Underleaves on primary shoots narrowly ovate, 450–1405 µm long, 405–1220 µm wide, asymmetric, usually one basal margin forming a decurrent wing down ventral-lateral stem surface, sometimes with apex obtuse to truncate, margins plane, except in the base that may be reflexed, or have a narrow, irregular flange, without pouches on the basal margins, lamina plane, not developing an inflated medial boss. Mid-basal cells of underleaves forming a distinct zone of larger cells. Branching exclusively terminal, of the *Frullania*-type; first branch underleaf asymmetrical, ovate, with one or both margins bearing flanges at stem insertion. Stems 360–420 µm diameter, oval in transverse section, cortex c. 130 cell rows in three layers, walls heavily thickened constricting cell lumen, thickening brown pigmented, intensity decreasing from outer to inner layers, transition to medullar cells abrupt, medullary cells in c. 80 rows, walls unpigmented and unthickened except for triangular trigones at cell wall angles. Asexual reproduction absent. Dioicous. Antheridial branches produced in regular opposite pairs, determinate, 1.9–3.3 mm long, bearing 3–7 pairs of antheridial bracts, each containing a single antheridium; basal one to two bracteoles fused with bract lobule on one side only, all others fused with both bract lobules, with degree of fusion increasing toward the branch apex where bract and lobule may be fused to their very apices; basal bract lobe occasionally bearing saccate lobes on anterior margin; antheridial bract lobes 1000–1200 µm long, 560–740 µm wide, bract lobules around 850–900 µm long, 600–650 µm wide, apices truncate, reflexed, weakly dentate. Gynoecial branches produced in pairs, sometimes sequential and appearing alternate, nearly sessile, comprising first branch underleaf and single 'gyre' of female bracts and bracteole only; bracteole and lobules of female bracts not fused; bracteole 1020–1115 µm long, 500–650 µm wide, heavily spinose-ciliate toothed on margins of upper half, lower half less so and typically bearing numerous hyaline papillae; female bract lobes asymmetrical, larger lobe 1360–2060 µm long, smaller lobe 1025–1250 µm long, 590–695 µm wide, ovate with obtuse apex, both heavily spinose-ciliate toothed on all margins except the basal quarter, which typically bears scattered hyaline papillae; female bract lobules similar size in both bracts, 795–930 µm long, 420–495 µm wide in larger, 780–885 µm long, 390–510 µm wide in the smaller, margins heavily spinose-ciliate on all except the basal quarter. Perianth broadly ovate to orbicular, 2200–2400 µm long, 1900–2100 µm wide, flat, with strongly incurved, narrow truncate mouth bearing spinose-ciliate teeth; perianth walls unistratose except for base where bistratose, outer walls of bistratose portion bearing heavy brown secondary thickening; calyptra unistratose throughout, calyptral perigynium absent; stem perigynium present, bulbous, 4–5 stratose throughout, enclosing sporophyte foot; female bracts and perianth wall both attached to the top of the stem perigynium, outer and inner free walls of the perianth bearing heavy brown secondary thickening. Sporophyte foot (inverted mushroom shaped, conical); seta massive, with c. 60 cortical and c. 150 medullary cell rows, cortical cells slightly smaller than medullary, both with nodular trigones at cell angles; capsule spherical, splitting into four valves, valves polystratose, bearing weak nodular thickenings in outer most cell layer, distributed in one-phase pattern; spores 35–50 µm diameter, with primary ornamentation of barbed echinae. Figure 12.

Variation: *Porella pulcherrima* is typically golden brown in colour, but in shaded microsites and forested habitats may be dark green, particularly when growing as an epiphyte on riparian shrubs. Within specimens shoot size and stature may vary, and as lobule shape is apparently correlated with shoot stature, lobules also vary. Larger shoots have relatively broader lobules with one or more prominent spinose-dentate teeth on the postico-lateral margin that point laterally or postically. A large morph is illustrated by Hattori (1986). Larger underleaves typically develop a flange at one or both bases. Large epiphytic plants may tend toward bipinnately branched shoot systems if they form pendants.

Recognition: *Porella pulcherrima* can be recognized by 1) the undulate, reflexed and appendaged acroscopic lobe margin, 2) the outer postical part of the lobe strongly reflexed, 3) the irregularly crenulate lobule margins, 4) the presence in some lobules of a triangular, backward pointing, tooth on the basiscopic lobule margin, 5) the asymmetric underleaves with one or both basiscopic margins decurrent down the lateral stem surface, the underleaves never bear pouches, 6) the presence of nodular trigones in leaves, lobules and underleaves. Male plants have a distinctive pinnate appearance due to the regular production of antheridial branches that are up to 11 pairs of bracts in length. Male and female plants are frequently, but not always, a warm golden brown in herbaria. Female plants have spinose-ciliate bract margins.

