

## A revision of Australian *Plagiochila* (Lophocoleinae: Jungermannioopsida)

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### Abstract

Fifty-five *Plagiochila* species are recognized for Australia and New Zealand, of which nine are new, all from Australia with eight of the new species from the Wet Tropics Bioregion of north-east Queensland and the ninth from the south-eastern mesic archipelago of eastern New South Wales and south-east Queensland. Four of the new species belong in the challenging, and neglected, section *Vagae*. Three new Australian records are reported, *P. daviesiana*, *P. monospiris*, and *P. streimannii*; and one species, *P. alta*, is a new record for New Zealand. Six species, *P. annotina*, *P. circumdentata*, *P. colensoi*, *P. deltoidea*, *P. gigantea* and *P. ramosissima*, are excluded from Australia as these are all New Zealand endemics reported in error for Australia. *Plagiochila baylisii*, previously considered a New Zealand endemic, is reported new for Australia. Four species are excluded from Australia, *P. furcata*, *P. inflata*, *P. renitens* and *P. sciophila*, as they are based on misidentifications or are not supported by voucher material. Another interpretation of the confusion surrounding the name *Plagiochila baileyana* is presented, wherein *Plagiochila baileyana* is accepted as a species distinct from *P. gigantea*, while *Plagiochila aculeata* is returned to synonymy of *P. fasciculata*, and *Plagiochila subfasciculata* Colenso is reinstated. The number of *Plagiochila* species in Australia increases from 32 to 41, but the number of species in New Zealand decreases from 28 to 27 as a result of this study. New combinations at species level are also proposed for a variety of *P. blepharophora* from Fiji and two varieties of *P. gymnoclada* from Sumatra and Java, two species which morphological data suggests are grossly polyphyletic as they are currently circumscribed.

### Introduction

The genus *Plagiochila* currently contains around 600 accepted species (Söderström *et al.* 2016) globally distributed in mesic environments, including lowland tropical rainforest and alpine herbfields. Different species partition microsites, including rock, soil, decaying wood, tree trunks, branches, and twigs, and within a forest all microsites except leaf surfaces maybe routinely colonized by various *Plagiochila* species. For example, in tropical montane forest of the Wet Tropics bioregion in Queensland *Plagiochila baileyana* Steph. occupies saturated humic soil on the forest floor, *P. conturbata* Steph. and *P. aenea* M.A.M.Renner grow on granite boulders, *P. monospiris* Inoue & Grolle grows on decaying wood, *P. arbuscula* (Brid. ex Lehm.) Lindenb. grows on tree trunks, and *P. queenslandica* Steph. and *P. daviesiana* Steph. grow on tree trunks, branches and twigs. On the west coast of the South Island, New Zealand, *Plagiochila circumdentata* Steph. and *P. incurvicolla* Hook.f. & Taylor grow on rocks and sand within and alongside streams, *P. banksiana* grows on damp soil,

often on streambanks, *P. intertexta* Hook.f. & Taylor may inhabit damp rocks, *P. gigantea* Lindenb. grows in depressions on the forest floor, *P. stephensoniana* Mitt. and *P. trispicata* Colenso, grow around tree trunk bases, *P. annotina* Lindenb., *P. incurvicolla*, and *P. strombifolia* Mitt. grow on tree trunks, and *P. circinalis* Lindenb. grows on branches and twigs. In some situations, including the tree trunks in the previous example, several species may co-occur within the same microsite. In lowland tropical rainforests in the Queensland Wet Tropics three species, *P. daviesiana* Steph., *P. teysmannii* Sande Lac., and *P. bantamensis* (Reinw., Blume et Nees) Mont. can be found syntopic on twigs and branches within riparian forest. Species packing within and partitioning among microsites combine with the wide range of microsites and climatic breadth occupied resulting in high *Plagiochila* species diversity, both within the Australasian region and elsewhere.

The first *Plagiochila* collections from Australasia were made by Archibald Menzies (1754–1842) at Dusky Bay in Fiordland, New Zealand during his appointment as naturalist on the global voyage of HMS *Discovery* under Captain George Vancouver. Menzies collected at least four *Plagiochila* species at Dusky Bay (now Dusky Sound). Three of these, *Plagiochila annotina*, *P. gigantea*, and *P. ramosissima* were described by William Jackson Hooker (1818) on the basis of his gatherings and have the distinction of being the first *Plagiochila* reported from New Zealand and Australia. New species were still being described from Menzies specimens more than fifty years after their collection, when Lindenberg (1843) described *Plagiochila deltoidea* Lindenb. and included a Menzies gathering in the original material. The next *Plagiochila* reported from Australasia was *Plagiochila circinalis* (Lehm. & Lindenb.) Lehm. & Lindenb., (Lehmann 1832) described as a species of the portmanteau genus *Jungermannia*, on the basis of collections by Charles Fraser (c. 1788–1831), first colonial botanist and superintendent of the Botanic Gardens, Sydney, who made trips to Tasmania in 1820 and 1826 (Orchard 1999).

The next significant *Plagiochila* collections from Australia and New Zealand were made during the voyage of HMS *Erebus* and *Terror*, which made landings at Lord Auckland's Island, Campbell Island, Van Diemen's Land (Tasmania), and the Bay of Islands in the North Island of New Zealand during their Antarctic Voyage. At these localities, the expedition's botanist Joseph Dalton Hooker collected bryophytes and in Tasmania and New Zealand received bryophytes from local collectors. In Tasmania Hooker received collections made by R.C. Gunn. At the Bay of Islands he received collections made by the Reverend William Colenso, who had travelled from Hawke's Bay to meet with Hooker. The Bay of Islands in the early 1840s proved an important locus that would set the course of New Zealand bryology for the next four decades. In addition to HMS *Erebus* and *Terror*, HMS *Favorite*, with Dr Andrew Sinclair (1794–1861) aboard as surgeon, visited the Bay of Islands in 1841. Here Sinclair met with the younger Hooker, who was aboard HMS *Erebus* as assistant surgeon, Dr David Lyall (1817–1895), aboard HMS *Terror* as surgeon, and the Rev. William Colenso Esq. Together these four collected around the Bay of Islands. Given the subsequent contribution of specimens each gentleman made toward Hooker's *Flora of New Zealand*, it is possible that they all discussed Hooker's plans for the completion of that project. The specimens assembled by Hooker from the Antarctic Voyage were studied by Thomas Taylor, who co-authored 10 new *Plagiochila* species from New Zealand and Tasmania with Hooker (Hooker and Taylor 1844a, 1844b).

Dr Lyall went on to serve as surgeon aboard the paddle sloop HMS *Acheron* between 1848 and 1851 and with her was dispatched for a coastal survey of New Zealand, an appointment that facilitated collections from around New Zealand; while Sinclair became Colonial Secretary of New Zealand under Governor FitzRoy at Auckland. Colenso, Lyall, and Sinclair all continued to collect bryophytes, sending their specimens to Hooker, who in turn sent material to William Mitten, author of the bryophyte sections following the death of Taylor in 1848. The association between these four botanists was commemorated in the dedication of Hooker's *Flora of New Zealand* (Hooker 1855), and in species described by Mitten. Two new *Plagiochila* species described by Mitten honoured Hooker's colonial collectors, *P. sinclairii* Mitt., and *P. stephensoniana* Mitt., the latter named for W. Stephenson (c. 1810–c. 1863) who gathered material in the Wellington region. Subsequently, and following the publication of Hooker's *Flora*, Colenso began describing new *Plagiochila* species based on his own gatherings, mostly made in the North Island (Colenso 1887, 1888), and he has the distinction of being the first New Zealand resident botanist to describe new New Zealand liverworts.

Other early collections of *Plagiochila* were opportunistic, some occurring within circumstances of historical significance. One notable, perhaps notorious, example is provided by a specimen of *Plagiochila kirkii* Mitt. ex Steph. gathered by Captain Sir James Evarard Home 2<sup>nd</sup> Bart. C.B. (1798–1853) of HMS *North Star*, 26 guns, from Kerikeri Falls in October 1845, during the ship's deployment in the 'Flagstaff War'—the first conflict of the New Zealand Wars. HMS *North Star* left the Bay of Islands for England on 11 January 1846 and arrived home, with its specimens, on 19 December 1846. This sizeable specimen, a rectangle of bark neatly cut from a tree probably with a small tomahawk, now resides in the Natural History Museum, London.

Mitten's treatment in Hooker's *Flora of New Zealand* (Hooker 1855) recognized 18 *Plagiochila* species, some of which are now attributed to other genera including *Dinckleria* Trev. and *Chiastocaulon* Carl within the Plagiocbilaceae (Groth and Heinrichs 2003; Patzak *et al.* 2016), but also to *Calypstrocolea* within the Adelanthaceae. Mitten described six new species, four of which are accepted today.

During the early phase of European settlement of Australia and New Zealand, resident botanists either volunteered themselves or were appointed to make known the botany of their new colonies. These botanists sent a mixture of their own and other's collections back to the northern hemisphere, where active bryologists resided. Australia's first government botanist, Alan Cunningham (1791–1839) travelled to Australia in 1816, and participated in several collecting expeditions between 1818 and 1831. Cunningham's collection focus was vascular plants, but he did collect non-vascular plants on Lord Howe Island and New Zealand. Other resident botanists who collect or communicated significant collections of non-vascular plants in the mid- to late 19<sup>th</sup> Century included Ferdinand von Mueller (1825–1896), government botanist in Victoria who was appointed in 1853, Thomas Kirk (1828–1898) in New Zealand who in 1868 became Curator at Auckland Museum, and Fredrick Manson Bailey (1827–1915) the first government botanist for the state of Queensland, commencing that position in 1881. Notable among Bailey's collections are those from Bellenden Ker, made during an expedition to the summit in 1889. The 1889 Government Scientific Expedition to the Bellenden Ker Range expedition was led by Archibald Meston and included F.M. Bailey (Dowe and Broughton 2007). They established a base camp on the Mulgrave Plain and explored the Mulgrave River, Harvey Creek, and Russell River areas, including an ascent of Mt Bellenden Ker returning via the Mulgrave River (Dowe and Broughton 2007). The ascent and descent of Bellenden Ker took more than a month, 15 June to 17 July (Dowe and Broughton 2007).

In Tasmania, William Anderson Weymouth (1841–1928) and Leonard Rodway (1853–1936) both sent specimens to Europe, as did Isaac Robinson from Norfolk Island. Thomas Wrench Naylor Beckett (1839–1906), who had settled in Christchurch, collected from along the eastern side of the main divide and up and over Arthur's Pass onto the West Coast—along with Berggren in 1874–75 the first bryologists to collect along this route, from New Zealand. The most significant collector and correspondent of this period though, was probably The Reverend William Walter Watts (1856–1920), who had arrived in Australia from England in 1887. For six years he was minister in Ballina, northern NSW, before moving to Young and Gladesville. Watts made prolific collections of mosses and liverworts, particularly around the Richmond River, and exchanged specimens with Brotherus and Stephani (Ramsay 1980). On Watts' death the NSW herbarium purchased his complete herbarium (Ramsay 1980).

The resulting specimen flow fueled the description of many new species, particularly when Franz Stephani (1842–1927) took it upon himself to fill the gap in expertise left by the deaths of Thomas Taylor (1775–1848), J.B.W. Lindenberg (1781–1851), C.G.D. Nees von Esenbeck (1776–1858), C.M. Gottsche (1808–1892), and the aging William Mitten (1819–1906). Stephani was, for a time, the world's foremost authority on liverworts and viewed literally tens of thousands of specimens during the preparation of his *Species Hepaticarum*, including many from Australia and New Zealand. Stephani even saw duplicates of many of the specimens Colenso had sent to Hooker at Kew, and was not averse to describing new species based upon them. Stephani was a prodigious describer of new species and published no less than 22 new *Plagiochila* species from Australia and New Zealand in his *Species Hepaticarum* from specimens sent to him from Tasmania and New Zealand, including *P. beckettiana* Steph., (Colenso, Beckett), *P. circumdentata* (Beckett), *P. kirkii* Mitt. ex Steph. (Kirk), *P. taylorii* Steph. (Weymouth), and *P. decurvifolia* Steph. (Weymouth). Despite being sometimes maligned for having 'taxonomic capacities too limited for the job' (Gradstein 2006 p. 560) Stephani could be a careful observer and did recognize as new many species we accept today. Although it could be argued that this was an artifact of being an early player on the board, in which circumstance even an entirely haphazard approach to species description would identify genuinely new species, Stephani's work is generally more nuanced than this. There is also an element of bias against Stephani stemming from the modern trend toward application of species concepts that are inappropriately broad. Indeed, in this revision of Australian *Plagiochila*, five of Stephani's species are reinstated from synonymy where they have languished due to subsequent misinterpretation of species circumscriptions or type specimens. To some extent, contemporary criticism of Stephani reflects our own failings as much as it identifies his.

The first regional treatment dedicated to *Plagiochila* was completed for the New Zealand species by Eliza Amy Hodgson (1888–1983), a remarkable woman who, with limited resources but much dedication, published a series of treatments for some of the larger and more challenging New Zealand liverwort genera, some of which remained current into the 21<sup>st</sup> century. Hodgson began her revision of *Plagiochila* by outlining the recognised difficulties inherent in species circumscription, including their being 'difficult of recognition and puzzling to identify' and 'difficult to define species limits' (Hodgson 1944 p. 270). Hodgson recognized 25 species in New Zealand, 19 of which are attributable to *Plagiochila* as currently circumscribed (Hodgson 1944). The only

new taxon described by Hodgson (1944) was *Plagiochila gregaria* var. *ovalifolia* E.A.Hodgs., treated below as a straight synonym of *P. gregaria* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees. After Hodgson's work, it was nearly 30 years before the next regional revision of *Plagiochila* was completed, by Inoue and Schuster (1971) who recognized 25 species of *Plagiochila* for Tasmania and New Zealand including three new species, *P. caducifolia* Inoue & R.M.Schust. *P. baylisii* Inoue & R.M.Schust., and *P. fragmentissima* Inoue & R.M.Schust. The treatment presented by Inoue and Schuster (1971), in its nuanced interpretation of morphological variation and attention to detail with an emphasis on homology, can be regarded as the first modern revision of *Plagiochila* in the Australasian region. Following on from that work, the second modern revision was presented for species of mainland Australia by Inoue (1986) on the basis of the specimens then available, including recent collections from the Wet Tropics made by Marie Hicks. Inoue (1986) described no new species but did report four species new to Australia and extended the ranges of a number of southern species into the Australian Wet Tropics. Subsequent collecting efforts have identified additional species and helped clarify the circumscription of others treated by Inoue. Indeed, the greatest changes in species composition and circumscription resulting from this revision apply to the flora of the Wet Tropics bioregion, which reflects how well studied this region is. Our knowledge of Plagiophilaceae in the Australian Wet Tropics remains incomplete, and new finds, including new species, should be anticipated as the geographic coverage of future collecting effort becomes more comprehensive, even in recently revised genera, see for example Renner and Worboys (2018).

Three new species were described from New Zealand at the end of the 20<sup>th</sup> Century, *Plagiochila bazzanioides* J.J.Engel & Merrill from Rangitoto Island (Engel and Merrill 1999); *Plagiochila hatcheri* J.J.Engel & Merrill from Stewart Island, and *P. kermadecensis* J.J.Engel & Merrill from Raoul Island. Though each of these species is accepted in this revision, all have earlier names, two having already been synonymized (Engel and Merrill 2010) the third, *P. bazzanioides*, is predated by *P. kirkii* Steph. which is reinstated in this treatment.

The summation of this work is that 32 species of *Plagiochila* have been reported for Australia since 1843 and not definitely excluded (Lindenberg 1843; Hooker and Taylor 1844a, 1844b; Bastow 1886; Weymouth 1902; Inoue and Schuster 1971; Inoue 1986; Glenny and Jarman 2008; Engel and Merrill 2010a, 2010b, 2013), around 16 of which are shared with New Zealand. Currently 28 *Plagiochila* species are recognized for New Zealand (Engel and Merrill 2009, 2010a, 2010b, 2013; de Lange *et al.* 2014), not including *Cryptoplagiochila radiculosa* (Mitt.) S.D.F.Patzak, M.A.M.Renner & Heinrichs (Patzak *et al.* 2016). Species circumscription, identity, and nomenclatural priority have been the subject of recent taxonomic research in preparation for the third volume of the Liverwort Flora of New Zealand series (Engel and Glenny 2008), and this effort has resolved many areas of persistent confusion, for example surrounding the application of the names *Plagiochila retrospectans* and *P. fuscella* (Engel and Merrill 2009), the identity of *Plagiochila hatcheri* (Engel and Merrill 2010a), and the status of some early but neglected names.

This might suggest that the diversity of *Plagiochila* in New Zealand is more or less completely known, but this is not necessarily the case, as discussion of *P. deltoidea* and *P. baylisii* below demonstrates. The application of names, a problem quite separate from the circumscription of entities to name is, in this study, also the cause of some deliberation.

Interpretation of types is often a matter of considerable complexity, with good reason. Stephani's types in Geneva are usually fragmentary, his herbarium having been divided a couple of times prior to its purchase by G, and some specimens now comprise single shoot systems, or fragments thereof. For species whose shoots exhibit hierarchical structuring wherein leaves on primary and secondary shoots differ in size and shape, and differences between species manifest most conspicuously on primary shoots, types that comprise fragments of secondary or tertiary shoots alone may be very difficult, if not impossible, to assign to a known species with confidence. Even types comprising relatively intact shoot systems with tractable hierarchy are difficult to relate to known species within complexes of closely related, morphologically similar and simultaneously variable forms as, for example, in the *Plagiochila arbuscula* complex (Renner *et al.* 2018). Despite considerable challenges, however, species circumscription, specimen identification, and type-specimen assignment are all possible using morphological data so long as the interpretation of morphology is methodical, nuanced, and coupled to recognition of both variability and hierarchical structuring. Some revisions of *Plagiochila* for Australia, New Zealand, and the Pacific are not well characterized by these criteria.

This revision for Australia seeks to build on the platform laid by the flora research program being completed in New Zealand.

#### *Phylogenetic context*

All studies referred to above are based on morphological data, being completed or started before the inclusion of molecular data in liverwort taxonomic studies became routine. The first study of *Plagiochila* including molecular data was published by Heinrichs *et al.* (2002), and insight into relationships from that and subsequent

molecular phylogenetic investigations has impacted the classification of Plagiochilaceae at all levels. The genera *Dinckleria* and *Chiastocaulon* have been reinstated from synonymy with *Plagiochila* (Groth and Heinrichs 2003; Heinrichs *et al.* 2006; Patzak *et al.* 2016), while *Rhodoplagiochila* R.M.Schust. was sunk (Heinrichs *et al.* 2004a). The sectional classification for *Plagiochila* has been progressively refined as knowledge of phylogenetic relationships gradually emerged from molecular phylogenetic studies (Heinrichs *et al.* 2003, 2004b, 2005a; Renner *et al.* 2017a, 2017b), and recently the sectional classification was overhauled in line with relationships inferred from a global sample of taxa including a near complete sample of Australasian species (Renner *et al.* 2017c). Molecular data have also provided insights informing species circumscription. Heinrichs *et al.* (2003) noted incongruent morphological and molecular divergence, within both closely and distantly related pairs of *Plagiochila* species. Heinrichs *et al.* (2004c) considered molecular data in their decision to adopt a broad species concept for the morphologically variable *P. bifaria*, and the intercontinental distribution of *P. corrugata* and *P. punctata* (Taylor) Taylor was confirmed using molecular sequence data (Heinrichs *et al.* 2004d, Heinrichs *et al.* 2005b). Revisions of *Dinckleria* and *Chiastocaulon* for Australia employed automated species delimitation methods based on genetic distances (Automatic Barcode Gap Detection: ABGD) and tree topology using the General Mean Yule Coalescent (GMYC) estimated from a three marker molecular dataset (Renner *et al.* 2016a, 2016b, 2017a). A revision of the *Plagiochila arbuscula* complex integrated molecular and morphological data; and used Geometric Morphometric Methods (GMM) to circumscribe differences in patterns of leaf shape variation among lineages within this complex. Differences so identified were then reflected onto type specimens of challenging interpretation to achieve data-based assignment of types, which resulted in the reinstatement of two species (Renner *et al.* 2018).

The strong floristic linkages between Australia and New Zealand, particularly between south-east Australia and New Zealand have long been recognized and are reflected in the number of species distributed on both sides of the Tasman Sea (Inoue and Schuster 1971; Inoue 1982). Treating Australia and New Zealand in a single revision is further justified by three factors, firstly the reciprocal exclusion of species currently thought shared by Australia and New Zealand, and contrarily the new Australian records for species thought endemic to New Zealand, both of which result from study of Australian specimens, but which have bearing on the New Zealand flora. Secondly, the species circumscriptions reached in this study on the basis of a synthesis of molecular and morphological data differ for some species from those in the forthcoming Flora of New Zealand treatment, and these differences have implications for species recognized in New Zealand. Finally, there is always the possibility that species currently New Zealand endemics will be detected in Tasmania, and vice versa. For these reasons the floras of Australia and New Zealand are both treated in this work.