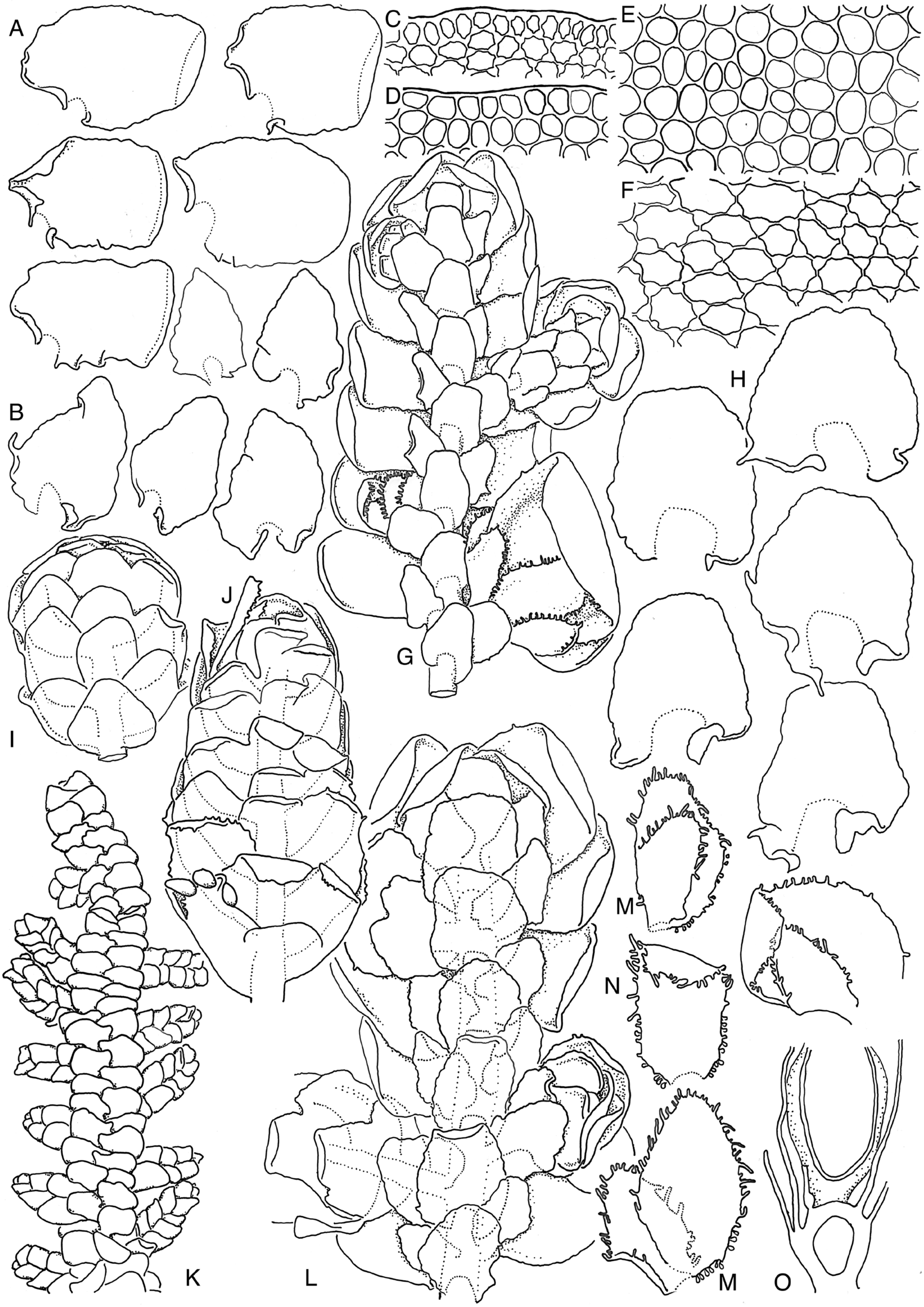

Figure 12. *Porella pulcherrima* Herzog ex S.Hatt. A. Five leaf lobes from primary shoots CHR135707. B. Five lobules from primary shoots CHR135707. C. Cells of dorsal leaf lobe margin AK312097. D. Cells of ventral leaf lobe margin AK312097. E. Medial leaf lobe cells AK312097. F. Basal leaf lobe cells AK312097. G. Female primary shoot in ventral view AK312097. H. Five underleaves from primary shoots CHR135707. I. Androecial branch CHR502583. J. Androecial branch CHR502583. K. Male primary shoot in dorsal view with regular production of determinate androecial secondary shoots CHR502583. L. Male primary shoot in ventral view CHR502583. M. Female bracts CHR523850. N. Female bracteole CHR523850. O. Longitudinal section of mature perianth with sporophyte emergent from calyptra, with the bulbous stem perigynium to which perianth wall and female bract are inserted, and on which archegonia are elevated above the original gynoecial disc level with the female bracts WELT-H5673. Scale bar: K: 3 mm; A, G, I, J, L: 800 µm; B, H, M, N, O: 500 µm. L: 100 µm C, D, E, F: 40 µm.