This revision builds upon the work completed by Inoue and Schuster (1971), Inoue (1986) and Engel and Merrill (2009a, 2010a, 2010b), and recognizes 55 species from Australia and New Zealand. Nine are new species, all from Australia, with eight from the Queensland Wet Tropics Bioregion and one from south-eastern Australia. Four of these new species belong in section *Vagae*. Three species are new Australian records – *P. daviesiana*, *P. monospiris*, and *P. streimannii* again all from the Wet Tropics; and one species, *P. alta* Steph., is a new record for New Zealand. The concentration of novelties within this Bioregion reflects how little studied this part of Australia is, as was reflected in Inoue's (1982) synopsis of speciation and distribution of *Plagiochila* in Australasia and the Pacific, at which time only 12 species were recognized from mainland Australia, mostly from the south east. The Australian records for six species -- *P. annotina*, *P. circumdentata*, *P. colensoi*, *P. deltoidea*, *P. gigantea* and *P. ramosissima*--are rejected, these species become New Zealand endemics as a result; while one other New Zealand endemic is reported new for Australia (*P. baylisii*). Four species are excluded from the Australasian region entirely, *P. furcata*, *P. inflata*, *P. renitens*, and *P. sciophila*. Another interpretation of the confusion surrounding the name *Plagiochila baileyana sensu* Inoue and Schuster (1971) is presented, wherein *Plagiochila baileyana* is accepted as a species distinct from *P. gigantea*, while *Plagiochila aculeata* is treated as a synonym of *P. fasciculata*, and *Plagiochila subfasciculata* Colenso is reinstated to accommodate some of the plants assigned to *P. baileyana* by Inoue and Schuster (1971), and to *P. aculeata* by Engel and Merrill (2010). Arrangement of species is by section, following the sectional circumscription presented by Renner *et al.* (2017c), the sections are ordered by phylogeny, with sect. *Denticulatae* first, sect. *Austrocaules* second, and the others following with sect. *Vagae* presented last.

This revision strives for better understanding of phylogenetic and morphological diversity within *Plagiochila*. It does not strive to provide a final answer in terms of the diversity, distribution, and circumscription of species in Australia, or the names that should be applied to them. Indeed, perhaps the most interesting components of this treatment are the areas of residual uncertainty, about which this treatment seeks explicit disclosure, that future improvement in our understanding might be more readily achieved. Further details in areas where species circumscription and the application of names might be improved are described under the species treatments below. Indeed, some significant challenges to species circumscription manifest in this study, some are intrinsic to the plants themselves, others to current circumstances, and it is unlikely that I have overcome

them all. Among intrinsic factors are the hierarchical structuring of shoot morphology, where shoot systems comprise a structured ordinal hierarchy of differentiated shoots that decrease in size with increasing shoot order, and express size-correlated patterns of morphological variation. Many diagnostic differences among species are associated with characters expressed at the larger end of this spectrum of size-correlated variation, in other words, on primary shoots. Type specimens, particularly of species belonging to *Plagiochila* sect. *Vagae* may comprise secondary, tertiary and quaternary shoots. It is then exceptionally challenging to relate type specimens with species. The hierarchical structuring of *Plagiochila* shoot systems seems under-appreciated by previous studies. Published descriptions and illustrations of leaf shape are usually of unknown shoot order, or orders, and species circumscription and identification both suffer because this obscures relevant patterns of structural variation. Inoue and Schuster (1971) sought to incorporate data from new sources into a framework of traditional interpretation, and this served well in the circumscription of species when fresh and fertile material were available. Unfortunately, this approach did not always serve the purposes of effective interpretation of type material, and the identification of sterile, and male or female material in some species, remains challenging as illustrated by the following examples:

- 1) the synonymisation of *P. alta* Steph. (sect. *Belangerianae*) with *P. teysmannii* (sect. *Vagae*) (So 2000).
- 2) the synonymisation of *P. serrifolia* with *P. vitiensis* (Inoue 1986)
- 3) the synonymisation of *P. multifurcata* with *P. queenslandica* (Inoue 1986)
- 4) the synonymisation of *P. queenslandica* with *P. metcalfii* (So 2000)
- 5) application of the name *P. baileyana* Steph. to plants from New Zealand (Inoue & Schuster 1971).

This study seeks a novel interpretation of some older taxonomic character systems from the vegetative gametophyte that explicitly acknowledges the existence of hierarchical structuring within shoot systems and overlapping parameters of variation among species in an effort to achieve durable attribution of type material to entities resolved on the basis of morphological and molecular data. For this reason, species circumscriptions rely heavily on characters from the sterile gametophyte, as these are present in all specimens including types.

Access to type material has imposed some limitations on this study, and an understanding of how those limitations have influenced my nomenclatural decisions will help future investigations understand why I have recognized new species, reinstated synonyms, or not. My efforts to relate Australian species to relevant type material, involved a two-week visit to Geneva in 2014 to examine as many regional types as possible. I examined many, but really needed to see them all again at this study's end. Where I am aware of the need to assess my new species with respect of close relatives overseas, I have made this need explicitly clear alongside my justification for the recognition of the new species. In other instances, I reinstate species from synonymy and apply reinstated names to Australian plants because I am more confident of the application of the synonym than the name which may have priority. *Plagiochila daviesiana* represents an example of this. In this, and indeed in other instances, I suspect it will not be possible to arbitrate over various applications of some names, *P. daviesiana* versus *P. junghuhniana* among them, until topotype material has been collected and the patterns of morphological variation expressed by that material fully appraised and if needed quantified, and the specimens included in a molecular dataset to place the plants within the *Plagiochila* phylogeny. Unfortunately, no *bona fide* specimens of *P. junghuhniana* have yet been included within a molecular phylogeny. The inclusion of well-characterized topotype material in future studies is a pressing need.

Finally, the application of names can be impacted by the typification of species. In Volume 1 of his Index Hepaticarum, Bonner (1962) inadvertently lectotypified many *Plagiochila* species on material held in Geneva, because he identified specimens he regarded as types, in accordance with the code. I thank the late Prof. Dr Jochen Heinrichs for pointing out that many hepaticologists, myself included, have overlooked this fact.

## Character analysis

### *Shoot system replication*

Inoue and Schuster (1971) characterized well the difference between leafy shoot systems with determinate vs unlimited growth, and indeed a distinction between these two kinds of shoot architecture can be made when opposing ends of the spectrum of variation in shoot architecture in *Plagiochila* are compared. At one end of this spectrum are shoot systems expressing a sharp distinction between an erect leafy sector, and a creeping, basal, microphyllous stolon. In these shoot systems the stolon proliferates basally, arising exclusively from other stolons, and never or very rarely are stolons produced *de novo* by leafy shoots. Leafy shoots always start as stolons, before turning away from the substrate and transitioning to leafy growth, simultaneously

producing a new stolon by intercalary branching near the point of upturning. Shoots replicate basally by the production of new stolons. Examples of species with this growth mode include *P. arbuscula*, *P. circinalis* and *P. queenslandica*, and all species of sect. *Vagae* have shoot systems that replicate basally.

At the other extreme are shoots that replicate apically by producing intercalary branches from within their leafy sectors. These intercalary branches are initially microphyllous and stolon-like but immediately turn upward and transition to leafy growth. Examples of species with this growth mode include *P. gigantea*, *P. retrospectans*, and *P. lamellata*. However, these two growth modes are linked by a range of intermediates that serve to blur any clear distinction between the two. *Plagiochila banksiana* grows primarily by production of leafy shoots from other leafy shoots. This species does not often express any stolon shoot sectors. The same is true of *P. intertexta*, though this species does often produce short isolated basal stolons amidst its prostrate and proliferating leafy shoots. On the other hand, while *Plagiochila minutissima* has shoots divided into stolon and leafy sectors, this species may produce stolons *de novo* just about anywhere, including within leafy and stolon sectors. Shoot growth habit may also differ among species with the same growth mode, for example the shoot systems of *Plagiochila gigantea* are erect, while those of the outwardly similar *P. baileyana* are procumbent, so that while having the same architecture the appearance of the plants *in situ* is quite different.

#### *Leafy shoot organization*

*Plagiochila* species may produce monomorphic leafy shoots, or hierarchically structured leafy shoots wherein different branch orders express differences in stature, with stature decreasing with increasing branch order. The largest shoots are always those arising from the basal stolon, and secondary, tertiary, and even quaternary shoots are always smaller by degrees. Hierarchically structured shoots may be pinnate or bipinnate, as in *Plagiochila arbuscula*, or dichotomous as in *P. queenslandica*. In sect. *Vagae* vegetative branching in all species is pseudodichotomous; the branch displaces the leading shoot causing a fork. The symmetry of pseudodichotomy varies among species; in most the fork forms a right angle or close to it but in other species such as *P. streimannii* the displacement of the leading shoot is but slight, and the pseudodichotomy is not immediately apparent, except that the leading shoot alternates left to right more than is quite usual between successive branches.

Neither Inoue and Schuster (1971), Inoue (1984), nor So (2000) explicitly noted hierarchical structure in shoot morphology.

#### *Branching*

Branch types provide significant clues to the identity of plants and different branching modes in stolons and subfloral innovations contribute to circumscribing some of the major lineages within *Plagiochila*. There is a structural component to branch production that is a function of shoot system organization, and this is a critical component in the interpretation of branching type that has not been fully appreciated. Branching within stolon sectors and leafy sectors are often by entirely different modes, and within leafy sectors vegetative branching often differs in mode from branching to produce shoots bearing reproductive structures.

Within the stolon sector, most *Plagiochila* species issue new stolons via lateral-intercalary branches. However, two Australasian species, *P. deltoidea* and *P. ratkowskiana*, produce ventral-intercalary branches within their stolon sectors. These ventral-intercalary branches appear to originate deep within the stem, possibly in the outer layers of the medulla, as they split the stem cortex longitudinally as they erupt and mature. This difference in the branch type by which new stolons are produced provides a valuable character for differentiating *P. deltoidea* from species to which it is superficially similar including *P. fasciculata*, *P. hartziana*, and *P. strombifolia*, particularly when material is sterile.

Within leafy shoot sectors two vegetative branch types predominate, *Frullania*-type and lateral-intercalary branching. Some species produce vegetative branches exclusively by one branch type or the other; in *P. abietina*, *P. arbuscula* and *P. queenslandica* for example vegetative branching is exclusively (or nearly so) *Frullania*-type, whereas in *P. lamellata*, *P. aenea* and *P. rutlandii* it is exclusively lateral-intercalary. Other species including *P. fasciculata*, *P. incurvicolla*, and *P. hartziana* produce both *Frullania*-type and lateral-intercalary vegetative branches and the relative frequency of each type varies among species, in this example lateral-intercalary vegetative branches are uncommon in *P. fasciculata* while they predominate in *P. incurvicolla*. Ventral-intercalary vegetative branching is absent from all *Plagiochila* species, except when shoot tips are damaged and the apex removed, in which case new vegetative shoots are produced close to the apex by lateral-intercalary branching alone, or a combination of lateral- and ventral-intercalary branching. If a plant produces normal ventral-intercalary vegetative branches, then it belongs to either *Dinckleria* or the *Chiastocaulon* lineage. Species whose vegetative branches are otherwise exclusively *Frullania*-type will produce lateral-intercalary branches in response to apex damage, so the state of the shoot apex should be checked when making an assessment of the vegetative branch types.

Subfloral innovations are borne immediately below the gynoecium in most *Plagiochila* species, such that exceptions like *P. abietina* are notable. In most *Plagiochila* species the subfloral innovations issue by lateral-intercalary branching, but in species of sect. *Denticulatae* the subfloral innovations are produced by ventral-intercalary branching and lateral-intercalary branching. Usually the subfloral branch is ventral-intercalary when one subfloral innovation is present, and lateral-intercalary when two or more are present, but both types may be associated with a single gynoecium.

In the male plants of many *Plagiochila* species male branches are produced in terminal pairs, or fascicles of three or more male branches at the apex of leafy shoots, with branches issuing from the base of the first (leading) male branch producing others. The branch type associated with the proliferation of male branches is usually *Frullania*-type, such that some species with exclusively lateral-intercalary vegetative branching may produce *Frullania*-type male branches, and the production of male branches is the only circumstance in which *Frullania*-type branches are manifest in those species. *Plagiochila deltoidea* and *P. ratkowskiana* both produce ventral-intercalary branches in association with male branches, either at the branch base or from among the male bracts, and these may proliferate male branches or produce a vegetative branch.

#### *Leaf shape*

Leaf shape varies among species of *Plagiochila* and presents a critical source of species-circumscribing features despite considerable within-individual and within-species variation. Within individuals leaf shape often expresses variation correlated with size. The breadth of this size-correlated variation within individuals is often greater than the differences in leaf shape expressed among species, and as such ranges of shape and size variation overlap across species and no morphological discontinuity may be evident when leaf shape or size are considered independently. However, in many species of *Plagiochila* differences in leaf shape and size manifest in the size and shape of the largest leaves associated with primary shoots, which may provide diagnostic, if subtle, differences useful for species circumscription and specimen identification, as demonstrated by Renner *et al.* (2018). Correspondingly, the shape of leaves from secondary, tertiary, and quaternary shoots, tend to be smaller and may not provide diagnostic differences among species, due to the convergence in allometric relationships within smaller size ranges.

#### *Leaf orientation and spacing*

Leaf orientation varies among species, some like *P. retrospectans* and *P. fuscella* have transversely orientated leaves, while others like *P. bantamensis* and *P. vitiensis* have nearly longitudinally orientated leaves.

Leaf spacing may show different tendencies among species, particularly closely related species, which provide clues to identity though these are probably best regarded as non-definitive clues only. As an example, *P. fasciculata* typically has imbricate primary shoot leaves, while *P. subfasciculata* typically has remote to contiguous primary shoot leaves, so an initial appraisal of leaf spacing can be corroborated or falsified by assessment of leaf shape and dentition. *Plagiochila apatila* and *P. nebulosa* have leaves more closely spaced than some other sect. *Vagae* species such as *P. minax*. Other species express considerable variation in leaf spacing, such as *P. incurvicolla* within which individuals vary from taller morphs with widely remote leaves to short plants with contiguous to imbricate leaves. *Plagiochila deltoidea* is another species in which leaf spacing varies, so this character should be used with a degree of discretion.

#### *Leaf dentition*

Leaf dentition varies among species and is another critical source of species circumscribing characters. Teeth vary from triangular with a broad base and composed of quadrate to subquadrate cells, to spinose with a narrow base and composed of elongated cells to ciliate and composed of elongate rectangular cells. The number of teeth on leaf margin also serves to differentiate among some species, as does their distribution. In particular the presence of teeth on the dorsal leaf margin is important in distinguishing between some similar pairs of species, for example *P. sydneyensis* from other species of sect. *Cucullatae*, and *P. baylisii* from *P. circinalis*. The number of teeth shows a broad positive correlation with leaf size; within species the larger the leaf the more teeth on its margin.

#### *Leaf cells*

A thickened border is present in some species of sect. *Denticulatae* such as *P. gigantea* and *P. retrospectans*. This border consists of continuous golden-brown pigmented thickening on the walls of the marginal two or three tiers of leaf cells, and this is sometimes discernable with a hand lens in the field. *Plagiochila lamellata* may also produce a similar leaf border in the same manner. The presence of a leaf border is a feature of most, but not all species of sect. *Denticulatae*, being absent from *P. gregaria* or *P. fragmentissima*, and variably expressed in *P. rutlandii*.

The degree of trigone development varies among *Plagiochila* species, some species such as *P. circinalis* are capable of producing block-like trigones, while others such as *P. bantamensis* produce triangular trigones only. So, while this character is potentially informative, the capacity for intra-specific variation in trigone production limits this somewhat.

Leaf-cell size and thickening both vary within and among species and have not been critically assessed as part of this study, so are not used as species circumscribing characters. However, species of sect. *Cucullatae* generally have larger, more leptodermous cells than other *Plagiochila* species, and this gives the plants a distinctive glassy appearance in the herbarium. Leaf cell size provides a useful source of characters for differentiating between *P. apatila* and *P. nebulosa*, as discussed below. *P. nebulosa* has distinctly elongate leaf marginal cells and leaf teeth cells in comparison to *P. apatila*.

#### *Underleaves*

Many *Plagiochila* species produce underleaves, though in most these underleaves are highly reduced. These reduced underleaves are often triangular, but some species have bi-lobed vestigial underleaves. *Plagiochila streimannii* produces what are probably the most conspicuous and well-developed underleaves among Australasian species. *Plagiochila bantamensis* also produces conspicuous underleaves, and in these two species the presence of large underleaves serves to differentiate them from others in their respective sections that do not produce underleaves. However, both species are distinctive and can be recognized without assessing the underleaves. Multiramous ciliiform underleaves are produced by *P. arbuscula*, *P. alta*, *P. pacifica*, and *P. trispicata*, but these fragment and dislocate to the point of absence from mature shoot sectors, except for *P. pacifica* in which underleaf remnants, comprising the basal-most cells of the underleaf remain on mature shoot sectors. In all species of the *P. arbuscula* complex the fully-formed underleaves can only be found among the embryonic leaves at the shoot apex.

#### *Paraphyllia and lamellae.*

Paraphyllia and lamellae are produced by several species and are usually consistently produced by the species that possesses them. The distribution of paraphyllia and lamellae on the stem varies among species and this is useful for identification. Paraphyllia may be restricted to the dorsal or the ventral sides of the stem, as in *P. circumdentata*, and *P. kirkii* or distributed all around the stem surface as in *P. abietina* or confined to the ventral stem surface as in *P. obtusa* and *P. streimannii*. In *Plagiochila abietina* paraphyllia are usually uniseriate projections, but larger paraphyllia comprising small flanges of tissue, sometimes bearing one or two teeth, are also produced. Large branched and ciliate paraphyllia are produced by *P. obtusa* and *P. streimannii*; in both these species paraphyllia are restricted to the ventral side of the stem. Paraphyllia in *P. circumdentata* and *P. kirkii* are chartaceous, but in the latter some paraphyllia are long and approach lamellae. A single long linear lamella is present on the dorsal stem surface adjacent each leaf insertion line in *P. lamellata*.

#### *Asexual reproduction*

Several modes of asexual reproduction occur in Australian *Plagiochila* species. The manifestation of these various modes is more informative of broader relationships than species circumscription, nevertheless the presence of a given type of asexual reproduction can often usefully localize an unknown plant to one or two likely groups of species. Most species of sect. *Vagae* produce gemmae borne on the ventral surface of the leaves. These form by budding, then proliferation of single leaf cells, and quickly assume the form of a small shoot. They may be particularly dense in some individuals. Several species reproduce via caducous leaves, and these may dislocate whole or in pieces. The leaves of *P. minutissima* and *P. spinulosa* dislocate as a whole from their base, while the leaves of *P. bantamensis* dislocate as fragments starting at the leaf apex and working inward toward the stem as the leaf ages.

#### *Male bracts*

The male bracts of *Plagiochila* exhibit useful variation. The male bracts in species of sect. *Denticulatae* are remote to contiguous, and the bract lobe rolls down and sits below the next male bract, so stops below, an arrangement called hypostatic. The other arrangement is exemplified by species of sect. *Vagae* whose male bracts are imbricate, the bract lobe then laying upon the next male bract, so stopping on, an arrangement called epistatic. Male bract lobes may be toothed or entire, and their apex rounded to acute, and some similar species pairs may be readily distinguished on this basis, for example *P. strombifolia* has entire male bract lobes, while *P. fasciculata* has dentate male bract lobes.

## Taxonomic Treatment

*Plagiochila* (Dumort.) Dumort. Recueil Observ. Jungerm. 14 (1835)

Basionym: *Radula* sect. *Plagiochila* Dumort., Syll. Jungerm. Europ. 42 (1831)

Type: *Plagiochila asplenioides* (L.) Dumort. Recueil Observ. Jungerm. 14 (1835)

Shoots in nearly all species divided into microphyllous basal stolon and leafy upper sector. Branching within the stolon lateral- or ventral- intercalary. Vegetative branching within the leafy sector various, *Frullania*-type, lateral-intercalary, or ventral-intercalary. Leaves succubously inserted, sometimes nearly transverse, usually unlobed, rarely bifid, usually with toothed margins, teeth various. Underleaves usually reduced or absent, but in sect. *Cucullatae* well developed, bifid, and ciliate. Stems with differentiated cortex, walls typically thickened and brown pigmented. Dioecious. Androecia intercalary on shoots. Gynoecia terminal, on primary shoots or any subordinate shoot order, in some species such as *P. abietina* on abbreviated shoots, with two leaf-like bracts and sometimes a bracteole. Perianth laterally compressed, ventral face reduced or absent. Subfloral innovations by lateral and/or ventral intercalary branching.