Distribution and ecology: Endemic to New Zealand, where known from the eastern side of both islands from Otago in the south through Canterbury, Marlborough and Nelson and in the southern North Island. The current known northern limit is Mokai Patea on the western side of the Ruahine Range. *Porella pulcherrima* is widely but sparsely distributed in the South Island east of the main divide. It occurs at Helicopter Hill on the eastern side of Arthurs Pass, where the first author has made collections from the same isolated patch temporally separated by more than a decade, and around Mt Cook village, but is not known to occur west of the main divide. *Porella pulcherrima* is known in the North Island by fewer than 10 collections.

Porella pulcherrima is a lithophyte or epiphyte with broad altitudinal tolerance and may be found in a variety of microhabitats between sea level and 1500 m. At its highest known station, at 1500 m on Tapuaenuku in the Inland Kaikoura Range, *P. pulcherrima* grew as a lithophyte among boulders in subalpine herbfield, similar microhabitats were occupied at other high elevation sites. *Porella pulcherrima* is the only *Porella* species in New Zealand that extends into the alpine zone. It also occurs in forests, where it may grow as a lithophyte on bedrock outcrops, bluffs, or on boulders, on a variety of bedrock types. At The Knolls, near Ngapara, *P. pulcherrima* was collected from the dry south facing side of a limestone bluff, with *Chiloscyphus calcareus*, *Colobanthus brevisepalus*, *Palamocladium sericeum*, *Syntrichia phaea*, *S. errata*, and *Tortula muralis*, or as an epiphyte on tree trunks and branches. At Helicopter Hill, *P. pulcherrima* grew on a greywacke rock bank, and at Mt Pleasant it grew on basalt boulders. There is some overlap with *P. atroviridis* in the tolerance of *P. pulcherrima* to basicolous substrates, so lithophytes on limestone cannot be assumed to be *P. atroviridis* by virtue of substrate occupancy alone. In cooler and drier subalpine scrub, *P. pulcherrima* is frequently epiphytic, particularly on *Discaria toumatou* (as in AK303425). As an epiphyte, *P. pulcherrima* may grow syntopic with *P. elegantula*, as in CHR 523852, collected by *K.W. Allison*, 24 Nov 1948, from Akatore south of Dunedin as an epiphyte in coastal bush, with the note that the mixed collection of female *P. elegantula* and male *P. pulcherrima* were "growing together on the same side of tree".

At many sites where *P. pulcherrima* is an epiphyte, it also occurs lithophytically on adjacent rock, such as at Mahoe Bush in the Horse Range, Otago.

Representative specimens examined: North Island: Wellington Land District, Ruahine Ecological District, Mokai Patea Range, Mokai Patea Station, 39°41.23′S, 176°03.02′E, 800 m, 20 Oct 2011, *G. Pritchard* (CHR 617487); Wellington, Southern Hawke Bay, Waipukurau, A'Deane Bush Scenic Reserve, 39°55′56.8″S 176°17′58.7″E, 290 m, 21 Feb 2012, *M.A.M. Renner 6261* (NSW896399), ibid, *M.A.M. Renner 6263* (NSW896402); Wellington Land District, Paengaroa Scenic Reserve, Hautapu Valley via Mataroa Road north west of Taihape, NZTM18333685E 55608174N, 560 m, 7 May 2011, *G. Pritchard PSR-1*, (CHR 616086); South Island: Marlborough Province, Richmond Range, Mt Richmond, 41°28′S, 173°24′E, 1300 m, 8 Jan 1983, *J. Child H4328* (F1086573); Marlborough Province, Tapuaenuku, Tounge Spur, 42°00′S, 173°39′E, 5,000 ft, 11 Jan 1977, *J. Child H3929* (F1087583); North West Nelson, Kahurangi National Park, Cobb Valley, Trilobite Hut, 41°07′48.0″S, 172°36′30.6″E, 840 m, 19 Feb 2012, *M.A.M. Renner 6258* (NSW896392); Spenser Ecological Region, Lewis Ecological District, Nina Valley track just west of footbridge over Lewis River, 640 m, 42°28′11″S, 172°23′50″E, 22 Jan 2007, *J.E. Braggins 07/021C* (AK303425); Spenser Ecological Region, Rotoroa Ecological District, Lake Rotoroa, start of Braeburn Walk, near carpark close to lake margin, 480 m, 41°47′44″S, 172°35′55″E, 14 Nov 1987, *J.E. Braggins 87/256* (AK284724); Kakanui Ecological Region, Duntroon Ecological District, Ngapara, The Knolls, 240 m, 44°55′S, 170°40′E, 17 Jan 2008, *P.J. de Lange 7256 & M.J. Thorsen* (AK301712); Puketeraki Ecological Region, Cragieburn Ecological District, Cragieburn Recreational Reserve, Helicopter Hill, 820 m, 43°9′S, 171°44′S, 17 Mar 2002, *M.A.M. Renner s.n.* (AK286352); Banks Ecological Region, Akaroa Ecological District, Rocky Peak, 400 m, 43°48′S, 172°54′E, Mar 1985, *J.E. Braggins 85/051A* (AK255855); Lowry Ecological Region, Culverden Ecological District, even miles north-north-east of Waiau, Lottery Bush Scenic Reserve, 1200 ft, 42°33′S, 173°5′E, 7 Dec 1982, *M. Stolp s.n.* (AK181845, CHR 349063, F1096288); Otago, Mt Pleasant, 1500 ft, 20 Jun 1970, *J. Child* (BM); Otago, 1883, *Hector* (BM); Dunedin, Leith Valley, Tyson's Stone Wall, 20 Jun 1969, *J. Child* (BM); Horse Range, 500 ft, 19 Oct 1972, *J. Child* (BM); Otago Province, Mt Watkins, 45°34′S, 170°34′E, 2,000 ft, 16 Aug 1969, *J. Child H93* (F1033842); Otago Province, The Crater N of Middlemarch, Taieri Ridge, 45°27′S, 170°15′E, 1,500 ft, 14 Oct 1969, *J. Child H156* (F1033841); ibid, 2000 ft, 10 Oct 1970, *J. Child H379* (F1033815); Otago Province, Horse Range, 45°17′S, 170°33′E, 500 ft, 19 Oct 1972, *J. Child H1466* (F0133844); Otago Province, Mt. Pleasant, 45°31′S, 170°39′E, 1,500 ft 20 Jun 1970, *J. Child H265* (F1033828); Southland Province, 20 miles NS of Riverton, south coast, 46°15′S, 167°50′E, 160 m, 2 Nov 1972, *J. Child H1590-A* (F1033433).

Notes: Unfortunately, Herzog was not able to publish the results of his investigations into New Zealand *Porella*. Hattori found two specimens in Jena herbarium annotated by Herzog as *Madotheca pulcherrima* Herz. sp. nov. and published the name *Porella pulcherrima* Herzog ex S.Hatt. (nom. inval.) (Hattori 1971). Fifteen years later Hattori validly published *P. pulcherrima* Herzog & S.Hatt. (Hattori 1986). A specimen collected by J.H. McMahon in Marlborough and held in CHR ex herb E.A.Hodgs. No 176 was determined by Herzog "Bryopteris integerrima det. Herzog in litt. Apr. 1947" (CHR 555669). This specimen was subsequently annotated by Herzog "Is this same as my H918 det. *M. pulcherrima* Herz. n. sp?"

So (2002) noted for lobules of *P. pulcherrima*: "as remarked by Hattori (1986a: 36) *P. pulcherrima* is closely related to *P. elegantula*, a common New Zealand species, the major difference seems to be the bluntly dentate-angular stem underleaves. From the range of specimens examined from New Zealand, dentate margins of leaf lobules and underleaves are also seen in several collections, notably those by Berggren (*351* & *361*), as well as the type material of *P. amoena*." So may have confused homology statements in her comments regarding lobule teeth by equating the spinose-ciliate margins appearing around the entire margins of lobules, as frequently produced by *P. elegantula* lobules in the immediate vicinity of gynoecial branches (never present in male plants), with the singly broad-based, elongate, postical-pointing triangular tooth produced from the basiscopic lobule margin which is present on lobules in *P. pulcherrima* independent of their association with gynoecial, or androecial branches (present in male and female plants). Teeth of this kind are never produced by *P. elegantula*, but they are also produced by *P. atroviridis*.

So (2002) noted that "another difference mentioned by Hattori is the saccate base of the underleaves in *P. elegantula*. However, this feature is not well developed in all specimens examined." The expression of lobule pouches is variable within some specimens of *Porella amoena* but this may be related to the site plants were growing. Basal lobule and underleaf pouches will be found in all specimens of *P. elegantula* on thorough examination. They have never been found in *P. pulcherrima* because *P. pulcherrima* never produces them. Critical evaluation of the morphology of the underleaf base suggests that even when pouches are absent in *P. elegantula*, the underleaf base never forms a long decurrent wing running down the stem side as it does in *P. pulcherrima,* such that the underleaves of these two species are distinct, and do not form a continuum, as So (2002) had implied.

Porella robusta M.A.M.Renner & Glenny, *sp. nov.*

Type: New Zealand: North Island, Western Volcanic Plateau Ecological Region, Pureora Ecological District, Pureora Forest Park, south of Titiraupenga, Centre of the North Island Track Car Park, 728 m, 38°31′40″S, 175°40′34″E, 15 Jan 2015, *P.J. de Lange 12466, T.J. de Lange & F.J.T. de Lange* (holotype: AK356184; isotypes: CHR, G, NSW).

Diagnosis: *Porella robusta* is distinguished by its large size, with primary shoots up to 4 mm wide; the reniform underleaves whose antical margin is reflexed and whose lamina bears a conspicuous medial boss immediately above the stem insertion; and the oblong, weakly falcate lobules.