### Key to Australasian *Plagiochila*.

- 1 Leafy shoots bipinnate, pinnate or irregular. Vegetative branching *Frullania*-type or lateral-intercalary, not pseudodichotomous. Asexual production, if present, by caducous leaves. Paraphyllia, if present, confined to dorsal stem surface or distributed on all stem surfaces. .... 13
- 1 Leafy shoots pseudodichotomous, vegetative branching *Frullania*-type. Asexual reproduction, if present, by gemmae produced from the leaf ventral surface. Paraphyllia, if present, confined to the ventral stem surface. .... sect. *Vagae* 2
- 2 Stems with paraphyllia on their ventral surface. .... 3
- 2 Stems without paraphyllia on their ventral surface. .... 4
- 3 Leaves falcate, with 2–7 triangular teeth around the apex. Underleaves conspicuous, larger than paraphyllia. .... *P. streimannii*
- 3 Leaves elliptic, with up to 25 spinose-ciliate teeth, sometimes on all margins. Underleaves similar in size to paraphyllia. .... *P. obtusa*
- 4 Leaves on secondary, tertiary and quaternary shoots rectangular to narrowly-rectangular, apex bifid, often no other teeth present on leaf margin. .... *P. daviesiana*
- 4 Leaves on secondary, tertiary and quaternary shoots elliptic to ovate to ovate-triangular, apex truncate to rounded, with two or more teeth at apex and additional teeth on ventral leaf margin at least. .... 5
- 5 Ventral leaf margin undulate ..... *P. norfolkiensis*
- 5 Ventral leaf margin plane ..... 6
- 6 Leaf margins conspicuously dentate ..... 7
- 6 Leaf margins often entire, or with inconspicuous triangular teeth ..... 8
- 7 Leaves triangular-oblong, apex truncate, margins entire ..... *P. acutifolia*
- 7 Leaves elliptic-oblong, apex rounded or truncate, margins usually with small triangular teeth ..... *P. paucidens*
- 8 Primary shoots 3.2–3.7 mm wide ..... 9
- 8 Primary shoots 5.0–5.5 mm wide ..... 11
- 9 Leaves on primary shoots oblong-triangular ..... 10
- 9 Leaves on primary shoots triangular-ovate ..... *P. queenslandica*
- 10 Leaves on primary shoots with 14–20 spinose teeth regularly spaced around apex and along ventral margin; cells in teeth elongate, narrowly rectangular. Male bract lobes obtuse, otherwise entire ..... *P. nebulosa*

- 10 Leaves on primary shoots with 11–15 triangular teeth around apex and on ventral margin, scattered and irregularly spaced, cells in teeth isodiametric to rectangular, not elongate. Male bract lobes with 4–7 triangular teeth on margin. .... *P. apatila*
- 11 Primary shoot leaves with 3–20 triangular teeth ..... 12
- 11 Primary shoot leaves with 15–40 sharp triangular teeth ..... *P. teysmannii*
- 12 Leaves on primary shoots oblong-triangular, with 3–10 teeth, often two teeth at leaf apex prominent. .... *P. minax*
- 12 Leaves on primary shoots asymmetrically ovate, with 8–20 teeth, teeth at apex not prominent..... *P. meridionalis*
- 13 Stolons originating by ventral-intercalary branching .....sect. *Austrocaules* 14
- 13 Stolons originating by lateral-intercalary branching ..... 15
- 14 Leaves rotund, with 0–10 small triangular teeth. Medial leaf cells to 41  $\mu\text{m}$  long and 28  $\mu\text{m}$  wide..... *P. ratkowskiana*
- 14 Leaves asymmetrically ovate, with 7–24 triangular, acuminate teeth. Medial leaf cells to 25  $\mu\text{m}$  long and 18  $\mu\text{m}$  wide..... *P. deltoidea*
- 15 Leaf cells with triangular to block-like trigones, with or without medial wall thickenings, but not with vermiculately thickened walls ..... 16
- 15 Leaf cells with bulging trigones and medial wall thickenings, often alternating either side of the cell wall to form vermiculately thickened walls ..... *P. aenea*
- 16 Lamellae either absent, or admixed with numerous paraphyllia ..... 17
- 16 A single lamella present adjacent each stem insertion line, paraphyllia absent.....*P. lamellata*
- 17 Subfloral innovations originating by lateral-intercalary branching. Male bracts epistatic. Leaf border absent. .... 26
- 17 Subfloral innovations originating by ventral intercalary branching when one subfloral innovation is produced, or by a mix of lateral- and ventral-intercalary branches. Male bracts hypostatic, but epistatic in *P. gregaria* and *P. fragmentissima*. Leaf border present, but absent in *P. gregaria* and *P. fragmentissima* .....sect. *Denticulatae* 18
- 18 Leafy shoots prostrate, branching irregular, stolons absent or inconspicuous. .... 19
- 18 Leafy shoots procumbent or erect, branching irregular or pinnate, stolons present and either a basal system or at the base of each ramet. .... 20
- 19 Leaves ovate-rotund, with spinose-ciliate teeth. .... *P. banksiana*
- 19 Leaves triangular-ovate with spinose teeth. .... *P. intertexta*
- 20 Leaf with a golden border formed by continuous heavy thickenings on walls of the outer two or three tiers of leaf cells closest to the margin ..... 21
- 20 Leaves without a distinct border as above ..... 24
- 21 Leaves with 15–60 spinose teeth. Vegetative branching *Frullania*-type. Leaves succubously orientated..... 22
- 21 Leaves with 0-100 small and sharp-triangular teeth. Vegetative branching lateral-intercalary. Leaves transversely orientated. .... 23
- 22 Leaves on primary shoots obovate. Shoots flabellate, procumbent. .... *P. baileyana*
- 22 Leaves on primary shoots elliptic. Shoots dendroid, erect. .... *P. gigantea*
- 23 Leaf apex without a single larger triangular-spinose tooth. .... *P. fuscella*
- 23 Leaf apex with a single larger triangular-spinose tooth..... *P. retrospectans*
- 24 Leafy shoot systems monomorphic, irregularly branched above system of basal stolons..... 25
- 24 Leafy shoot systems di- or trimorphic, pinnate or bipinnate. Secondary shoots smaller in stature than primary shoot, bearing smaller leaves with more numerous and prominent teeth than primary shoot leaves. .... *P. rutlandii*

- 25 Leaves asymmetrically triangular ovate, with teeth around the apex and on the ventral margin.  
Perianths with a prominent wing along the length of the dorsal keel. .... *P. fragmentissima*
- 25 Leaves broadly asymmetrically ovate, entire or with a few teeth around the apex.  
Perianths with a low wing at the base of the dorsal keel ..... *P. gregaria*
- 26 Teeth ciliate ; leaves with or without a pouch ..... sect. *Cucullatae* 27
- 26 Teeth triangular to spinose; leaves never with a pouch..... 31
- 27 Dorsal leaf margin with ciliate teeth ..... 28
- 27 Dorsal leaf margin entire or with acutely triangular teeth ..... 29
- 28 Leaves oblong-falcate, leaf pouch spheroidal. Primary shoots 2.5–4.5 mm wide..... *P. bantamensis*
- 28 Leaves rotund to ovate, leaf pouch absent, ventral margin revolute at base only.  
Primary shoots 10–13 mm wide. .... *P. sandei*
- 29 A fusiform to pyriform leaf pouch present on larger leaves. .... *P. sydneyensis*
- 29 A leaf pouch not developed, ventral margin revolute at base only. .... 30
- 30 Leaves triangular-ovate, with numerous spinose-ciliate teeth around apex and on  
ventral leaf margin. .... *P. blepharophora*
- 30 Leaves elliptic, oblong or oblong-ovate, with sharp triangular to spinose-ciliate  
teeth tending to cluster toward the leaf apex. .... *P. vitiensis*
- 31 Vegetative branching lateral-intercalary only..... 43
- 31 *Frullania*-type vegetative branching present ..... 32
- 32 Stems without paraphyllia..... 33
- 32 Stems with paraphyllia ..... *P. abietina*
- 33 Primary shoots 3.0–5.5 mm wide. Basal-most male bracts lamellate. Shoot systems pinnate..... 34
- 33 Primary shoots 5.0–9.0 mm wide. Basal-most male bracts not lamellate.  
Shoot systems pinnate or bipinnate ..... 39
- 34 Plants mid-green, mat. Leaves with 10–30 teeth ..... 35
- 34 Plants dark green-black to bronze-black or black, glossy. Leaves usually with 0–3 teeth ..... *P. hartziana*
- 35 Dorsal leaf margin entire ..... 36
- 35 Dorsal leaf margin with spinose teeth at base immediately above stem insertion..... *P. baylisii*
- 36 Leaves asymmetrically triangular-ovate, teeth triangular. .... 37
- 36 Leaves ovate, teeth triangular-acuminate to aciculate. .... 38
- 37 Leaves on primary shoots remote to contiguous, triangular-oblong to more or less elliptic,  
1550–2450 mm long × 950–1575 mm wide; ventral margin straight in outer half and  
shallowly ampliate at base or continuously curved in more elliptic leaves; apex and  
ventral margin bearing 3–16 triangular teeth; apex usually with 2 prominent teeth,  
inner quarter of ventral margin at base of ampliate portion usually entire ..... *P. subfasciculata*
- 37 Leaves on primary shoots contiguous to imbricate, triangular ovate, 1600–2870 mm long ×  
1220–2330 mm wide; ventral margin curved in outer half and ampliate at base, apex and  
ventral margins, including ampliate portion, bearing 13–23 triangular teeth; sometimes  
two or three teeth at the apex slightly larger; inner quarter of ventral margin at base of  
ampliate portion usually with one to three teeth ..... *P. fasciculata*
- 38 Plants forming turfs of densely packed, irregularly branched, leafy shoots ..... *P. incurvicolla*
- 38 Plants forming turfs of loosely packed, openly pinnate to subpinnately  
branched leafy shoots. .... *P. conturbata*
- 39 Primary shoot leaves oblong-triangular, apex often truncate. Primary shoots 5–7 mm wide..... 40
- 39 Primary shoot leaves triangular ovate, apex rounded. Primary shoots  
7–9 mm wide. .... *P. stephensoniana*
- 40 Leafy shoot-systems bipinnate. Underleaf remnants absent from mature shoot sectors ..... 41

- 40 Leafy shoot-systems pinnate. Underleaf remnants present on mature shoot sectors ..... *P. pacifica*
- 41 Primary shoot leaves longer than wide, more oblong than ovate. .... 42
- 41 Primary shoot leaves nearly the same dimension at their widest and longest, more ovate rather than oblong. .... *P. arbuscula*
- 42 Primary shoot leaves oblong-triangular, 2880–5020  $\mu\text{m}$  long  $\times$  1660–3500  $\mu\text{m}$  wide, with an ampliate base, apex rounded or truncate, dorsal margin straight to shallowly concave; with 6–23 triangular to long triangular teeth distributed discontinuously around the apex and along the ventral margin, usually with a gap in the middle of the ventral margin, in some leaves extending along the dorsal margin to the base, teeth smaller in stature around the apex than the base, where they may be long and curved. .... *P. trispicata*
- 42 Primary shoot leaves oblong, 1570–2885  $\mu\text{m}$  long  $\times$  820–1505  $\mu\text{m}$  wide, with a shallowly ampliate base, apex truncate, dorsal margin shallowly convexly curved at its middle or, less commonly, straight; margins with 7–16 triangular teeth distributed discontinuously around the ventral margin, usually with a gap along the ventral margin, in some leaves extending along the dorsal margin, teeth similar in stature around apex and base ..... *P. alta*
- 43 Leafy shoots dimorphic, irregularly or regularly pinnate or dendroid. .... 44
- 43 Leafy shoots monomorphic, irregularly branched. .... 48
- 44 Primary shoots 1.5–4.0 mm wide. Leaves rotund to asymmetrically ovate. .... 45
- 44 Primary shoots 3.5–5.5 mm wide. Leaves triangular ovate to triangular oblong.....*P. aemula*
- 45 Leaves persistent. Leaf cell surfaces smooth throughout. .... 46
- 45 Leaves caducous. Leaf cell surfaces striolate-papillose on basal cells.....*P. spinulosa*
- 46 Shoots erect or spreading, pinnate or irregular, but secondary shoots not radiating and spreading..... 47
- 46 Shoots erect, dendroid, secondary shoots long, radiating and spreading, often in a single plane, arising from a robust erect primary shoot. .... *P. ramosissima*
- 47 Underleaves present, vestigial, triangular. Oil-bodies granular. Teeth sharp triangular, mixed sizes. .... *P. colensoi*
- 47 Underleaves absent. Oil-bodies homogeneous. Teeth acicular, narrower, acuminate, evenly sized ..... *P. incurvicolla*
- 48 Stems with paraphyllia on dorsal surface..... 49
- 48 Stems without paraphyllia..... 50
- 49 Leaves ovate-triangular. Teeth on ampliate leaf margin straight..... *P. circumdentata*
- 49 Leaves narrow triangular falcate. Teeth on ampliate leaf margin curved. .... *P. kirkii*
- 50 Leaves round..... 51
- 50 Leaves oblong to oblong-triangular ..... 52
- 51 Male branches straight. .... *P. microdictyon*
- 51 Male branches circinate..... *P. circinalis*
- 52 Primary shoots 0.8–3.8 mm wide ..... 53
- 52 Primary shoots 3.0–6.5 mm wide ..... 55
- 53 Leaf insertion not attaining dorsal stem mid-line. Shoots 0.8–2.4 mm wide..... 54
- 53 Leaf insertion attaining dorsal stem mid-line. Shoots 2.5–3.8 mm wide..... *P. vampira*
- 54 Shoots 1.6–2.4 mm wide. Leaves persistent. ....*P. monospiris*
- 54 Shoots 0.8–1.3 mm wide. Leaves caducous..... *P. minutissima*
- 55 Dorsal leaf margin with spinose teeth along its length. Male bract lobes denticulate. Perianth dorsal keel with spinose wing. .... *P. annotina*
- 55 Dorsal leaf margin entire, at least in basal two thirds. Male bract lobes entire. Perianth dorsal keel with low, entire wing ..... *P. strombifolia*

***Plagiochila* sect. *Denticulatae* Schiffn.**, Hep. Fl. Buitenzorg: 106 (1900)

Type: *Plagiochila nobilis* Gottsche (lectotype designated by So & Grolle 2000)

= *Plagiochila* sect. *Fragmentissimae* (Inoue et R.M.Schust.) R.M.Schust., Hepaticae and Anthocerotae of North America 4: 449 (1980)

Basionym: *Plagiochila* subsect. *Fragmentissimae* Inoue et R.M.Schust., Journal of the Hattori Botanical Laboratory 34: 154 (1971)

Type: *Plagiochila fragmentissima* Inoue & Schuster.

Nine species from Australasia belong to sect. *Denticulatae*, whose other species occur in Malesia and on the eastern side of the Pacific in southern South America with a few species distributed along the Andes into Central America as far north as Costa Rica (Patzak *et al.* 2016). The section may be circumscribed by a unique combination of features. The stolon branching is lateral-intercalary, and shoot systems may be modular with a basal stoloniferous section and upper leafy sector, replicated sympodially from a basal stolon network, or monopodially from stolons produced from among leaves. Leafy shoot systems are monomorphic, dimorphic, or trimorphic, and shoots are hierarchically arranged. Lateral-intercalary vegetative branching occurs in all species, some species also produce *Frullania*-type terminal branching (*P. baileyana*, *P. gigantea*). Spinose teeth two or three cells broad at base and uniseriate above, composed of elongate cells with differentially and continuously thickened cell walls on the leaf margins are characteristic of the section; but not all species have these teeth: *P. gregaria* and *P. fragmentissima* have fairly typical triangular teeth and the leaves of *P. fuscella* may be entire. Leaf marginal cells may bear heavy golden-brown pigmented thickening on their cell walls, this too is characteristic of some but not all species in the section. Subfloral innovations are produced by ventral-intercalary branching when one subfloral innovation is present, and while sect. *Denticulatae* is the only section to produce ventral-intercalary subfloral innovations, the subfloral innovation branching mode switches to lateral-intercalary branches when two or more subfloral innovations are present.

***Plagiochila baileyana* Steph.**, Bulletin de l'Herbier Boissier, sér. 2 3: 327 (1903) = Species Hepaticarum 2: 311 (1903)

Type citation: Australia, Queensland, Bellenden Ker Range (Bailey).

Type: Australia: Queensland, Bellenden ker District, Bellenden Ker, Palm Camp, 1889, F.M. Bailey (ex herb. Brotherus 627?) (lectotype designated by Bonner (1962): G 00064091! as *Plag. baileyana* St. n.sp. Original.; isolectotypes: BM! MEL 1039230!)

*Plagiochila baileyana* Steph. ex F.M.Bailey, A synopsis of the Queensland Flora, suppl. 3: 102. (1890) *nom. inval.*

Type citation: Palm Camp, Bellender-Ker, 4000ft

**Etymology:** after Fredrick Manson Bailey (1827–1915) the first government botanist in the state of Queensland who collected the type on the 1889 Government Scientific Expedition to the Bellenden Ker Range led by Archibald Meston (White 1950).

**Notes:** Bailey's Palm Camp collection was made on the Bellenden Ker expedition either on the way up (20–21 June 1889) or on the way back down (28 June–1 July 1889) Bellenden Ker. Palm Camp is on the ridge to the west and north of current Bellenden Ker centre peak, at around 1200 m altitude (Dowe and Broughton 2007). The specimens labeled F.M. Bailey 627 contain two elements, the other being *P. conturbata*, as in the duplicate now in NY, discussed further below under *P. subfasciculata*.

**Description:** Plants with flabellate branched, procumbent leafy shoots comprising repeated monopodial units of a basal stolon and upper leafy sector, stolons arising from within the leafy sector near its base by lateral-intercalary branching; forming diffuse mats; mid-green to bronze-green, shoot systems to 120 mm long and 70 mm wide, dimorphic; primary shoots 2.0–4.0 mm wide, secondary shoots smaller, arising by *Frullania*-type branches. Stems of primary shoots flexuose, without lamellae, paraphyllia, or paraphyses, reddish-brown, to 350 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 4–6 layers, cortical cell walls strongly and continuously thickened, reddish-brown, outer layer with thinner walls than inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls without secondary thickening, primary walls yellow- to yellow-brown pigmented. Rhizoids on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves on stolons reduced, entire, remote to contiguous. Leaves on primary shoots contiguous, succubously inserted and orientated, obovate, 2685–3210 µm long × 1535–1825 µm wide, on secondary shoots 1700–2265 µm long × 1120–1615 µm wide, dorsal margin shallowly curved, ventral margin straight at base; dorsal margin entire or with a few

scattered teeth, apex and ventral margin with (15–)23–33 teeth, teeth spinose comprised of two to four cells, apical cell triangular, slightly elongated and acute-tipped; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, not attaining ventral stem midline leaving, variably along a shoot, one or two cortical cell rows leaf-free, attaining the dorsal stem midline, stem visible between leaves. Marginal leaf cells short rectangular to rectangular, 21–27  $\mu\text{m}$  long  $\times$  6–13  $\mu\text{m}$  wide, occasionally quadrate, long axis perpendicular to leaf margin, walls of one to three tiers of marginal cells with continuous golden-brown thickening; medial leaf cells hexagonal to polyhedral, 26–32  $\mu\text{m}$  long  $\times$  18–22  $\mu\text{m}$  wide, walls without secondary thickening, unpigmented, with small concave to triangular trigones; cells in leaf base elliptic to long rectangular, 40–71  $\mu\text{m}$  long  $\times$  14–18  $\mu\text{m}$ , walls continuously thickened. Cell surfaces smooth. Oil-bodies 4–7 per cell, ellipsoid, pale grey-brown, internally homogeneous, surface granular. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, fascicles of two or three male branches produced at the apex of vegetative shoots by *Frullania*-type branching at the base of the leading male branch; lateral- and ventral-intercalary branches not associated with male branches; bracts in 3–10 pairs, contiguous but not closely packed, bracts resembling sterile leaves but with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts unornamented. Gynoecia at apices of leafy shoots; bracts elliptic-obovate, 2600–3400  $\mu\text{m}$  long  $\times$  1200–2000  $\mu\text{m}$  wide; apex and ventral margin with numerous spinose teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from below the female bracts, 1 per gynoecium in the absence of sporophyte production, absent when sporophytes are present. Perianth ligulate, 3800–4700  $\mu\text{m}$  long  $\times$  1550–1750  $\mu\text{m}$  wide at mouth, dorsal and ventral keels not winged, laterally compressed but with a weakly inflated base, lateral walls plane; labia rounded, each bearing 25–35 spinose teeth. Fig. 1.