Description: Forming extensive pure mats of overlapping pinnately to bipinnately branched shoots, usually descending and pendulous from a creeping base adherent to substrate, free at least around the apex, which arches outward away from the substrate toward the horizontal; shoots typically bronze-green, occasionally with brown or golden brown pigments on older shoot sectors, never with reddish pigments, lobe margins not becoming hyaline in herbarium. Male and female plants weakly dimorphic, male plants smaller in stature, otherwise similar, in both sexes primary shoot systems 2.8–4.0 mm long, up to 10 cm long. Rhizoids brown, in dense tuft from underleaf base. Leaf lobes broad ovate to rotund, 2400–3950 µm long, 1850–2650 µm wide; apex broadly rounded, incurved, margins entire, except at antical and postical stem insertions, interior part of antical margin reflexed, with or without small lobed projections and one or two broad undulations, sometimes with a small irregular appendage, postical margin often with a small reflexed lobe at the insertion, then ± straight and plane with the occasional exception of one small undulation; antical margin ± continuously and shallowly curved. Medial leaf lobe cells isodiametric, to short elliptic, 21–28 µm long, 15–24 µm wide, walls thin or with weak medial thickenings, between bulging trigones, cell wall pigments absent; basal cells oblong to stretched hexagonal 32–54 µm long, 23–32 µm wide, walls thin, medial thickening absent, trigones coarse, strongly bulging and angular, rarely confluent; cells on dorsal margin oblong with evenly thickened walls and indistinct trigones, on ventral margin cells quadrate to oblong, with evenly thickened walls. Oil-bodies 12–30 per cell, ellipsoidal, 3.0–7.0 × 1.5–4.0 µm. colourless, homogeneous, and smooth, arranged in a loose submarginal ring. Lobules on primary shoots oblong and weakly falcate, 1200–1800 µm long, 670–875 µm wide, apex rounded; margins entire, plane, lacking undulations inner margin slightly arched, outer margin slightly curved; inner and outer base usually both with tear-drop shaped pouches, the inner slightly larger than the outer, not continuing along the lobule margins at the stem insertion which are plane; lobule bases not auriculate. Mid-basal cells of lobules forming an indistinct zone of larger cells. Lobules on secondary shoots similar but smaller, 950–1300 µm long, 550–775 µm wide and usually with one pouch only, typically at the base of the inner margin, the base of the outer margin minutely auriculate, or vice versa, and the inner lobule margin may be straight or arched. Underleaves on primary shoots oblong with a semi-circular end, 1100–1550 µm long overall, 930–1250 µm wide, margins strongly reflexed around the rounded apex, and to a lesser extent degree along the lateral markings above the pouches where forming two indistinct channels either side of a prominent, large, strongly inflated rotund central boss, underleaf base not forming a decurrent wing, with spheroidal or oblate spheroidal pouches on both sides; insertion U-shaped, transverse across ventral stem midline; mid-basal cells of underleaves forming a zone of larger cells, often associated with the 'boss'; on secondary shoots underleaves similar, but more rotund in shape by virtue of having shorter straight sides above the stem insertion, 750–1275 µm long overall, 900–1250 µm wide, also always with two pouches at their base, as for the primary shoot underleaves. Branching exclusively terminal, of the *Frullania*-type. Branch half-leaf not differentiated from adjacent leaf-lobes, or slightly smaller than adjacent leaf lobes but of like shape. Branch underleaf asymmetrically ovate to obovate, margins and apex often irregularly reflexed, with one or both margins bearing pouches at stem insertion. Stems on primary shoots 450–550 µm diameter, oval in transverse section, cortex c. 150 or more cell rows in three layers, walls heavily thickened constricting cell lumen, thickening brown pigmented, intensity decreasing from outer to inner layers, transition to medullar cells abrupt, medullary cells in c. 80 rows, walls unpigmented and unthickened except for triangular trigones at cell wall angles. Asexual reproduction absent.

Antheridial branches scattered, determinate, 1.2–2.1 mm long, bearing 3–6 pairs of antheridial bracts, each containing a single antheridium; antheridial stalk two cell columns, side by side. Bracteoles ligulate, apex broadly rounded to obtuse, reflexed, fused to bract lobules on both sides near base. Antheridial bract lobes hugging bract lobules, bract lobules 450–825 µm long, 350–475 µm wide, apices plane, rounded to obtuse, reflexed. Gynoecial branches short, sessile, hidden beneath leaves, comprising first branch underleaf and single 'gyre' of female bracts and bracteole only. Bracteole and lobules of female bracts not fused. Bracteole c. 1200 × 900 µm, shortly and sparsely spinose-ciliate toothed on margins of upper half, mostly around the apex, lower half less so and typically bearing scattered hyaline papillae. Female bract lobes asymmetrical, both 1350–1550 µm long, differing in width with the larger c. 1350 µm wide, the smaller lobe c. 800 µm wide, ovate with obtuse apex, both sparsely spinose-ciliate toothed on all margins except the basal quarter, which typically bears scattered hyaline papillae. Female bract lobules similar size in both bracts, 1150–1320 µm long, 650–700 µm wide, oblong-ovate, sparsely spinose-ciliate

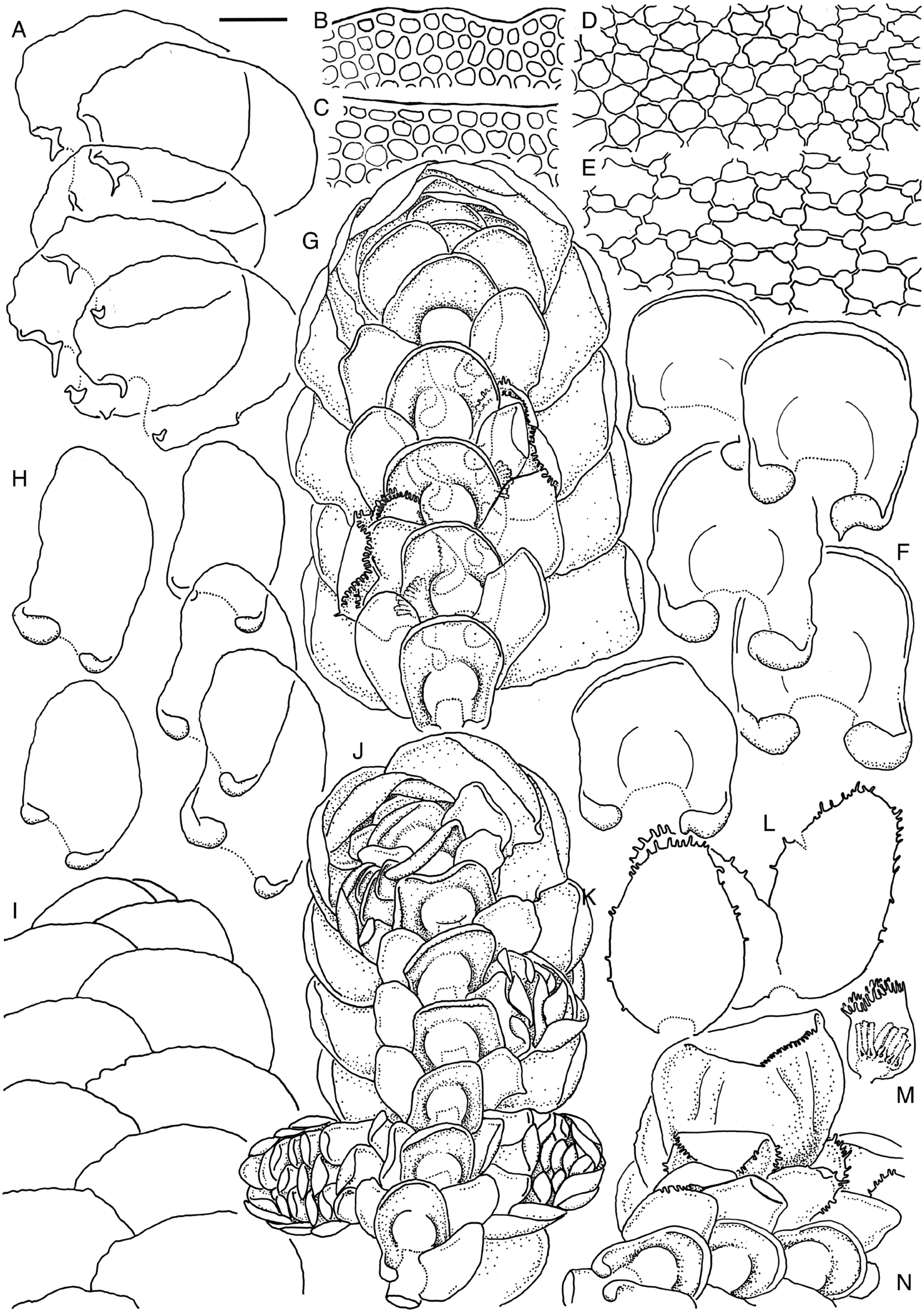

Figure 13. *Porella robusta* M.A.M.Renner & Glenny. A. Five leaf lobes from primary shoots AK357752. B. Cells of dorsal leaf lobe margin AK357752. C. Cells of ventral leaf lobe margin AK357752. D. Medial leaf lobe cells AK357752. E. Basal leaf lobe cells AK357752. F. Five underleaves from primary shoots of female AK357752. G. Primary shoot of female in ventral view AK357752. H. Five lobules from primary shoots AK357752. I. Primary shoot of female in dorsal view AK356184. J. Primary shoot of male in ventral view with androecia on determinate secondary shoots AK356185. K. Female bracteole AK357752. L. Female bract AK357752. M. Proto-perianth surrounding gynoecial disc AK357752. N. Perianth, bracts and bracteole on lateral branch arising from a secondary shoot AK356184. Scale bar: A, G, I, J, N: 800 µm; H, I, L, M: 500 µm; B, C, D, E: 40 µm.

toothed on all margins except the basal quarter. Perianth broadly ovate to orbicular, 2500–2700 µm long, 600–750 µm wide flat but with ventral face often bulging, often reflexed along a transverse or slightly oblique line in the upper quarter, with narrow truncate mouth bearing spinose-ciliate teeth, perianth walls unistratose except for base where bistratose, outer walls of bistratose portion bearing heavy brown secondary thickening. Calyptra unistratose throughout, calyptral perigynium absent. Stem perigynium present, bulbous, 4- or 5- stratose throughout, enclosing sporophyte foot. Female bracts and perianth wall both attached to the top of the stem perigynium, apparently having been elevated away from the first branch underleaf by growth of the stem perigynium. Outer and inner free walls of the stem bearing heavy brown secondary thickening. Sporophyte not seen. Figure 13.