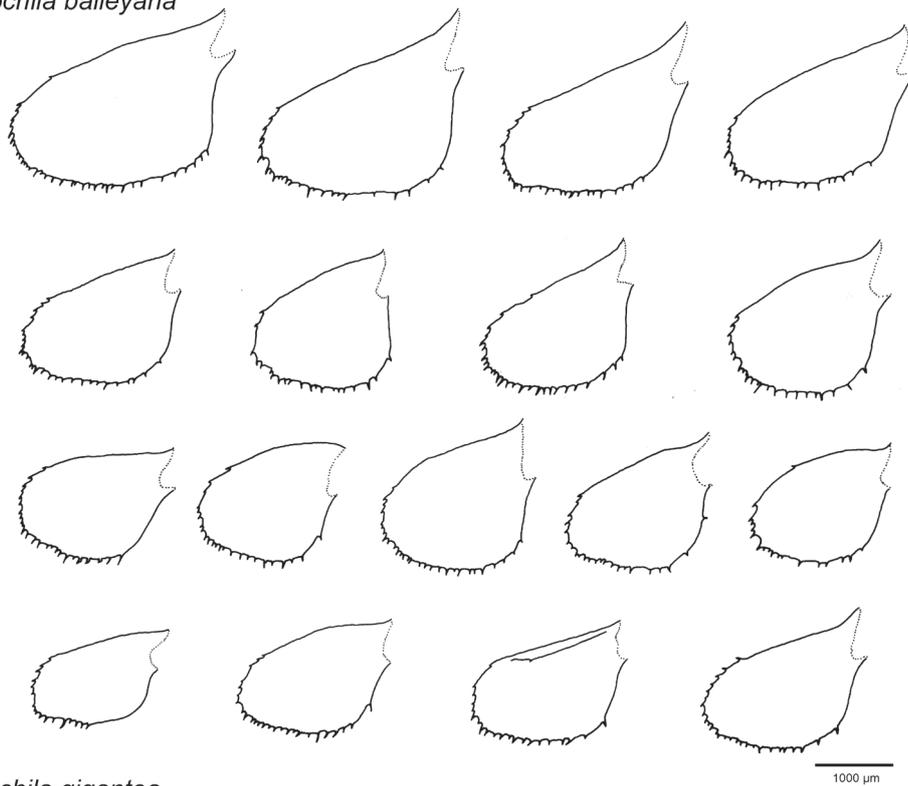
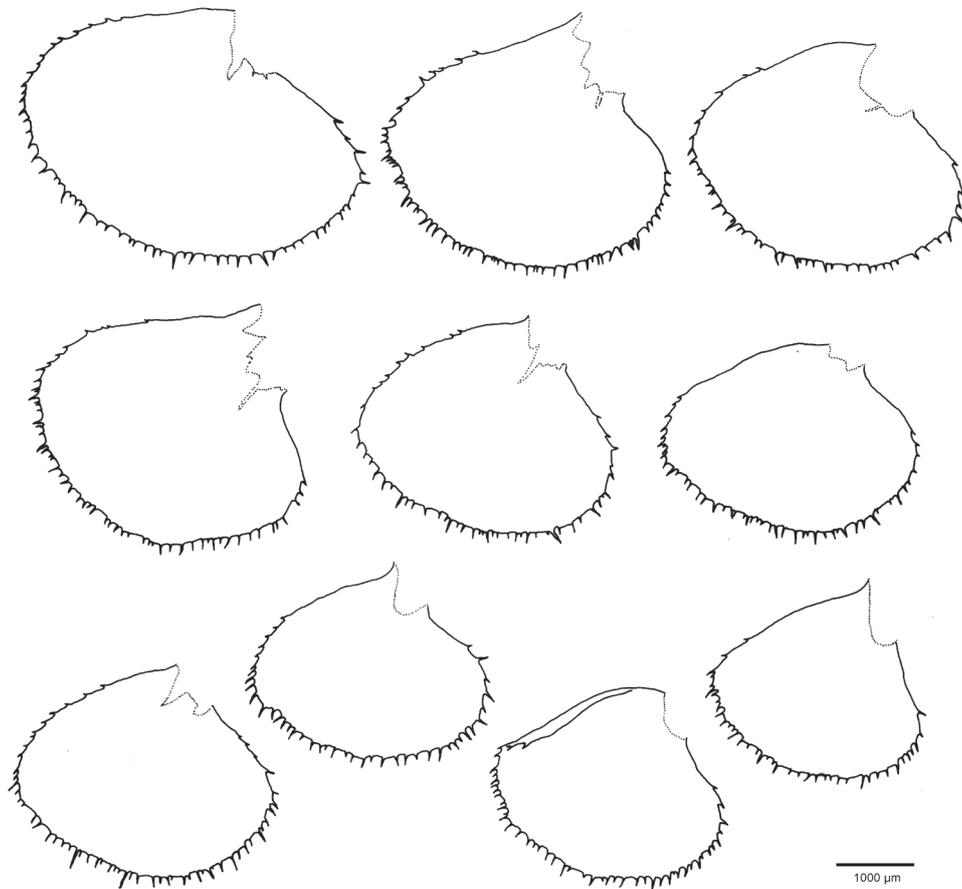
**Recognition:** *Plagiochila baileyana* is distinctive in the procumbent habit of its monopodial shoot systems which are pinnate-flabellate with *Frullania*-type vegetative branching, the numerous spinose-dentate teeth around the leaf margin, and the presence of a leaf border formed by cells with continuously thickened, golden-brown cell walls.

Though similar to *P. gigantea* in details of leaf armature and cell wall architecture, the procumbent growth habit of *P. baileyana* differs from the erect habit of *P. gigantea*, a feature readily observed in the field. In the field *Plagiochila baileyana* forms mats of decumbent shoots, wherein the basal stolon, though initially erect, arches forward and downward, splaying the leafy shoot sector outward in close proximity to the substrate. This contrasts with the growth habit of the outwardly similar New Zealand endemic *P. gigantea*, wherein the stolons are erect, and the leafy shoot sector radiates outward around the central axis in much the same manner as *Hypnodendron* alliance. The two species also differ in leaf shape, *Plagiochila baileyana* has obovate primary-shoot leaves, while *P. gigantea* has broadly elliptic-ovate primary-shoot leaves and this character is probably the best basis for identifying herbarium specimens (Fig. 1). To assess shape adequately leaves must be dissected from shoots and slide-mounted.

**Notes:** The type of *Plagiochila baileyana* comprises a fragmented collection mostly of secondary and tertiary branches, with a couple of primary branches. The distinctive procumbent habit is no longer evident in the specimen, whose shoots scarcely now approach 2 cm long, let alone the 7 cm described by Stephani. This species presents one instance wherein Stephani's protologue provides a clearer conception of the species than the extant type specimens now do, even the more copious isotype in BM. In particular Stephani's description of the habit and the leaf shape clearly encapsulate salient differences between this species and the related *P. gigantea*, with which this species was synonymised by Engel and Merrill (2010a) on the basis of the shared leaf dentition and distinctive architecture and colour of the marginal cell walls. This proposed synonymy was rejected by molecular phylogeny reconstruction, which showed *P. baileyana* was more closely related to *P. intertexta* than *P. gigantea* (Renner *et al.* 2017a, Fig. 1).

**Distribution and Ecology:** *Plagiochila baileyana* is endemic to Australia, where it is confined to tropical montane rainforests above approximately 1200 m in the Wet Tropics Bioregion of north-east Queensland. *Plagiochila baileyana* has a scattered distribution from Thornton Peak in the north to Mount Bartle Frere in the south, and including Mount Bellenden Ker and the Windsor Tableland (M. Grixti *pers. comm.*). Plants inhabit riparian vegetation in permanently wet microsites often beneath overhanging vegetation. On Bartle Frere this species grew on permanently wet soil in seepage sites under *Helmholtzia*, microsites in which the plants were hydrated even during the dry season when all surrounding bryophytes were desiccated. On Thornton Peak *P. baileyana* grew on granite boulders on a steep slope in hyperhumid cloud forest with a range of other large moisture-dependent bryophyte species.

The name *Plagiochila baileyana* has been widely applied to specimens from Tasmania and New Zealand. See the treatment of *P. subfasciculata* below for discussion of how this application came about.

*Plagiochila baileyana**Plagiochila gigantea*

**Fig 1.** *Plagiochila baileyana* and *P. gigantea* leaves from primary shoots. *Plagiochila baileyana* leaves all from *M.A.M. Renner 7318 & L.J. Gray* (NSW 880459); *Plagiochila gigantea* all from *Glenny 118* (NSW) respectively.

**Representative specimens examined:** Australia: Cook: Summit ridge of Mount Bellenden Ker, between the radio mast and W end of centre peak, 17°56'36"S 145°51'06"E, 1370–1420 m, 13 Jun 2001, *D.C. Cargill 109* (CANB 644592.1); Cook, 5 km N of Tinaroo Dam, 17°05'54"S 145°35'26"E, 1025 m, 20 Aug 2000, *B.S. Wannan 1899* & *R.L. Jago* (NSW 623679); *M.A.M. Renner 7311* & *L.J. Gray* (NSW 880456); *ibid.*, *M.A.M. Renner 7318* & *L.J. Gray* (NSW 880459).

***Plagiochila banksiana*** Gottsche, *Annales des Sciences Naturelles; Botanique*, sér. 4, 8: 329 (1857)

*Type citation:* None provided.

*Type:* New Zealand, 1843, *Raoul*, ex herb. Mont., Mus. Paris ex herb. Stephani (lectotype designated by Bonner (1962): G 00121028!)

=*Plagiochila laeta* Mitt., *Handbook of the New Zealand Flora*: 752 (1867)

*Type citation:* Northern Island, *Colenso*

*Type:* n.v.

=*Plagiochila limpida* Herzog, *Transactions and Proceedings of the Royal Society of New Zealand* 68: 42 (1938)

*Type citation:* ... by Makaretu Falls, Wairoa, leg. E.A. Hodgson (n.1)

*Type:* n.v.

=*Plagiochila banksiana* var. *echinophora* Inoue et R.M.Schust., *Journal of the Hattori Botanical Laboratory* 34: 62 (1971) *syn. nov.*

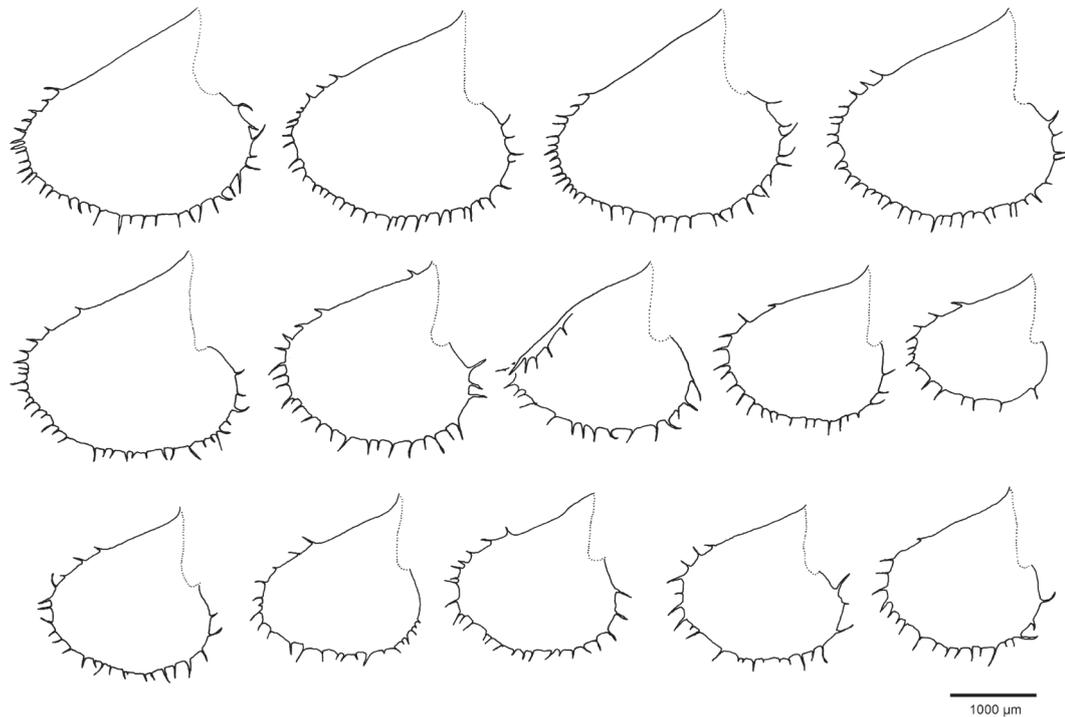
*Type citation:* New Zealand, S. of Haast Pass, Otago Prov., South Island, leg. *Schuster 49724a* (MASS)

*Type:* n.v.

**Etymology:** named for Sir Joseph Banks who, with Daniel Solander, were aboard *HMB Endeavour* on Cook's first voyage to New Zealand.

**Description:** Plants irregularly branched, prostrate leafy shoots; robust system of basal stolons absent, but microphyllous shoots may be present in basal sectors of the plant; forming diffuse mats; mid-green, shoots to 90 mm long, monomorphic; primary shoots 2.0–4.0 mm wide, secondary shoots smaller, arising by lateral-intercalary branches. Stems of primary shoots without lamellae, paraphyllia, or paraphyses, reddish-brown, to 600 µm diameter, transversely elliptic, surfaces smooth; cortical cells in up to 4 or 5 layers, cortical cell walls continuously thickened, light reddish-brown, outer layer with thinner walls than inner cortical cell layers, inner cells with thickening tapering toward medulla, all cortical cells smaller than medulla cells, cortex sometimes weakly differentiated in which case walls are thinner and with faint pigmentation; medulla cell walls without secondary thickening, primary walls yellow- to yellow-brown pigmented. Rhizoids arising from the lateral merophyte at the base of leaves and from the ventral merophyte. Leaves on primary shoots contiguous to imbricate, succubously inserted and orientated, ovate-rotund, 1500–3000 µm long × 1200–2800 µm wide; dorsal margin entire or with a few scattered teeth, apex and ventral margin with 15–38 teeth, teeth spinose-ciliate comprised of two to four cells, apical cell triangular, slightly elongated and acute-tipped; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, not attaining ventral stem midline leaving, variably along a shoot, one or two cortical cell rows leaf-free, not attaining the dorsal stem midline, stem visible between leaves. Marginal leaf cells rectangular, 20–35 µm long × 10–15 µm wide, long axis parallel to leaf margin, walls of one to three tiers of marginal cells with or without weak continuous thickening; medial leaf cells hexagonal to polyhedral, 25–45 µm long × 35–45 µm wide, walls without secondary thickening, unpigmented, with small concave to triangular trigones; cells in leaf base elliptic to long rectangular, 25–75 µm long × 20–35 µm, walls unthickened except for triangular trigones. Cell surfaces smooth. Oil-bodies 5–12 per cell, fusiform to ellipsoid, hyaline, internally homogeneous, surface granular. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, produced singly at the apex of vegetative shoots; lateral-intercalary branching from within male branch present in some plants, *Frullania*-type and ventral-intercalary branches not associated with male branches; bracts in up to 20 pairs, imbricate but not closely packed, bracts resembling sterile leaves in shape and dentition but smaller and with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts unornamented. Gynoecia at apices of leafy shoots; bracts rotund, larger than subtending leaves; apex and ventral margin with numerous spinose teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by ventral-intercalary or lateral-intercalary branching from between the female bracts. Perianth campanulate, 1800–2400 µm long and 1300–1600 µm wide at mouth, dorsal and ventral keels narrowly winged; labia rounded, each bearing 4–15 spinose-ciliate teeth. Fig. 2.

*Plagiochila banksiana*

**Fig 2.** *Plagiochila banksiana* leaves, all from *P.J. de Lange* 9934 (AK 323586).

**Recognition:** *Plagiochila banksiana* can be recognized by the combination of prostrate or procumbent leafy shoots, absence of a well-defined network of basal stolons, broad-ovate leaves with spinose-dentate margins (Fig. 2), cells with weakly thickened cell walls and small triangular trigones. The stem anatomy of *P. banksiana* is unusual, in having a cortex of 3 or 4 tiers of cells whose walls are only moderately thickened. The male bracts of *P. banksiana* are leaf-like with a lobe nearly the same size and shape as the adjacent leaves.

**Distribution and Ecology:** *Plagiochila banksiana* is a native of southern temperate Australasia with a range including the New Zealand mainland and outlying islands including the Chatham Islands. *Plagiochila banksiana* is widely distributed throughout the North and South Islands, from Te Pahi to Fiordland. *Plagiochila banksiana*'s only Australian occurrence is on Macquarie Island (Inoue and Seppelt 1985) and here, as in New Zealand, it is common in seepages and alongside streams in bryophyte communities typical of wet sites including *Acrocladium*, *Brachythecium salebrosum*, *Breutelia pendula*, *Chiloscyphus*, *Dicranoloma*, *Drepanocladus uncinatus*, *Metzgeria*, *Riccardia cochleata*, *Temnoma palmatum*, *Thuidium*. On Macquarie Island in association with *Poa foliosa* grassland, *Carex trifida* sedgeland, and *Azorella polaris*-*Pleurophyllum* herbfields. *Plagiochila banksiana* also grows on rocks within the flood zone of streams and rivers, or partially submerged on boulders, within waterways. The species occurs on a variety of substrates including basalt, ignimbrite, and schist.

**Representative specimens examined:** **Australia:** *Verremy* [sic] as *Plagiochila Beta deltoidea* Ldbg. (G 026167); **Macquarie Island:** Skua Lake, Quadrat 4, 54°37'S 158°50'E, 22 Nov 1983, G.R. Copson (HO 577576); Skua Lake, Quadrat 2, 54°37'S 158°50'E, 22 Oct 1983, G.R. Copson (HO 577577); Skua Lake, 54°37'S 158°50'E, 22 Oct 1983, G.R. Copson (HO 577578); Sawyer Creek Gorge, 54°38'08"S 158°53'18"E, 30 m, 11 Nov 1979, R.D. Seppelt 6605 (HO 577581); Sawyer Creek Gorge, edge of lower waterfall, 54°38'S 158°53'E, 25 m, 23 Nov 1981, R.D. Seppelt 11963 (HO 577599); Boiler Rocks, 54°33'S 158°52'E, 15 m, 13 Dec 1979, R.D. Seppelt 7225 (HO 577583); Sawyer Creek valley, above main water fall, 54°38'S 158°53'E, 80 m, 19 Nov 1979, R.D. Seppelt 6894 (HO 577582); north west of Handspike Corner, 54°30'S 158°53'E, 15 m, 3 Jan 1980, R.D. Seppelt 7403 (HO 577584); *ibid.*, R.D. Seppelt 7406 (HO 577585); *ibid.*, 20 Jan 1980, R.D. Seppelt 10230 (HO 577588); *ibid.*, 25 Oct 1984, R.D. Seppelt 14587 (HO 577605); Hurd Point, coastal slopes behind field Hut, 54°46'S 158°50'E, 100 m, 17 Jan 1980, R.D. Seppelt 7791 (HO 577586); 1.5 km north east of Bauer Bay refuge hut, 54°33'S 158°53'E, 120 m, 6 Nov 1981, R.D. Seppelt 11694 (HO 577589); west coast raised beach terrace between Boiler Rocks and Douglas Point, 54°33'S 158°52'E, 20 m, 16 Nov 1981, R.D. Seppelt 11804 (HO 577590); Finch Creek Valley, west of Sandy Bay, 54°34'S 158°54'E, 150 m, 23 Nov 1975, R.D. Seppelt 9572 (HO 577587); Raised beach terrace between Boiler Rocks and Douglas Point, 54°33'S 158°52'E, 20 m, 16 Nov 1981, R.D. Seppelt 11809 (HO 577591);

Razor Back Ridge, 54°30'S 158°56'E, 100 m, 5 Nov 1983, *R.D. Seppelt 14427* (HO 577603); Hasselborough Bay, 54°30'S 158°56'E, 10 m, 7 Nov 1983, *R.D. Seppelt 14466* (HO 577604); Nuggets Creek, 54°32'S 158°56'E, 20 m, 22 Nov 1984, *R.D. Seppelt 14776* (HO 577606); 50 m west of Gadgets Gully dam, 54°30'S 158°55'E, 110 m, 9 Feb 1995, *R.D. Seppelt 19540* (HO 577607); creek on south side of Tractor Rocks, 54°30'S 158°56'E, 3 Feb 1995, *R.D. Seppelt 19958* (HO 577608). **New Zealand: North Island:** North Cape, Te Pahi, North Cape Scientific Reserve, Pararaki Stream, at the confluence of eastern and western tributaries, 34°24'15"S 173°01'56"E, 100 m, 22 Feb 2011, *P.J. de Lange 9934* (AK 323586); Central North Island, Eastern Volcanic Plateau, Whirinaki, near Minginui, Whirinaki River, Mangamate waterfall, 39°31'21"S 176°46'52"E, 320 m, 6 Dec 2007, *P.J. de Lange 7359* & *P.B. Cashmore* (AK 303499); **South Island:** Nelson Province, Gridiron Bivvy, Flora track, NW Nelson, 41°11'S 172°44'E, 1000 m, 20 May 1983, *J. Child H4773* (F 1088173); Arthurs Pass, east of pass, Pegleg Creek, north of the road, 42°54'S 171°34'E, 950 m, 1 Feb 1986, *J.E. Braggins 86/041B* (AK 258044); Hokitika Gorge track from footbridge, at river access about 1 km upstream of footbridge, 42°57'34"S 171°36'E, 75 m, 26 Nov 1995, *J.E. Braggins 95/649A* (AK 303869); Lake Monowai, 19 km WSW of Manapouri, 45°35'S 167°22'E, 180 m, 16 Nov 1990, *J.A. Curnow 3480* (CANB 9406344); **Chatham Islands:** Rekohu (Chatham Island) Tuku-a-Tamatea Nature Reserve, Tuku-a-Tamatea River, 44°04'S 176°36'W, 200 m, 13 Sep 2007, *P.J. de Lange CH1143* & *P.B. Heenan* (AK 302541).

***Plagiochila fuscella*** (Hook.f. & Taylor) Taylor & Hook.f. ex Gottsche, Lindenb. & Nees, *Synopsis Hepaticarum* 5: 648 (1847)

Basionym: *Jungermannia fuscella* Hook.f. & Taylor, *London Journal of Botany* 3: 373 (1844)

*Type citation:* Lord Auckland's group.

*Type:* Auckland Islands, Lord Auckland's group, Nov 1840, *J.D. Hooker*, *Voyage of H.M. Discovery Ships Erebus and Terror* (lectotype designated here: FH 00458014!)

=*Plagiochila beckettiana* Steph., *Bulletin de l'Herbier Boissier*, sér. 2 4: 788. (1904) = *Species Hepaticarum* 2: 466. (1904)

*Type citation:* New Zealand (Colenso, Beckett)

*Type:* New Zealand, insula merid., Waimate (Canterbury) in damp bush, May 1901, *T.W.N. Beckett 247*, ex herb. *Levier 2784* (lectotype designated by Bonner (1962): G 00121210!)

=*Plagiochila orbiculata* Colenso, *Transactions and Proceedings of the New Zealand Institute* 21: 48 (1888)

*Type citation:* On ground, sides of Mount Tongariro, County of East Taupo; 1887; *Mr. H. Hill*.

*Type:* New Zealand, Mt Tongariro, county of East Taupo, 1887, *Colenso 1357* (lectotype designated by Bonner (1962): G).

=*Plagiochila rotundifolia* Colenso, *Transactions and Proceedings of the New Zealand Institute* 20: 246 (1887) [1888]

*Type citation:* Among small herbage, shaded woods, base of Mount Tongariro, County of East Taupo; 1887; *Mr. H. Hill*.

*Type:* n.v.

=*Plagiochila taylorii* Steph., *Bulletin de l'Herbier Boissier*, sér. 2 4: 781 (1904) = *Species Hepaticarum* 2: 459 (1904)

*Type citation:* Tasmania (Weymouth).

*Type:* Tasmania, Mt Wellington, St Crispin's, 2000 ft, on rocks, 24 Jan 1899, *W.A. Weymouth 550*, (lectotype designated by Inoue and Schuster (1971): NY; isolectotypes: BM! HO 305177! HO 85834! MEL 300793!)

=*Plagiochila fuscella* var. *novae-zelandiae* (E.A.Hodgs.) J.J.Engel & G.L.Merr., *Nova Hedwigia* 89: 294 (2009) *syn. nov.*

Basionym: *Plagiochila retrospectans* var. *novae-zelandiae* E.A.Hodgs., *Transactions and Proceedings of the Royal Society of New Zealand* 73: 293. (1944)

*Type citation:* New Zealand Bealey River, coll. Berggren, n.3685e, 1874

*Type:* n.v.

**Notes:** Engel and Merrill (2010a) redundantly lectotypified *P. beckettiana* on the same specimen as Bonner (1962) and identified a lectotype for *J. fuscella* but their lectotypification did not fulfill the rather stringent requirements of the ICN.

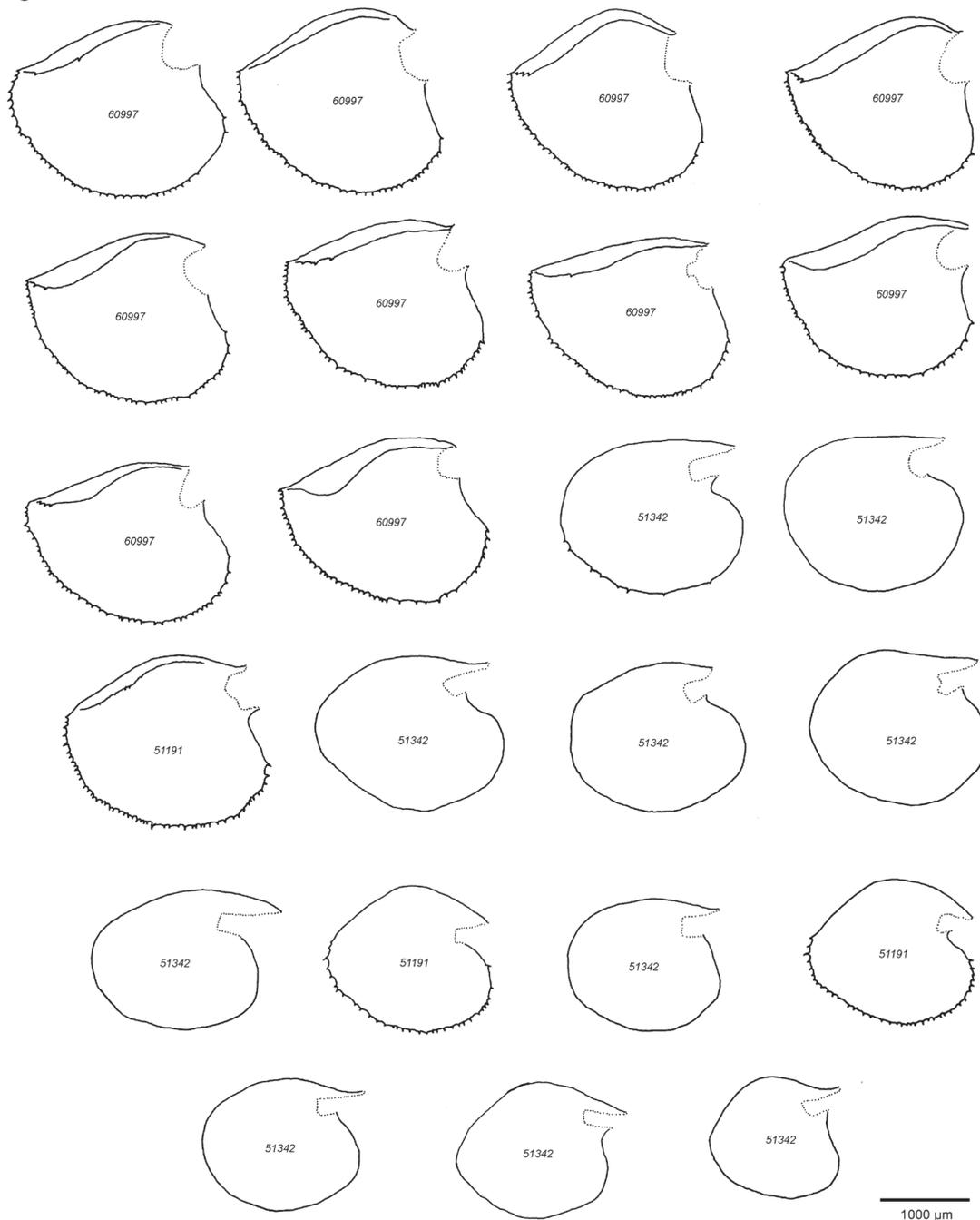
A new lectotype for *P. orbiculata* was identified by Engel and Merrill (2010a): New Zealand, *Colenso* 1329 sub *Plagiochila alpina* *Colenso* (WELT: isolectotype: G 00120994!), however Bonner (1962) had already inadvertently lectotypified this species. *Plagiochila rotundifolia* is a synonym of *P. fuscella* *fide* Engel & Merrill (2009). Inoue and Schuster (1971) were not able to study the type of *P. rotundifolia*, but Stephani (1892) gives it as a synonym of *Adelanthus falcatus* *fide* Hamlin (1972); *Colenso's* collection (n. 1424a) in WELT agrees with *Plagiochila retrospectans* *fide* Hamlin (1972). Inoue and Schuster (1971) designated Weymouth no. 550 in NY as the lectotype of *P. taylorii* and listed the name under synonymy of *P. stephensoniana*; Engel and Merrill (2013) clarified the status of *P. taylorii*, and placed it in synonymy of *P. fuscella*. Engel and Merrill (2010) recognized *Plagiochila fuscella* var. *novae-zelandiae* for plants with reniform leaves, teeth on the leaf margins, and thickened marginal cell walls. All these characters vary as a function of exposure. The number of marginal teeth also varies within and among specimens.

**Etymology:** fusc- dark brown, -ella diminutive suffix, in reference to plant colour.

**Description:** Plants with irregularly branched, erect leafy shoots comprising repeated monopodial units of a basal stolon and upper leafy sector, stolons arising from within the leafy sector near its base by lateral-intercalary branching; forming dense turfs; dark-green to bronze-green, shoot systems to 60 mm long and 25 mm wide, monomorphic; shoots 1.0–1.5 mm wide, arising by lateral-intercalary branches. Stems without lamellae, paraphyllia, or paraphyses, reddish-brown, to 400  $\mu\text{m}$  diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 4–6 layers, cortical cell walls strongly and continuously thickened, constricting the cell lumen in middle cortical layers, reddish-brown, outer layer with thinner walls than inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls without secondary thickening except those beneath the cortex, on whose walls thickening tapers over 2 or 3 tiers toward the stem centre, primary walls faint red-brown pigmented. Rhizoids on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on leafy shoots imbricate, succubously inserted but transversely orientated, rotund-ovate, 1550–2500  $\mu\text{m}$  long  $\times$  1500–2350  $\mu\text{m}$  wide, dorsal margin shallowly curved, ventral margin amplate; margins entire or with up to 100 teeth on apex and ventral margin, teeth small and triangular, comprised of one or two cells, apical cell triangular, slightly elongated and acute-tipped; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular 7–17  $\mu\text{m}$  long  $\times$  8–15  $\mu\text{m}$  wide, long axis parallel or perpendicular to leaf margin, walls of one to three tiers of marginal cells with continuous golden-brown thickening; medial leaf cells quadrate to polyhedral, 8–18  $\mu\text{m}$  long  $\times$  10–23  $\mu\text{m}$  wide, walls unpigmented, with conspicuous cordate to bulging trigones and occasional medial thickening; cells in leaf base long rectangular, to 60  $\mu\text{m}$  long  $\times$  15  $\mu\text{m}$  wide, walls continuously thickened. Cell surfaces smooth. Oil-bodies 1–4 per cell, ellipsoid, granular. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, often in a terminal tuft produced by serial lateral-intercalary branching at the apex of a leafy shoot itself bearing a male branch, male branches nodding, ventral-intercalary and *Frullania*-type branches not associated with male branches; bracts in 3–8 pairs, imbricate and closely packed, bracts resembling sterile leaves but with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts unornamented. Gynoecia at apices of leafy shoots; bracts ovate-rotund, larger than subtending leaves but otherwise similar; apex and ventral margin with numerous spinose teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral- or ventral-intercalary branching from between the female bracts. Perianth ligulate, to 5500  $\mu\text{m}$  long  $\times$  2500  $\mu\text{m}$  wide at mouth, dorsal and ventral keels not winged, laterally compressed but with a weakly inflated base, lateral walls plane; labia truncate or emarginate, each bearing 18–24 spinose teeth. Fig. 3.

**Distribution and Ecology:** *Plagiochila fuscella* is a native of southern temperate Australasia, and occurs in Australia and New Zealand. In Australia *P. fuscella* is widely distributed in Victoria, Tasmania, and Macquarie Island in wet sites associated with watercourses and seepages in forest, grassland, and herbfield. In Victoria *P. fuscella* is restricted to higher elevation sites in the Great Dividing Range. In New Zealand *P. fuscella* is widely distributed in the South Island but is rarer in the North Island, where it is restricted to cool hyperhumid forests in association with mountains and ranges. *Plagiochila fuscella* is often a rheophyte, growing within the flood zone of watercourses on bedrock, boulders, sand or soil, but it also grows in seepage sites associated with cliffs, and in saturated herbfield associated with soaks, tarns, and springs. On Macquarie Island *P. fuscella* has been collected in a wide range of microhabitats, including fellfield terraces in short grassland ecotones, with *Azorella macquariensis*, *Polytrichum*, *Campylopus*, *Dicranoloma*, *Syzygiella colorata*, and *Racomitrium crispulum*; in sheltered recesses alongside streams with *Bartramia papillata*, *Chiloscyphus bidentatus*, *Lepidozia*, and *Peltigera*; on wet stones and earth bank at edge of waterfall, with *Acrocladium*, *Breutelia elongata*, *Temnoma palmatum*, and *Dicranella cardotii*; in short grassland with *Breutelia pendula* and *Thuidiopsis furfurosa*; on stones at the edge of a small lake; and within rockfield formed by pillow basalt.

*Plagiochila fuscella*

**Fig 3.** *Plagiochila fuscella* leaves from primary shoots, from *H. Streimann* 51191 (CANB 9306641), *H. Streimann* 51342 (CANB 9306792), and *H. Streimann* 60997 (CANB 9910339.1)

**Recognition:** *Plagiochila fuscella* can be recognized by the combination of succubously inserted but transversely orientated, ovate to reniform, imbricate leaves whose margins are either entire, or bear few to numerous small triangular teeth composed of one to three cells whose walls are usually continuously thickened to a degree greater than the subtending medial leaf cell walls, at least on the free external wall; vegetative branching by lateral-intercalary mode only; the decurrent wing formed by the dorsal leaf insertion; and the ventral-intercalary subfloral innovation when only one is present.

*Plagiochila fuscella* could be confused with *P. retrospectans*, but differs by the absence of a pronounced, larger, spinose-dentate tooth close to the outer extremity of the dorsal leaf margin. *Plagiochila fuscella* and *P. retrospectans* also differ in leaf shape, the dorsal margin of *P. fuscella* leaves is more shallowly curved such that the leaf apex is above the leaf midline, whereas in *P. retrospectans* the dorsal margin is more curved, and the leaf apex is close to the leaf midline (Figs 3, 4).

*Plagiochila fuscella* could be confused with *Adelanthus falcatus*, but differs by the smaller, often more numerous teeth, the rotund to reniform leaf shape (not obovate) and the imbricate leaves.

**Representative specimens examined:** **Australia:** **Tasmania:** North West Coast: Emu Bay, Jan 1892, *J.H. Royce* ex herb. Weymouth No. 68 det Stephani (BM); South West, Waterfall Creek State Reserve, South Bruny Range, 43°24'S 147°19'E, 100 m, 28 Apr 1993, *A. Moscal* 25214 (HO 577324); South West, Wilson Bight, 43°33'S 146°05'E, 5 m, 14 Jan 1987, *A. Moscal* 13963 (HO 577366); North East, Groom River, 3.5 km SSE of Lottah, 41°15'S 148°02'E, 160 m, 23 Nov 1984, *A. Moscal* 26353 (HO 577342); eastern slope to Mackintosh Creek watershed, 480–680 m, 41°34'S 145°49'E, 5 May 2003, *A. Moscal* 31387A (HO 577373); Ben Lomond, Mount Barrow State Reserve, 41°22'S 147°26'E, 900 m, 26 Feb 1993, *A. Moscal* 24686 (HO 577416); Russell Falls to Lady Barron Falls track, Mt Field National Park, 42°41'S 146°42'E, 20 Dec 1980, *A.V. Ratkowsky* (HO 304472); Mt Freycinet, Freycinet National Park, 42°13'S 148°18'E, 620 m, 12 Jul 2003, *K. Felton* (HO 305596); Cradle Mountain-Lake St Clair National Park, track from Lees Paddocks to Kia Ora, 41°53'S 146°06'E, 630 m, 25 Sep 2000, *K. Felton* (HO511113); Central Highlands, Qualie Falls, Olivia Creek, 41°34'S 146°01'E, 700 m, 16 May 1996, *A. Moscal* 28324 (HO 577317); **Macquarie Island:** Lusitania Creek, 54°43'S 158°50'E, 50 m, 11 Jan 1980, *R.D. Seppelt* 9645 (HO 577657); *ibid*, 80 m, *R.D. Seppelt* (HO577658); *ibid*, 130 m, *R.D. Seppelt* 9700 (HO 577659); 500 m south east of Mt Flectcher, 54°44'S 158°49'E, 320 m, 11 Jan 1980, *R.D. Seppelt* 9717 (HO 577660); Bauer Bay, west coast, along creek north east of Bauer Bay hut, 54°33'S 158°53'E, 15 m, 8 Jan 1980, *R.D. Seppelt* 9772 (HO 577661); Green Gorge, 54°38'S 158°54'E, 40 m, 8 Feb 1980, *R.D. Seppelt* 9862 (HO 577663); south east side of Mt Haswell, 54°46'S 158°48'E, 300 m, 31 Jan 1980, *R.D. Seppelt* 9979 (HO 577667); eastern shore of Prion Lake, 54°35'S 158°54'E, 190 m, 9 Feb 1980, *R.D. Seppelt* 10213 (HO 577674); Pyramid Peak, 54°39'30"S 158°52'18"E, 240 m, 26 Feb 1980, *R.D. Seppelt* 10329 (HO 577677); 1 km west of Scoble Lake, 54°31'S 158°54'E, 200 m, 2 Mar 1980, *R.D. Seppelt* 10602 (HO 577684); Sawyer Creek valley, beside main waterfall, 54°38'S 158°53'E, 70 m, 5 Dec 1981, *R.D. Seppelt* 12117 (HO 577695); 500 m SW of Mt Elder, in water at east end of lake, 54°32'S 158°55'E, 340 m, 17 Dec 1984, *R.D. Seppelt* 14895a (HO 130040); 500 m SE of Mt Elder, on stones at edge of small lake, 54°32'14"S 158°55'00"E, 310 m, 17 Dec 1984, *R.D. Seppelt* 14895c (HO 577614); 350 m N of Island Lake, 54°31'S 158°53'E, 200 m, 3 Mar 1985, *R.D. Seppelt* 15600 (HO 130033); 500 m SW of Mt Elder, 54°32'S 158°55'E, 290 m, 17 Dec 1984, *R.D. Seppelt* 14895b (HO 130027); Sawyer Creek gorge, by main waterfall, 54°38'S 158°53'E, 5 Dec 1986, *R.D. Seppelt* 12116 (HO 129596); Green Gorge, 54°38'S 158°54'E, 29 Oct 1980, *R.D. Seppelt* 11393 (HO 127643); Green Gorge, SW side, 54°38'S 158°53'E, 18 Nov 1979, *R.D. Seppelt* 6903 (HO 577642); Green Gorge, south side of lake, 54°37'44"S 158°53'45"E, 6 m, 26 Mar 2003, *P.M. Turner* (HO577634); Skua Lake, 54°37'S 158°50'E, 22 Oct 1983, *G.R. Copson* (HO 577632); Sawyer Creek Valley, western side, 1 km south east of Mt Law, 54°38'S 158°52'E, 200 m, 17 Nov 1979, *R.D. Seppelt* 6732 (HO 577639); Sawyer Creek valley, above waterfalls, 54°38'S 158°53'E, 120 m, 19 Nov 1979, *R.D. Seppelt* 6954 (HO 577643); knoll on western side of Major Lake, 54°41'S 158°49'E, 210 m, 11 Jan 1980, *R.D. Seppelt* 7938 (HO 577655); west side of Lusitania Creek basin, 50 m, 11 Jan 1980, *R.D. Seppelt* 7697 (HO 577649); 1 km south of Mt Ifould, 54°38'S 158°51'E, 280 m, 11 Jan 1980, *R.D. Seppelt* 7832 (HO 577651); 500 m north west of Lusitania Bay hut, 54°43'S 158°50'E, 100 m, 11 Jan 1980, *R.D. Seppelt* 7692 (HO 577648); west side of Lusitania Creek basin, 54°43'S 158°50'E, 50 m, 11 Jan 1980, *R.D. Seppelt* 7697 (HO 577649); 1.5 km south of Mt Power, 54°33'S 158°55'E, 250 m, 19 Jan 1980, *R.D. Seppelt* 7929 (HO 577654); South east end of Red River Valley, 54°36'S 158°54'E, 150 m, 3 Dec 1979, *R.D. Seppelt* 7080 (HO 577644); Skua Lake, 54°37'S 158°50'E, 180 m, 22 Oct 1983, *G. Copson* (HO 577598); north side of Tiobunga Lake, 54°41'42"S 158°49'15"E, 185 m, 11 Jan 1980, *R.D. Seppelt* 7875 (HO 577653); north side of Mt Aurora, 54°43'S 158°50'E, 350 m, 11 Jan 1980, *R.D. Seppelt* 7848 (HO 577652);

**New Zealand: North Island:** *Colenso* 1917 *p.p.* (G 00121207); New Zealand, *Colenso* 1329 sub *Plagiochila alpina* *Colenso* (G 00120994); Northland, Mangamuka Stream, 37°13'07"S 173°29'04"E, 90 m, 17 Apr 1984, *J.E. Braggins* 84/22a, (AK 327191); Central Plateau, south of Turangi between Desert Road and Tongariro River, Tree Trunk Gorge, 39°10'19"S 175°48'07"E, 700 m, 27 May 1992, *J.E. Braggins* 92/18 (AK 320620);

**South Island:** Lake Peel, North West Nelson Forest Reserve, 33 km W of Motueka, 41°09'S 172°36'E, 1310 m, 4 Feb 1993, *H. Streimann* 51342 (CANB 9306792); Nina Valley track, 23 km SW of Springs Junction 42°28'S 172°23'E, 700 m, 3 Feb 1993, *H. Streimann* 51191 (CANB 9306641); Below Macdonald's West Coast Road, Teremakau River, May 1889, *T.W.N. Beckett* 419, ex herb. Levier (G 00120806); Westland, Otira Gorge, May 1899, *T.W.N. Beckett* 373, ex herb. Levier (G 00120988); Westland, Kelleys Range, May 1889, *T.W.N. Beckett* 420, ex herb. Levier (G 00121209); Canterbury, Waimate, May 1901, *T.W.N. Beckett*, ex herb. Levier 2782 (G 00121208); Westland, Kellys Creek, 3 Feb 1903, *T.W.N. Beckett* 342, as *P. beckettiana* Steph. n.sp. (BM).