Variation: *Porella robusta* is another species of fairly constant morphological expression, with consistent, if subtle, partitioning of size and shape variation among primary and secondary shoots. Male and female plants are of similar stature and have similar patterns of size and shape variation in underleaves and lobules.

Recognition: *Porella robusta* can be recognised by the 1) large stature of the primary shoots, at up to 4 mm wide; 2) the pinnate shoot systems wherein the primary shoot is not, or is hardly, offset by the branches; 3) the underleaves having a semi-circular apex whose margin is strongly reflexed around the whole apex; 4) the underleaf lamina having a pronounced, inflated medial boss; 5) the underleaves consistently possessing a pouch at the base on both sides; 6) the lobules on primary shoots being oblong and weakly falcate with entire margins, and two basal pouches; 7) the leaf lobe margins being nearly plane except close to the stem insertion; and 8) the spinose ciliate female bracts.

Porella robusta could be confused with other large *Porella* in New Zealand, including *P. amoena*, *P. elegantula* and *P. atroviridis*. From all of these, *Porella robusta* differs by its underleaves which have a distinctive semi-circular apex that is consistently strongly reflexed along its whole length, the underleaves also have a pronounced, strongly inflated medial boss, and always bear two basal pouches, one on each side at either end of the stem insertion.

Porella elegantula, by contrast, has underleaves whose apex is truncate, and folded over rather than reflexed. *Porella elegantula* also has shoot systems that are openly and pseudo-dichotomously branched. *Porella atroviridis* has rotund underleaves that are similar in their continuously curved apex, but this may or may not be reflexed along its whole length, there is no central boss, and the underleaves never bear pouches, rather they have irregular reflexed flanges at their base. *Porella atroviridis* also has entire female bracts. *Porella amoena* underleaves have plane margins, never exhibiting a continuously reflexed apical margin, and lack a pronounced central boss. The lobules on primary shoots of *Porella amoena* are usually folded inward toward the stem.

Distribution and ecology: *Porella robusta* is an epiphyte of trunks and large branches and lithophyte on large rocks in wet forests and is widespread from western Northland south to Fiordland, from sea level to around 600 m elevation. *Porella robusta* may grow in podocarp broadleaf forest, for example in gullies with west-south-westerly aspect with *Dacrydium cupressinum* emergent over a canopy dominated by *Pterophylla racemosa* and *Nothofagus fusca*, with *Dicksonia squarrosa*, *Melicytus ramiflorus*, and *Lophobyrtus bullata* in subcanopy, scattered *Beilschmiedia tawa* saplings, *Leptopteris hymenophylloides, Asplenium bulbiferum* and *Blechnum discolor* on forest floor, where it was pendulous from side of fallen *Dacrydium* trunk bridged over stream. *Porella robusta* may also grow as a lithophyte in situations of high light, for example in riparian secondary forest with *Coriaria arborea, Fuchsia excorticata, Aristotelia serrata, Carpodetus serratus, Melicytus ramiflorus* and *Cyathea smithii*, with *Blechnum novae-zelandiae* and *Asplenium bulbiferum* on forest floor on flat alluvial plain, where it grew on large alluvial boulders.

Porella robusta is broadly sympatric with *P. amoena* and *P. elegantula* and may grow in colonies mixed with these two species. It is also sympatric with *P. atroviridis* and may grow in close proximity to that species. At one site in Southland, three *Porella* species, *P. amoena, P. atroviridis,* and *P. robusta* were observed growing within arms-reach of each other.