***Plagiochila retrospectans* Lindenb., Species Hepaticarum 5: 123 (1843)**

*Type citation:* in Nova Hollandia (*Sieber*); in Brasilia (Com. de Lambert. Herb. Hookeri et Rudolphii)

*Type:* Nova Hollandia, *Sieer*, Lindenberg hep. no. 874 (lectotype designated here: W).

=*Jungermannia retrospectans* Nees, *Linnaea* 6: 619 (1831) *nom. illeg.* Nees, *non* Nees ex Spreng.

*Type citation:* Crescit in Nova Hollandia, *Sieber*.

*Type:* *n.v.*

=*Plagiochila opisthotona* (Hook.f. et Taylor) Taylor et Hook.f. ex Gottsche, *Lindenb. et Nees, Synopsis Hepaticarum* 5: 652 (1847)

*Basionym:* *Jungermannia opisthotona* Hook.f. et Taylor *London Journal of Botany* 3: 577 (1844)

*Type citation:* Van Diemen's Land

*Type:* Voyage of H.M. Discovery Ships Erebus and Terror, 1840, *J.D. Hooker* (FH!)

=*Plagiochila multidentata* Steph., *Species Hepaticarum* 6: 185 (1921)

*Type citation:* Nova Zelandia (Colenso legit)

*Type:* New Zealand, *W. Colenso a.1424* (G 00283135!)

=*Plagiochila apiculata* Steph. ex Weymouth, *Papers and Proceedings of the Royal Society of Tasmania* 1902: 131 (1903) *nom. inval.*

*Type citation:* Mount Wellington, St. Crispin's Track & Deep Creek Track W.A.W. nos 542, 549, 551/2, 555

=*Plagiochila apiculata* Steph. ex Dugas, *Contribution à l'Étude du Genre Plagiochila Dum.:* 92 (1928)

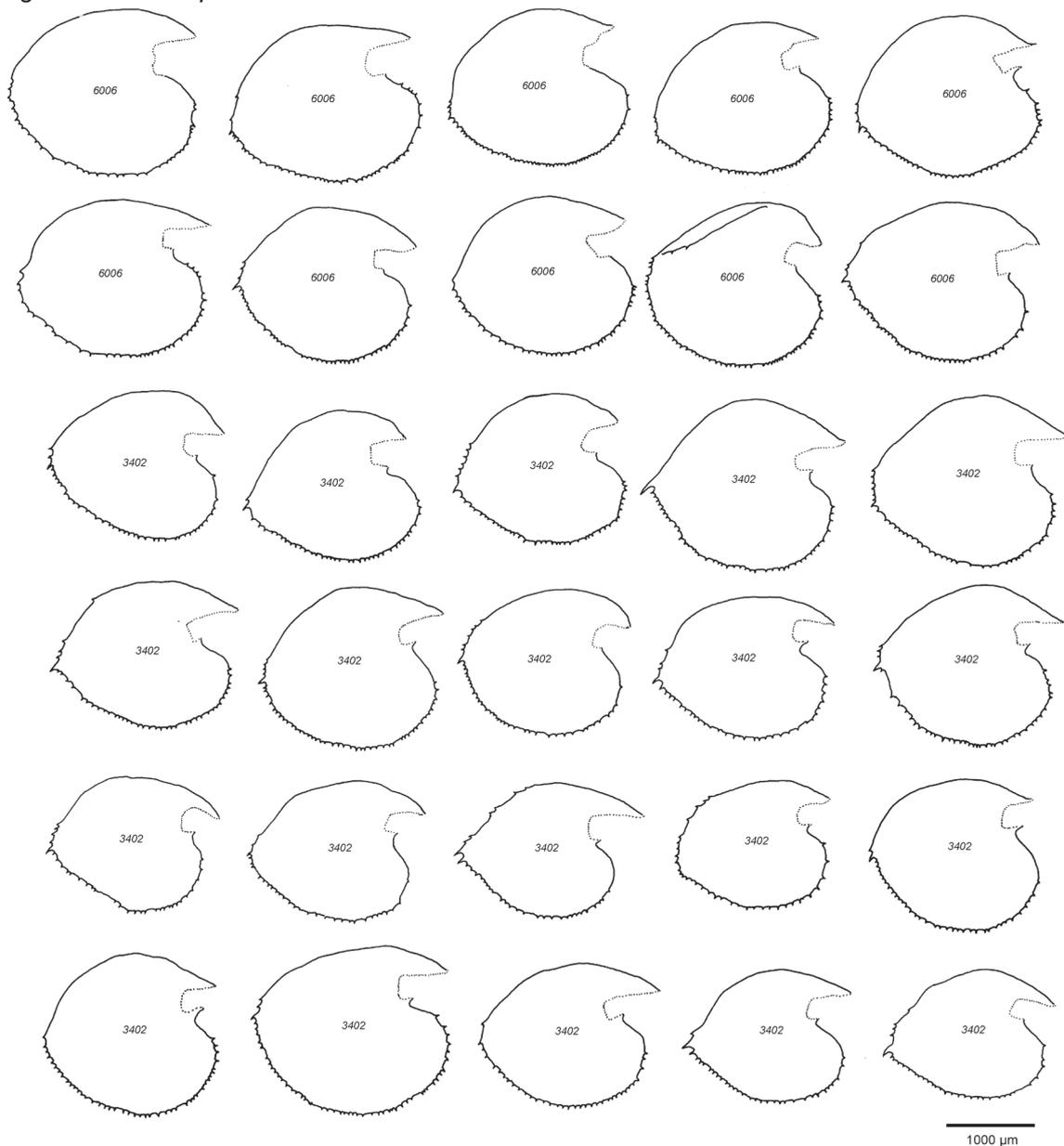
*Type citation:* Tasmania, leg. Weymouth, 1899

*Type:* *Weymouth 549* (HO 305168! BM! MEL 2277125!)

**Etymology:** backward looking, possibly referencing the nodding shoot apex

**Description:** Plants with irregularly branched, erect leafy shoots comprising repeated monopodial units of a basal stolon and upper leafy sector, stolons arising from within the leafy sector near its base by lateral-intercalary branching; forming dense turfs; dark-green to bronze-green, shoot systems to 60 mm long × 25 mm wide, monomorphic; shoots 1.0–1.5 mm wide, arising by lateral-intercalary branches, apex nodding. Stems without lamellae, paraphyllia, or paraphyses, reddish-brown, to 400 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 4–6 layers, cortical cell walls strongly and continuously thickened, constricting the cell lumen in middle cortical layers, reddish-brown, outer layer with thinner walls than inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls without secondary thickening except those beneath the cortex, on whose walls thickening tapers over 2 or 3 tiers toward the stem centre, primary walls faint red-brown pigmented. Rhizoids on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on leafy shoots imbricate, succubously inserted but transversely orientated, rotund-ovate, 1500–2500 µm long × 1500–2500 µm wide, dorsal margin curved, ventral margin ampliate; margins with up to 100 teeth on apex and ventral margin, teeth small and triangular, comprised of one or two cells, apical cell triangular, slightly elongated and acute-tipped, and with a single larger spinose-triangular tooth at the leaf apex; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular 7–17 µm long × 8–15 µm wide, long axis parallel or perpendicular to leaf margin, walls of one to three tiers of marginal cells with continuous golden-brown thickening; medial leaf cells quadrate to polyhedral, 7–17 µm long × 8–22 µm wide, walls unpigmented, with conspicuous cordate to bulging trigones and occasional medial thickening; cells in leaf base long rectangular, to 80 µm long × 18 µm wide, bulging trigones and medial wall thickenings. Cell surfaces smooth. Oil-bodies 2 per cell, ellipsoid, granular. Underleaves absent. Asexual reproduction absent.

Diocious. Androecia intercalary on shoots that continue vegetative growth, male branches nodding, ventral-intercalary and *Frullania*-type branches not associated with male branches; bracts in 3–6 pairs, imbricate, closely packed, and tapering, bracts resembling sterile leaves but with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts unornamented. Gynoecia at apices of leafy shoots; bracts ovate-rotund, larger than subtending leaves but otherwise similar; apex and ventral margin with numerous spinose teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral- or ventral-intercalary branching from between the female bracts. Perianth ligulate, to 4000 µm long × 2500 µm wide at mouth, dorsal and ventral keels not winged, laterally compressed but with a weakly inflated base, lateral walls plane; labia truncate, each bearing 16–24 spinose teeth. Fig. 4.

*Plagiochila retrospectans*

**Fig 4.** *Plagiochila retrospectans* leaves from primary shoots, from *N. Klazenga* 6006, (MEL 2131756) and *P.C. Jobson* 3402 (MEL 2235519).

**Notes:** The species currently known as *Plagiochila retrospectans*, was first described as *Jungermannia retrospectans* Nees, but unfortunately this was an illegitimate homonym blocked by *Jungermannia retrospectans* Nees ex Spreng. *Jungermannia retrospectans* Nees ex Spreng. was based on a different type from *J. retrospectans* Nees, and today *J. retrospectans* Nees ex Spreng. is a synonym of *Heteroscyphus argutus* (Reinw., Blume et Nees) Schiffn. Twelve years after the publication of *Jungermannia retrospectans* Nees, Lindenberg (1843) proposed the species *Plagiochila retrospectans* Lindemb. Even if Lindenberg had intended to publish Nees' name under *Plagiochila* as a new combination (Article 41.4) this could not have been achieved because no legitimate basionym was available for that combination (Article 6.10). Lindenberg's name in *Plagiochila* was therefore effectively a new name, even though it was based on the same type as *Jungermannia retrospectans* Nees. The interpretation by Engel and Merrill (2009), that Lindenberg's name was a new combination of Nees ex Sprengl's name, is incorrect because Lindenberg's description and syntypes describe and capture the plant of Nees, not the plant of Nees ex Spreng. *Plagiochila retrospectans* Lindemb. is therefore the correct citation.

Reference to locations 'Australia & Brasil' for the syntypes of *Plagiochila retrospectans* can be attributed the fact that the name Nova Hollandia was applied to both Australia and an early Dutch colony near Recife in Brasil, this confusion was only enhanced by the fact that two different Siebers collected in 'Nova Hollandia':

Franz Wilhelm Sieber in Australia and Friedrich Wilhelm Sieber in Brasil (Anders Hagborg *pers. comm.* 2015). *Plagiochila retrospectans* has not yet been effectively lectotypified. Inoue and Schuster (1971) identified the Australian plant as the type element but could not locate a specimen of it, while Engel and Merrill (2009) identified the Australian syntype of *J. retrospectans* Nees as the holotype of *J. retrospectans* Nees ex Spreng. A lectotype for *Plagiochila retrospectans* Lindenb. is therefore proposed above.

The name *Plagiochila squarrosa* Steph. n.sp. (nom. herb.) was applied by Stephani to a specimen from Tasman Peninsula on a rock, Newmans Creek, 2 Feb 1899, W.A. *Weymouth* 819 (BM!, HO 86208!) which is *P. retrospectans*. This name was never published.

Bonner (1962) listed a Petrie specimen gathered in 1898 in hb. G as the type of *P. multidentata*, but this is in conflict with the protologue.

**Recognition:** *Plagiochila retrospectans* can be recognized by the combination of succubously inserted yet transversely orientated, ovate to reniform, imbricate leaves with numerous (>80) small triangular teeth composed of 1 to three cells on the leaf margin, whose cell walls are usually continuously thickened to a degree greater than the subtending medial leaf cell walls, at the very least on the free external wall; and the presence of a single larger spinose tooth close to the apical end of the dorsal leaf margin; vegetative branching by lateral-intercalary mode only; the decurrent wing formed by the dorsal leaf insertion; and the ventral-intercalary subfloral innovation when only one innovation is present.

*Plagiochila retrospectans* could be confused with *P. fuscella*, but differs by the presence of a pronounced, larger, spinose-dentate tooth close to the outer extremity of the dorsal leaf margin. The two species also differ in leaf shape as described above under *P. fuscella*.

*Plagiochila retrospectans* could be confused with *Adelanthus falcatus*, but differs by the smaller, often more numerous teeth, the rotund to reniform leaf shape (not obovate) and the imbricate leaves.

*Plagiochila retrospectans* has been confused with *P. deltoidea* (e.g. HO 577123, HO 577113) but differs by the lateral-intercalary stolon branching (not ventral-intercalary) the numerous small spinose-triangular teeth on the leaf margin (not triangular teeth) the rotund to reniform leaf outline (not asymmetrically ovate), the leaf border of heavily and continuously thickened, often golden pigmented leaf cell walls (not present in *P. deltoidea*), the monopodial growth habit (not sympodial), and the ventral-intercalary subfloral innovation when only one is present (not lateral-intercalary).

**Distribution and Ecology:** *Plagiochila retrospectans* is indigenous to Australia and New Zealand, and in Australia occurs from south-east New South Wales through eastern Victoria, and Tasmania. Throughout this range *P. retrospectans* occupies microsites close to running water, typically on streamside boulders, logs, banks, and bedrock where it may form extensive pure turfs. On Macquarie Island *P. retrospectans* grew in saturated herbfield.

**Representative specimens examined:** **Australia: New South Wales:** Rutherford Creek, 11 km SE of Nimmitabel, 850 m, 36°34'S 149°36'E, 19 Feb 1982, *H. Streimann* 16719 (CANB 8212678); **Victoria:** Surf Coast, Angahook-Lorne State Park, near Lorne, walking track from Erskine Falls to Lorne along Erskine River, Erskine Falls end, 38°31'S 143°55'E, 1 Apr 2002, *N. Klazenga* 6006, (MEL 2131756); **Tasmania:** Burnie, Blythe River crossing, 4 km W of South Riana, 41°14'13"S 145°55'47"E, 260 m, 26 Feb 1995, *P.C. Jobson* 3402 (MEL 2235519); North East, Ferntree Glen Creek, St Marys Pass State Reserve, 41°33'S 148°12'E, 330 m, 2 July 1993, *A. Moscal* 25383 (HO 577358); North West, River Leven, Sith Cala Nature Reserve, 41°13'S 146°06'E, 20 m, 19 Oct 1994, *A. Moscal* 26136 (HO 577336); Dismal Swamp Nature Reserve, 41°59'S 144°51'E, 40 m, 23 Mar 2000, *A. Moscal* 30998 (HO 577411); West Coast, Huskisson River, 41°39'S 145°28'E, 140 m, *A. Moscal* 21059 (HO 577334); Whyte-Pieman Rivers junction, Pieman River State Reserve, 41°39'S 145°05'E, 20 m, 8 Feb 1995, *A. Moscal* 26561D (HO 577337); Cradle Mountain-Lake St Clair National Park, junction of Overland and Cuvier Valley tracks, 42°02'S 146°06'E, 765 m, 14 Jan 2004, *K. Felton* (HO 525703); Central Highlands: Mt Pelion East, 41°51'S 146°05'E, 880 m, *A. Moscal* 15042 (HO 577355); Mersey River 2.5 km south of Lewis Falls, 41°52'S 146°10'E, 750 m, 24 Sep 1987, *A. Moscal* 14759 (HO 577356); First Creek, 21 km south of Cressy, 41°53'S 147°59'E, 800 m, 27 Jan 1990, *A. Moscal* 18617 (HO 577365); near Shadow Lake, 42°06'S 146°08'E, 960 m, 7 Feb 1987, *A. Moscal* 14361 (HO 577346); Cathcart Bluff, 41°48'S 146°52'E, 860 m, 11 Jan 1990, *A. Moscal* 18363 (HO 577325); Below Lake Mackenzie Dam, H.E.C. Concession Area, 41°41'S 146°23'E, 1100 m, 12 Mar 2000, *A. Moscal* 30940B (HO 577319); Mt Field, The Watcher, 42°39'S 146°32'E, 1260 m, 11 Mar 1992, *A. Moscal* 22852 (HO 577354); Mt Field, Windy Moor, 42°39'S 146°39'E, 1190 m, 12 Apr 1992, *A. Moscal* 23316 (HO 577326); Mt Field, Lady Barron Creek, 42°41'S 146°38'E, 900 m, 12 Apr 1992, *A. Moscal* 23305 (HO 577353); Mt Field, Tyenna Peak, Humboldt Ridge, 42°43'S 146°34'E, 670 m, 21 May 1992, *A. Moscal* 23714 (HO 577351); East Coast: Mt Elephant, 41°37'S 148°15'E, 460 m, 11 Feb 1984, *A. Moscal* 6217 (HO 577345); Sandspit River Forest Reserve, 42°42'S 147°50'E, 200 m, 7 Jun 2000, *A. Moscal* 31048A (HO 577339); Sandspit

River, 8.5 km WNW of Cape Bernier, 42°43'S 147°50'E, 200 m, 30 Oct 1988, *A. Moscal 16644* (HO 577318); Newmans Creek, 43°06'S 147°51'E, 140 m, 28 Dec 1998, *A. Moscal 30013* (HO 577322); Oakwood Hill, 43°07'E 147°52'E, 100 m, 19 Aug 1998, *A. Moscal 29856* (HO 577321); Mahers Creek, 43°12'S 147°11'E, 200 m, 14 Nov 1991, *A. Moscal 21941* (HO 577328); Rainforest Lodge, Douglas-Aspley National Park, 41°44'S 148°13'E, 450 m, 24 Dec 1994, *A. Moscal 26415* (HO 577338); Myrtle Creek, Douglas-Aspley National Park, 41°48'S 148°08'E, 420 m, 26 Dec 1994, *A. Moscal 26479* (HO 577341); Orielson Rivulet, 12 km NNW of Sorell, 42°40'S 147°31'E, 250 m, 11 Sep 1988, *A. Moscal 16480* (HO 577348); Flash Tier (State Forest) 42°37'S 147°51'E, 370 m, 10 Dec 2000, *A. Moscal 31132* (HO 577361); Tatnells Creek (headwater) 3.5 km east of Taranna, 43°03'S 147°55'E, 435 m, 21 Jan 1999, *A. Moscal 30319* (HO 577414); Mt Raoul, Cape Raoul State Reserve, 43°13'S 147°47'E, 380 m, 8 Apr 1993, *A. Moscal 24882* (HO 577413); Agnes Creek, Fortescue Forest Reserve, 43°09'S 147°57'E, 3 m, 2 Dec 1998, *A. Moscal 30150* (HO 577412); Newmans Creek, Mt Koonia, 43°05'S 147°47'E, 160 m, 27 Sep 1998, *A. Moscal 29918* (HO 577409); South West: Wilson Bight, 43°33'S 146°04'E, 15 m, 14 Jan 1987, *A. Moscal 15546* (HO 577360); Ben Lommond, Mt Barrow, 41°23'S 147°25'E, 1280 m, 25 Feb 1993, *A. Moscal 24587* (HO 577359); Viormy Tasmanian Land Conservancy Property, Nive River, Skullbone Plains Road bridge, 42°04'44"S 146°28'14"E, 700 m, 25 Feb 2014, *L.H. Cave 1952* (HO 576853); Central Highlands, Mother Cummings Peak, 41°40'S 146°33'E, 845 m, 20 Feb 1986, *A. Moscal 12378c* (HO 577123 as *P. deltoidea*); North West, River Forth, 41°43'S 146°03'E, 345 m, 5 Sep 1987, *A. Moscal 14597* (HO 577113); Mt Wellington, on ground, 42°53'S 147°15'E, Jul 1917, *L. Rodway* (HO 87586 as *P. fasciculata*); Van Diemens Land, Gunn, ex R.K. Greville 1 Mar 1843, (FH, type of *Jungermannia loricata* Taylor ms). **Macquarie Island:** north side of Tiobunga Lake, 54°41'42"S 158°49'15"E, 185 m, 11 Jan 1980, *R.D. Seppelt 7875* (HO 577653); Gadgets Gully, 54°30'S 158°56'E, 150 m, 28 Oct 1980, *R.D. Seppelt 11379* (HO 577688).

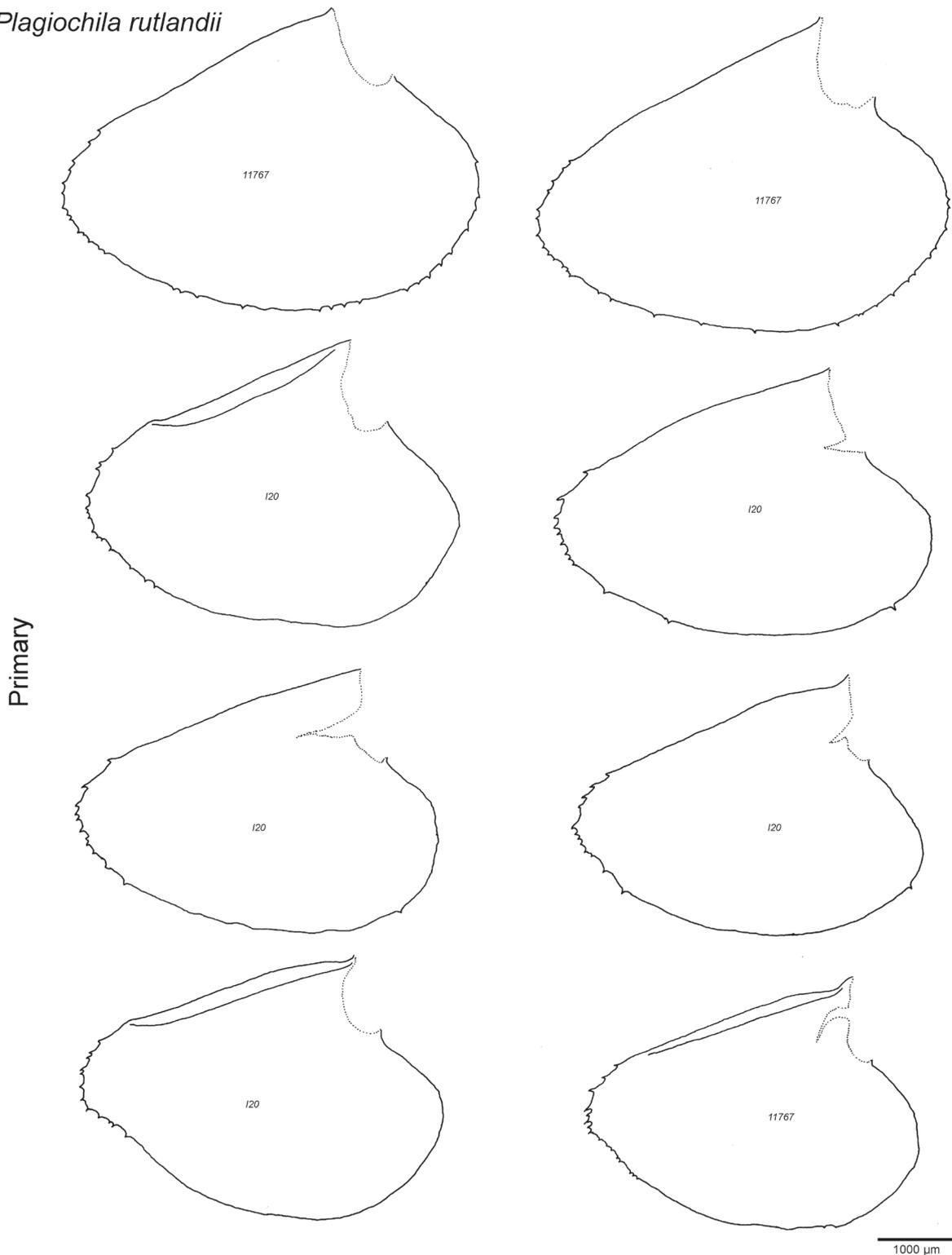
***Plagiochila rutlandii*** Steph., Bulletin de l'Herbier Boissier, sér. 2 4: 776 (1904) = Species Hepaticarum 2: 454 (1904)

*Type citation:* New Zealand (Stephenson, Rutland).

*Type:* New Zealand. South Island: Westland, Pelorus Sd., Aug 1890, *J. Rutland*, ex herb. Levier 430 (lectotype designated by Bonner (1962): G 00061554!); New Zealand, 1843, *W. Stephenson*, Pearson dedit, (residual syntype: G 00115867!)

**Etymology:** of Joshua Rutland (1836–1915), collector of some of the original material (Godley 1992).

**Description:** Plants with bipinnately branched, erect or suberect leafy shoots arising from a robust creeping basal stolon, stolons arising from other stolons by lateral-intercalary branching, not produced from leafy shoot sectors; forming tall turfs; dark-green, shoot systems to 120 mm long × 50 mm wide, trimorphic; primary shoots 5–8 mm wide, secondary shoots arising by lateral-intercalary branching. Stems without lamellae, paraphyllia, or paraphyses, reddish-brown, in primary shoots to 900 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 4 or 5 layers, cortical cell walls strongly and continuously thickened, constricting the cell lumen in middle cortical layers, reddish-brown, outer layer with thinner walls than inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls without secondary thickening except those beneath the cortex, on whose walls thickening tapers over 2 or 3 tiers toward the stem centre, primary walls faint red-brown pigmented. Rhizoids scattered on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots imbricate, succubously inserted and orientated, broadly ovate, 4400–6150 µm long × 3150–5250 µm wide, dorsal margin straight, ventral margin ampliate; margins entire except for 11–30 small spinose teeth around the apex, comprised of one or two cells, apical cell triangular, slightly elongated and acute-tipped; leaves on secondary shoots 2850–3350 µm long × 1950–3150 µm wide, with 29–67 teeth; leaves on tertiary shoots 1650–3050 µm long × 1200–2050 µm wide, with 17–38 teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, not attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular 12–30 µm long × 7–16 µm wide, long axis parallel or perpendicular to leaf margin, walls of one to three tiers of marginal cells with continuous thickening; medial leaf cells quadrate to polyhedral, 15–34 µm long × 13–23 µm wide, walls unpigmented, with triangular trigones; cells in leaf base long rectangular, 38–92 µm long × 13–18 µm wide, walls continuously thickened. Cell surfaces smooth. Oil-bodies 4–10 per cell, ovoid to ellipsoid, granular. Underleaves absent. Asexual reproduction absent.

*Plagiochila rutlandii*

**Fig 5.** *Plagiochila rutlandii* leaves from primary shoots, from P.J. de Lange 11767 (NSW 848797).

Dioicous. Androecia intercalary on shoots that continue vegetative growth, either singly or in fascicles of two or three male branches produced at the apex of vegetative shoots by *Frullania*-type branching at the base of the leading male branch; lateral- and ventral-intercalary branches not associated with male branches; bracts in 4–8 pairs, imbricate, bracts resembling small sterile leaves but with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts unornamented. Gynoecia at apices of secondary shoots; bracts elliptic, to 4000 µm long, larger than subtending leaves; apex and ventral margin with numerous spinose teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching

from between the female bracts in the absence of fertilisation. Perianth triangular, to 5500 µm long × 2500 µm wide at mouth, dorsal and ventral keels not winged, laterally compressed but with a weakly inflated base, lateral walls plane; labia rounded, each bearing around 20 spinose teeth. Fig. 5.

**Recognition:** *Plagiochila rutlandii* can be recognized by the combination of large, bi- or tri-pinnate shoot systems in which secondary and tertiary shoots originate by lateral-intercalary branching; the sympodial growth habit with large pinnate shoot systems arising from a system of creeping basal stolons; the large asymmetrically ovate leaves on primary shoots bearing triangular teeth around their apex and also on their ventral margin, in contrast to leaves on secondary and tertiary shoots which bear teeth around their apex and along their ventral margin.

*Plagiochila rutlandii* could be confused with other large *Plagiochila* species such as *P. gigantea* and *P. stephensoniana*. From *P. gigantea*, *P. rutlandii* differs by having vegetative branching of lateral-intercalary mode only (not *Frullania*-type); asymmetrically ovate primary-shoot leaves, not transversely elliptic (Fig. 5); the small triangular teeth on the leaf margin, not spinose, and the pinnate shoot architecture, not flabellate. From *P. stephensoniana*, *P. rutlandii* differs by having vegetative branching of lateral-intercalary mode only, not *Frullania*-type, and small triangular teeth on the leaf margin, not spinose-dentate.

**Distribution and Ecology:** *Plagiochila rutlandii* is endemic to New Zealand, where it occurs in rainforest habitats in the North and South Island. *Plagiochila rutlandii* is usually encountered below 600 m elevation and in association with water, and may grow in a range of microsites, including on rotting logs in low-lying boggy areas, on large rocks within streambeds, on stream banks, on exposed bedrock near waterfalls, and on rocks alongside forest tracks.

**Representative specimens examined: New Zealand: North Island:** Northland, Mangamuka Range, in valley of a northern tributary of Mangamuka Range, 35°10'49"S 173°24'38"E, 200 m, 17 Apr 1984, *J.E. Braggins 84/23k* (AK 321010); Puketi Forest, Waihoanga Gorge Kauri Walkway, Waihoanga Stream, 35°15'13"S 173°44'51"E, 250 m, 20 Mar 2006, *J.E. Braggins 06/091* (AK 303113); Hauraki Gulf, Hauturu (Little Barrier), summit ridge, 36°12'S 175°04'E, 595 m, 13 Jun 1984, *J.E. Braggins 84/213* (AK 312488); South Auckland, Erua Forest, Tupapakukura Waterfall Track, 39°10'55"S 175°21'23"E, 738 m, 24 Nov 2013, *P.J. de Lange 11767* (NSW 848797); Whanganui River, Tawhata, May 1947, *E.H. Bunn Lloyd 1* (AK 321070); Wellington District, Akatarawa, Waterfall Creek, above waterfall, 40°57'36"S 175°06'42"E, 9 Dec 1984, *J.E. Braggins 84/457c* (AK 316603); **South Island:** Marlborough, Pelorus Bridge, Circular Track, 41°17'55"S 173°34'21"E, 1 Oct 1983, *J.E. Braggins* (AK 316618); Catlins, Tautuku, Lake Wilkie, 46°35'S 169°26'E, 1 Nov 1970, *G.M. Taylor* (AK 320982)

***Plagiochila intertexta*** Hook.f. & Taylor, London Journal of Botany 5: 267 (1846)

*Type citation:* Norfolk Island, Allan Cunningham.

*Type:* A. Cunningham ex hb Taylor (lectotype designated by Bonner (1962): G; isolectotypes: Australia, Norfolk Is, Allan Cunningham 336, FH, MANCH, S(3); ex herb. Taylor, as *P. interrupta*, G 00128870!; ex herb. Lehmannianum as *Plagiochila intertexta* Taylor ab ipso BM!).

=*Plagiochila littoralis* Steph., Species Hepaticarum 6: 177 (1921)

*Type citation:* New Zealand. West Coast. (Colenso legit).

*Type:* New Zealand, West Coast, Colenso s.n. (lectotype designated by Bonner (1962): G) syn. fide So 2001.

=*Plagiochila sinclairii* Mitt. in Hooker, Flora Novae Zelandiae 2: 133 (1854)

*Type citation:* Northern Island: Auckland, Sinclair. Bark of trees. Tehawera, Colenso.

*Type:* New Zealand, Northern Island, Auckland, Sinclair s.n. (lectotype designated by Inoue and Schuster 1971: NY! isolectotype: BM!)

=*Plagiochila traversii* Steph., Bulletin de l'Herbier Boissier, sér. 2 4: 782 (1904) = Species Hepaticarum 2: 460 (1904)

*Type citation:* Chatham Island (Travers)

*Type:* New Zealand, Chatham Is, 1872, Travers (lectotype designated by Bonner (1962): G 00069880! isolectotypes: ex herb. Stephani BM! FH! HO 115870!).

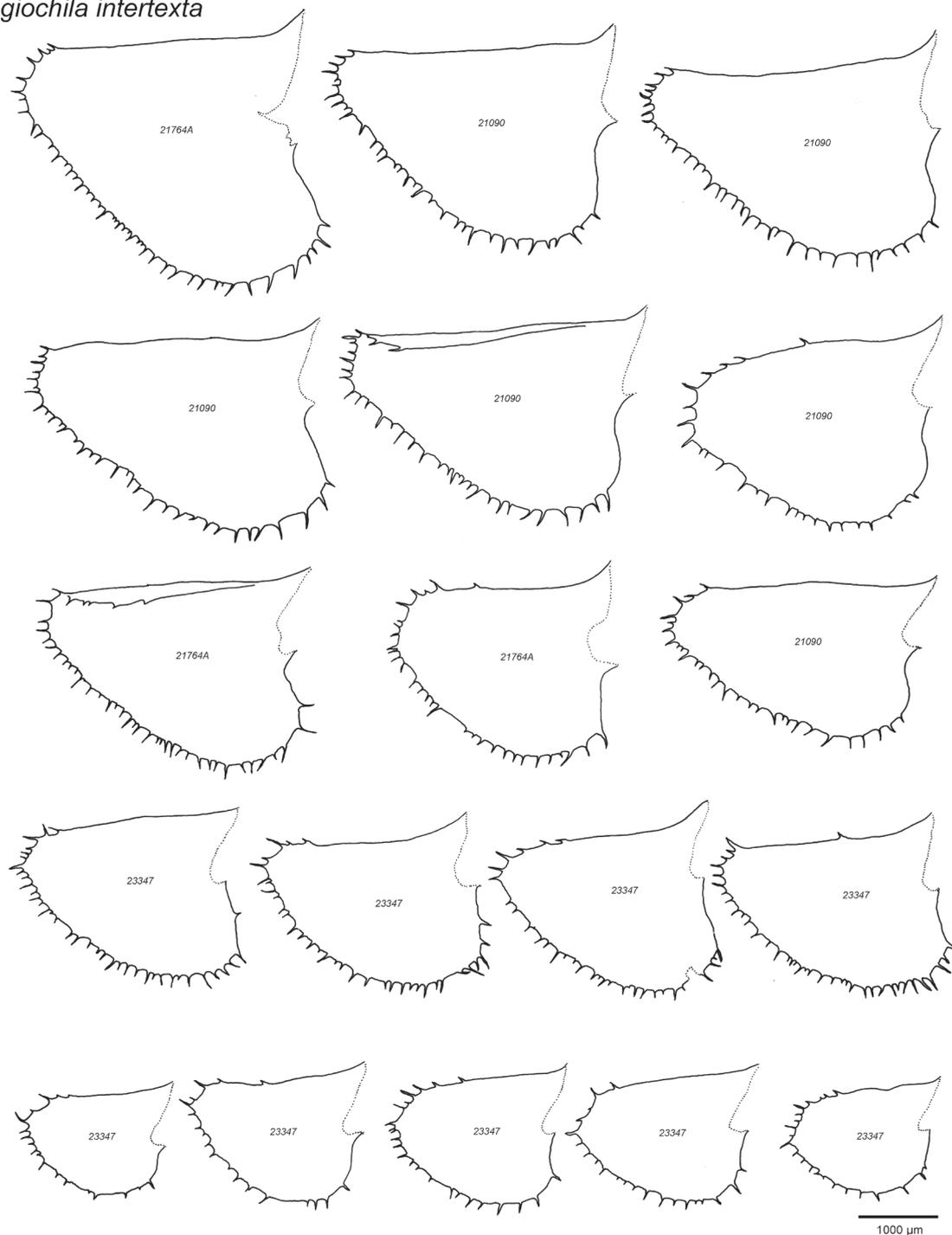
**Etymology:** interwoven, in reference to the comingled overgrowth of the prostrate shoots in this species.

**Description:** Plants with irregularly branched, prostrate leafy shoots arising from a weak creeping basal stolon, stolons issuing from other stolons by lateral-intercalary branching, not produced from leafy shoot sectors; forming interwoven mats; dark-green, shoot systems to 80 mm long, monomorphic; primary shoots 5–8 mm wide, branches arising by lateral-intercalary branching. Stems without lamellae, paraphyllia, or paraphyses, reddish-brown, in primary shoots to 500 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 4 to 6 layers, cortical cell walls strongly and continuously thickened, constricting the cell lumen in middle cortical layers, reddish-brown, outer layer with thinner walls than inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls without secondary thickening except those beneath the cortex, on whose walls thickening tapers over 2 or 3 tiers toward the stem centre, primary walls faint red-brown pigmented. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots imbricate, succubously inserted and orientated, triangular-ovate, 1860–4150 µm long × 1390–3450 µm wide, dorsal margin straight, ventral margin ampliate; dorsal margin entire, apex and ventral margins bearing 17–45 spinose teeth, comprised of 2–13 cells, up to four cells broad at base and uniseriate for up to five tiers, apical cell triangular, slightly elongated and acute-tipped; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular long axis parallel to leaf margin, one to three tiers of marginal cells with continuous yellow to golden-brown thickening on their cell walls; medial leaf cells isodiametric to broad elliptic polyhedral, 22–40 µm long × 19–28 µm wide, walls unpigmented, with triangular trigones; cells in leaf base long rectangular, 40–66 µm long × 20–25 µm wide, walls continuously thickened. Cell surfaces smooth. Oil-bodies 4–10 per cell, ovoid to ellipsoid, granular. Underleaves present, persistent, amorphous clusters of cells. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, either singly or in fascicles of two or three male branches produced at the apex of vegetative shoots by *Frullania*-type branching at the base of the leading male branch; lateral- and ventral-intercalary branches not associated with male branches, lateral- and ventral-intercalary branches not associated with male branches; bracts in 4–8 pairs, imbricate, bracts resembling small sterile leaves but with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts unornamented. Gynoecia at apices of shoots; bracts elliptic-ovate, to 3500 µm long, larger than subtending leaves; apex and ventral margin with numerous spinose-ciliate teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral- or ventral-intercalary branching from between the female bracts with or without fertilisation. Perianth triangular, to 4000 µm long × 3000 µm wide at mouth, dorsal and ventral keels not winged, laterally compressed but with a weakly inflated base, lateral walls plane; labia rounded, each bearing around 20–25 spinose-ciliate teeth. Fig. 6.

**Recognition:** *Plagiochila intertexta* can be recognized by the combination of asymmetrically ovate leaves whose dorsal margin is straight and entire, and whose other margins bear numerous, closely spaced long spinose teeth, and by the lateral-intercalary vegetative branching.