Representative specimens examined: North Island: Western Northland Ecological Region, Maungataniwha Ecological District, Quarry south side of Omataroa Ridge Road at start of Onekura ridge track, 5 Aug 1994, *J.E. Braggins* (AK287724); North Island, Western Northland Ecological Region, Tutamoe Ecological District, Waipoua Forest Sanctuary, Mataraua Plateau, Waouku Coach Road, 30 Sep 1994, *J.E. Braggins s.n.* (AK257575); Auckland Ecological Region, Hunua Ecological District, Hunua Range, Mangatangi Forks, 18 Apr 1970, *J.E. Braggins s.n.* (AK250556); Coromandel Peninsula, 8.5 km east of Tapy, 36°59′S, 175°30′E, 29 Dec 1981, *D. Vitt 29992* (F1078734); Te Aroha, Feb 1910, *B. Leland & E.W.B. Chase* (F1023797); Rotorua, Ngongotaha Mountain, Nov 1909, *J.E. Tilden* (F102376); Bay of Plenty, Mt Tarawera, in low forest above gate on road to airstrip, 4 Nov 1984, *J.E. Braggins 84/337A* (F1105559, F1105674); Tongariro National Park, Mt Ruapehu, Ohakune Road, 600 m, 22 May 1971, *D.S. Horning NZ-726* (F1045958); Tongariro National Park, *E.K. Cameron s.n.* (AKU063359); Egmont Ecological Region and District, Mt. Taranaki, Manaia Road, 26 Aug 1998, *J.E. Braggins 98/261B*, (AK254248); Taranaki Province, Pukeiti Bush near New Plymouth, 16 Nov 1954, *R.E. Hatcher 213A* (F); North Island, Tararua Ecological Region and District, Akatarawa Range, Waterfall creek, unnamed tributary of Bull Stream c. 2.5 km down from summit of road, 9 Dec 1984, *J.E. Braggins 84/420* (AK285282); Wellington Land District, Waikanae, Hemi Matangi Scenic Reserve, 40°52.667′S, 175°05.461′E, 500 m, *G. Pritchard HNW-12* (CHR 616087); Wellington, Akararawa, Waterfall Creek, 9 Nov 1984, *J.E. Braggins 84/420* (AKU069951). South Island: Pelorus Sound, Marlborough, Aug 1890, *J. Rutland*, comm. T.W.N. Beckett, ex herb Levier 402 as *M. stangeri* (G); Kenepuru Sound, Queen Charlotte Track, 41°12′ 55″S, 173°58′48″E, 295 m, 11 Feb 2012, *M.A.M. Renner 6061* (NSW895336, AK); Marlborough, Pelorus River catchment, head of Elvy Stream, 41°18′52″S, 173°34′24″E, 270 m, 12 Feb 2012, *M.A.M. Renner 6078* (NSW895353); Nelson Province, NW Nelson, Gridiron Bivvy, Flora Track, 41°11′S, 172°44′E, 1000 m, 20 May 1983, *J. Child H4775* (F1088170); Nelson, Apr 1892, *D. Grant*, comm. T.W.N. Beckett ex herb Levier 401 as *M. stangeri* (G); Whataroa

Ecological Region, Harihari Ecological District, Harihari, Feb 1949, *R.C. Lloyd s.n.* (AK164016); North-west Nelson Ecological Region, Whakamarama Ecological District, Mt Burnett, track to south summit, 30 Nov 1995, *J.E. Braggins 95/687A* (AK285927); Nelson Province, Flora Track, Gridiron Bivvy, 41°11′S, 172°44′E, 3,000 ft, *J. Child H4775* (F1088170); Westland, Paparoa National Park, Fox River, 42°02′26″S, 171°23′58″E, 20 m, 18 Feb 2012, *M.A.M. Renner 6228* (NSW895689); Westland Province, Kellys Creek, 42°48′S, 171°34′E, 140 m, 21 Aug 1970, *J. Child H347* (F1033818); Westland Province, Fox Glacier, 43°30′S, 170°2′E, 160 m, 25 Aug 1981, *J. Child H3736* (F1087658); Westland, Chesterfield, Kapitea Creek, 42°37′20″S, 171°07′29″E, 35 m, 17 Feb 2012, *M.A.M. Renner 6185* (NSW895512); Westland Province, South Westland, Lake Ellery, 44°5′S, 168°43′E, 60 m, 12 Dec 1981, *J. Child H4592* (F1088380); Aspiring Ecological Region, Okuru Ecological District, Haast Pass, roadside at summit, 3 May 2003, *J.E. Braggins & Y.-L. Qiu NZ03155B* (AK283765); Otago Province, Lee Stream, Hindon Road, 45°48′S, 170°17′E, 300 m, 31 Mar 1972, *J. Child H893* (F1033825); Otago Province, north of Dunedin, north side of Mt Cargill, 45°49′S, 170°34′E, 500 m, 7 Aug 1972, *J. Child H1373* (F1033811); Otago Province, NW of Dunedin, Flagstaff, Pineapple Track, 45°50′S, 170°28′E, 2 Aug 1969, *J. Child H79* (F1033840); Otago Province, Morrisons Creek north of Dunedin, 45°51′S, 170°30′E, 300 m, Jun 1974, *J. Child s.n.* (F1033372); ibid, 140 m, 9 Aug 1981, *J. Child H3447* (F1086803); ibid, *J. Child H3432* (F1086915); ibid, 18 Nov 1972, *J. Child H1659* (F1033457); Otago Province, Siberia Hut, WNW of Makarora, 44°12′S, 169°3′E, 600 m, 17 Jan 1976, *J. Child H2886* (F1033829); Southland Province, Fiordland National Park, Hollyford Valley, 500 m, 1 Apr 1972, *J. Child H1038* (F1033827); Southland Province, Fiordland National Park, Stillwater River, 45°S, 167°22′E, 3 Mar 1949, *V.D. Zotov* (F1027350).

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