*Plagiochila intertexta* could be confused with *P. gigantea*, but differs by the lateral-intercalary vegetative branching, not *Frullania*-type, and the leaf shape as described above, not broadly ovate (Figs. 1, 6). *Plagiochila intertexta* could be confused with *P. banksiana* but differs in the sympodial shoot system with a differentiated system of basal stolons, absent from *P. banksiana*, and the leaf asymmetrically ovate leaves, not rotund. *Plagiochila intertexta* could be confused with *P. baylisii*, but differs in the shape and dentition of leaves, with the straight and entire dorsal margin, not toothed at the base, and the exclusively lateral-intercalary vegetative branching, not mixed lateral-intercalary and *Frullania*-type. *Plagiochila intertexta* could be confused with *P. fuscella* or *P. retrospectans* but both these species have leaves whose dorsal margin is curved, and either entire margins, or margins armed with numerous small triangular teeth. *Plagiochila intertexta* could be confused with *P. deltoidea*, but *P. intertexta* has stolons arising by lateral-intercalary branching, not ventral-intercalary branching.

*Plagiochila intertexta*

**Fig 6.** *Plagiochila intertexta* leaves, from J.J. Engel 21090 (F 1141683), J.J. Engel 21764A (F 1141311), and J.J. Engel 23347 (F 1182057).

**Distribution and Ecology:** *Plagiochila intertexta* occurs on Norfolk Island, and throughout New Zealand, including the North and South Islands, and the Chatham Islands. Across this distribution *P. intertexta* inhabits rainforest habitats as an epiphyte, lithophyte, or terrestrial species in a wide range of situations. It has been collected growing on soil on a small river terrace with *Adiantum aethiopicum* under *Podocarpus totara*, at Tangihua; as an epiphyte on a *Beilschmiedia tawa* trunk at Manawatu Gorge; a vertical limestone rock face, and on rotting logs at Waitomo; and on rocks in a streambed at Tutamoe. *Plagiochila intertexta* (as *P. sinclairii* and *P. traversii*) was been reported from Tasmania, but all records are based on misidentifications of other species, including *P. baylisii*.

**Representative specimens examined:** **New Zealand: North Island:** Northland, Waima Forest, Hauturu Highpoint track in vicinity of Hauturu Trig, 35°31'S 173°28'E, 650–680 m, 23 Feb 1997, J.J. Engel 22576

(F 1141256); SE corner of Waipoua Forest, just north of Tutamoe, 35°38'S 173°38'E, 540 m, 9 Feb 1995, *J.J. Engel* 21090 (F 1141683); Tangihua Ecological District, Wairua Falls, bottom of falls, 35°45'S 174°05'E, 30 m, 18 Aug 1987, *J.E. Braggins* 87/078 (AK 259170); Northland, summit area of Mt Manaia, NW of Bream Head, 35°48'S 174°31'E, 8 Feb 1997, *J.J. Engel* 22233 (F 1141255); *ibid.* *J.J. Engel* 22235 (F); Otago, Mamaku Bush, May 1949, *T.C. Chambers* (AK 58669); Urewera National Park, Panekiri Range, near summit of Pukenui near Panekiri Bluff, 38°47'S 177°04'E, 1050 m, 24 Mar 1997, *J.J. Engel* 23347 (F 1182057); King Country, Waitomo, Stubbs farm, covenant, 38°16'S 175°01'E, 360 m, 29 Oct 1989, *J.E. Braggins* 89/115 (AK 315614); Manawatu Gorge, Totara Reserve Pohangina, Fern Walk, 40°08'56"S 175°50'32"E, 480 m, 9 Dec 2005, *J.E. Braggins* 05/083 (AK 294764); **South Island:** Nelson Lakes National Park, NE margin of Lake Rotoroa west of St. Arnaud, 41°48'S 172°37'E, 520 m, 21 Feb 1995, *J.J. Engel* 21510 (F 1141305); Westland, Ship Creek, 14.5 km N of Haast River, 43°46'S 169°10'E, sea level, 26 Feb 1995, *J.J. Engel* 21737 (F 1141684); *ibid.* *J.J. Engel* 21764A (F 1141311); Limestone Cavern track, upper reaches of a tributary to Pig Creek, 10 km NW of Monowai Power House, 45°45'S 167°30'E, 325 m, 18 Nov 1990, *J.A. Curnow* 3579 (CANB 9408665); **Chatham Islands:** *H.H. Travers* (AK 320974 ex WELT H1079c)

Representative misidentified specimens

*Plagiochila baylisii*

Tasmania: Port Davey, Southwest National Park, 43°25'S 146°10'E, 1960, *D. Martin* (HO 305615).

*Plagiochila fuscella*

Tasmania, Hobart Rivulet, 42°54'S 147°19'E, 4 Dec 1897, *W.A. Weymouth* 146 (HO 85967)

***Plagiochila fragmentissima*** Inoue & R.M.Schust., *Journal of the Hattori Botanical Laboratory* 34: 155 (1971)

*Type citation:* New Zealand: in deep, moist Beech-Rimu forest, near shore, Deep Cove, Doubtful Sd., ca. 10-250 ft, Fiordland Natl. Park, South Island, *RMS 53315* (MASS; dupl. in TNS).

*Type: n.v.*

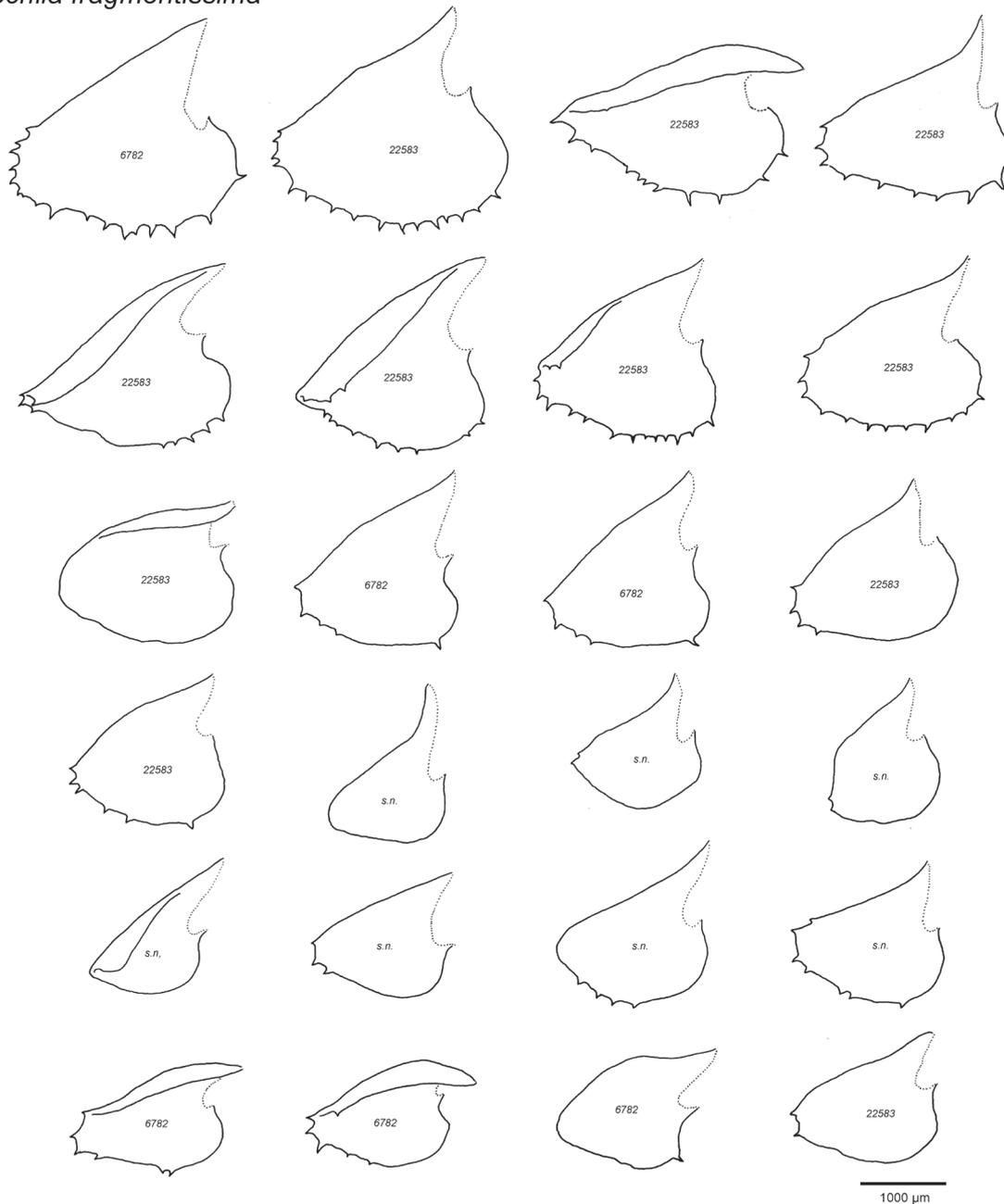
**Etymology:** in reference to the fragmenting leaves of the type specimen, unfortunately this is not a feature of the species.

**Description:** Plants with irregularly branched, erect leafy shoots arising from a creeping basal stolon, stolons arising from other stolons by lateral-intercalary branching, not produced from leafy shoot sectors; forming interwoven mats; mid-green to light green, shoot systems to 50 mm long, monomorphic; primary shoots 1.5–3 mm wide, branches arising by lateral-intercalary branching. Stems without lamellae, paraphyllia, or paraphyses, reddish-brown, in primary shoots to 500 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 4 or 5 layers, cortical cell walls strongly and continuously thickened, constricting the cell lumen in middle cortical layers, reddish-brown, outer layer with thinner walls than inner cortical cell layers, free external wall with limited thickening, all cortical cells smaller than medulla cells; medulla cell walls without secondary thickening except those beneath the cortex, on whose walls thickening tapers over 1 or 2 tiers toward the stem centre, primary walls hyaline. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots imbricate, succubously inserted and transversely orientated, broadly ovate to triangular ovate, 1700–2730 µm long × 1380–2280 µm wide, dorsal margin straight but in situ tightly rolled forming a distinct cnemis, ventral margin ampliate; dorsal margin entire, apex and ventral margins bearing 0–16 triangular teeth, comprised of 2–7 cells, up to four cells broad at base and capped by a triangular apical cell; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular 20–29 µm long × 11–24 µm wide, long axis parallel to leaf margin, walls with coarse quadrate to bulging trigones but not continuously thickened, free external wall of each cell with a single wave-shaped thickening projecting into the cell lumen; medial leaf cells quadrate to polyhedral, 27–52 µm long × 25–36 µm wide, walls unpigmented, with bulging cordate to nodular trigones, medial thickenings absent; cells in leaf base long rectangular, 30–66 µm long × 17–36 µm wide, walls with bulging nodular to knot-like trigones, and occasional medial thickening, trigones occasionally confluent. Cell surfaces smooth. Oil-bodies not seen. Underleaves absent. Asexual reproduction by caducous leaves fragmenting into irregular pieces, or absent; leaf-borne propagules absent.

Dioicous. Androecia unknown. Gynoecia at apices of shoots; bracts broadly elliptic-ovate, to 4000 µm long, larger than subtending leaves; margins with around 20 triangular to spinose-dentate teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral- or ventral-intercalary

branching from between the female bracts with or without fertilisation. Perianth campanulate, about 3000  $\mu\text{m}$  long  $\times$  3000  $\mu\text{m}$  wide at mouth, dorsal keel with a wing extending from the base to near the mouth, entire or with one or two spinulose teeth, ventral keel not winged, laterally compressed but with a weakly inflated base, lateral walls plane; labia rounded, entire or with a few small triangular teeth. Fig. 7.

*Plagiochila fragmentissima*



**Fig 7.** *Plagiochila fragmentissima* leaves, from M.A.M. Renner 6782 (NSW 899353), J.J. Engel 22583 (F 1141352), and J. Jarman & G. Kantvilas (HO 531518).

**Notes:** A specimen sub *P. strombifolia* Taylor from Van Diemen's Land, ex Macquarie River, 1836, R. Ball (FH 00458022!) is *P. fragmentissima*, but the specimen sheet bears a near-verbatim hand-written copy of Taylor's protologue, except that a description of the calyx is missing, and the specimen bears no perianths. This specimen is likely part of the original material of *Jungermannia strombifolia* Taylor, and is discussed further below under *Plagiochila strombifolia*.

**Recognition:** *Plagiochila fragmentissima* can be recognized by the combination of imbricate, asymmetrically triangular-ovate leaves with an ampliate base and revolute dorsal margin forming a distinct cnemis, and

whose apex and ventral margin bear 0–17 triangular teeth (Fig. 7); and stolons produced by lateral-intercalary branching. Fertile female plants are particularly distinctive with their campanulate (in lateral view) perianth with a prominent dorsal wing, and rounded labia that bear small triangular teeth. Despite the species epithet, specimens do not usually have fragmenting leaves.

*Plagiochila fragmentissima* could be confused with *P. gregaria*, particularly where the two species grow sympatrically, but the leaves of *P. gregaria* are broadly asymmetrically ovate and typically entire, or with a few teeth around the leaf apex only, they are also larger (Fig. 8). In contrast the leaves of *P. fragmentissima* are asymmetrically triangular-ovate, and bear triangular teeth around the apex and along the ventral leaf margin. The perianths of *P. fragmentissima* have a prominent dorsal wing, while those of *P. gregaria* do not, if a wing is present in *P. gregaria* it is at best low in stature and confined to the perianth base. The male branches of *P. gregaria* are produced in a cluster at the apex of vegetative shoots by repeated *Frullania*-type branching.

*Plagiochila fragmentissima* could be confused with *P. circinalis*, but as noted above the perianths of *P. fragmentissima* have a prominent dorsal wing, wide mouth and rounded labia that are either entire or sparsely dentate with triangular teeth. In contrast the perianths of *P. circinalis* are ligulate, do not have a dorsal wing, and have numerous spinose-dentate teeth on the mouth. For sterile or male specimens, the leaves of *P. circinalis* tend to be deeper relative to their length than in *P. fragmentissima*, and are smaller, have fewer teeth, undulate leaf margins, and a deep U-shaped stem insertion. But these features are all subject to some variation, and do not always serve to reliably differentiate these two species.

*Plagiochila fragmentissima* could be confused with *P. deltoidea*, but *P. deltoidea* has stolons originating by ventral-intercalary branching only, and the perianths of *P. deltoidea* do not have a dorsal wing, and have spinose-dentate to lacinate teeth on their labia.

*Plagiochila fragmentissima* could be confused with *P. baylisii*, but *P. baylisii* has a few small spinose teeth on the dorsal margin near the stem insertion, occasional *Frullania*-type vegetative branching, and homogeneous or few segmented oil-bodies.

*Plagiochila fragmentissima* could be confused with *P. strombifolia*, but *P. strombifolia* has spinose-ciliate teeth on the leaf margin, and homogeneous or few segmented oil-bodies.

**Distribution and Ecology:** *Plagiochila fragmentissima* occurs in Tasmania and the North and South Islands of New Zealand. *Plagiochila fragmentissima* is typically an epiphyte in forested habitats, where it grows on trunks, branches, and twigs of a range of tree species.

There is one specimen whose origin is given as New South Wales, collected by Allan Cunningham and communicated by Dr Hewitt Watson (FH 00284116), but *Plagiochila fragmentissima* is otherwise unknown from the Australian mainland. Possibly this record is the result of confusion about the specimen's origin, other Cunningham collections communicated by Dr Hewitt Watson are from New Zealand, where *P. fragmentissima* is known.

**Representative specimens examined: Australia: Tasmania:** 'Van Diemen's Land', ex Macquarie River, 1836, R. Ball (FH 00458022 this specimen is possibly part of the original material of *J. strombifolia* Hook.f & Taylor); Central Highlands, below Lake Mackenzie Dam, H.E.C. Concession Area, 41°41'S 146°23'E, 110 m, 12 Mar 2000, A. Moscal 30963 (HO 577104); Manuka Road in the Warra Long-Term Ecological Research Site in southern Tasmania, 43°06'S 146°41'E, 140 m, 30 Apr 2002, J. Jarman s.n. (HO 546905); Manuka Road in the Warra Long-term Ecological Research site, 43°06'S 146°41'E, 140 m, 17 May 2005, J. Jarman & G. Kantvilas (HO 531518); Mt Wellington, 42°54'S 147°14'E, 1000 m, 16 Apr 1980, A.V. Ratkovsky H1547 (HO 49895 p.p.); **New Zealand: North Island:** North Auckland Province, Waima Forest, Hauturu Highpoint track in vicinity of summit areas of Hauturu Trig, off Waiotemarama Track, 35°31'S 173°28'E, 650–680 m, 23 Feb 1997, J.J. Engel 22583 (F 1141352); Central Plateau, Maunganui o te Ao River catchment, Erua Forest, track to Tapapakurua Falls, 39°10'48"S 175°22'23"E, 850 m, 24 Nov 2013, M.A.M. Renner 6782 (NSW 899353); (?) New Zealand (specimen data gives New South Wales): Allan Cunningham, comm. Dr Hewitt Watson Feb. 1844, (FH 00284116).

***Plagiochila gregaria*** (Hook.f. & Taylor) Hook.f. & Taylor ex Gottsche, Lindenb. & Nees, Synopsis Hepaticarum 5: 654 (1847)

Basionym: *Jungermannia gregaria* Hook.f. & Taylor, London Journal of Botany 3: 564 (1844)

Type citation: New Zealand

Type: New Zealand, 1843, J.D. Hooker, Voyage of H.M. Discovery Ships Erebus and Terror (lectotype designated by Inoue and Schuster (1971): FH 00284114! isotype: S)

=*Plagiochila gregaria* var. *ovalifolia* E.A.Hodgs., Transactions and Proceedings of the Royal Society of New Zealand 73: 289 (1944)

Type citation: *n.v.*

Type: New Zealand, Ketetahi Track, National Park, Jan. 1932, leg. G.O.K. Sainsbury (*n.v.*)

=*Tylimanthus saccatus* var. *umbellaris* Berggr., On New Zealand Hepaticae: 29 (1898)

Type citation: *n.v.*

Type: New Zealand, South Island, Canterbury Prov, Bealey River, leg. *Berggren 3153* (isotype: *S n.v.*)

=*Plagiochila helmsii* Steph., Bulletin de l'Herbier Boissier, sér. 2 4: 782 (1904) = Species Hepaticarum 2: 460 (1904)

Type citation: New Zealand, Southern Island (Helms).

Type: New Zealand, *Helms*, (lectotype designated here: G 00113228! (male); New Zealand, *Helms*, (residual syntype: G 0061442! (female)).

**Etymology:** in reference to the terminal cluster of androecial branches.

**Notes:** The syntype series of *Plagiochila helmsii* comprises two specimens, one male, one female, and both sexes were described in the protologue. Bonner (1962) inadvertently achieved a narrowing of the typification of this name by identifying Helms's collections in Geneva as the type. The two syntype specimens in Geneva were interpreted as duplicates of a single Helms gathering, number 522, by Engel and Merrill (2010a) and presented as different 'sheets' of the same holotype specimen. However, the female specimen grows with *Frullania ptychantha* and *Macromitrium*, while the male specimen grows with *Dicnemon calycinum*. These associated species and substrate – being a layer of black humic matter within which stolons are embedded – are both consistent with growth as epiphytes on tree trunks, but given that the species assemblages differ between specimens, and the males and females are pure in both specimens, not admixed, the specimens may be derived from separate collecting events. Further, pencilled numbers in the same hand as on the *P. helmsii* specimens occur on many of Stephani's types, suggesting that the number 522 on the packets is not a Helms collecting number. In Species Hepaticarum Volume 2 (Stephani 1904) *Plagiochila helmsii* is presented as species number 522 within the genus *Plagiochila*, suggesting the number was probably added to the packets after the specimens had been incorporation into Geneva, possibly by Bonner during his work on Index Hepaticarum (M. Price pers. comm.), in which case it bears no relevance to the gathering of the original syntype material. All other observed pencilled numbers on type packets in G similarly corresponded with their presentation in Stephani's Species Hepaticarum (pers. obs.). Because two specimens, possibly derived from separate gatherings by Helms, are included within the syntype series of *P. helmsii* lectotypification is required. Selection of either specimen will not change the way *P. helmsii* is currently applied, as both unambiguously belong to the entity currently referred to by the name *P. gregaria*, but because the androecial characters in combination with the leaf characters are the greatest point of difference between *P. gregaria* and its sister species *P. fragmentissima*, I designate the male plant as the lectotype. This specimen is also the more copious and intact of the two. This narrowing of the lectotypification for *P. helmsii* is consistent with treatment of other liverworts with mixed-sex types (e.g. Engel and Merrill 2010a).

**Description:** Plants with irregularly branched, erect leafy shoots arising from a creeping basal stolon, stolons arising from other stolons by lateral-intercalary branching, not produced from leafy shoot sectors; forming interwoven mats; mid-green to light green, shoot systems to 50 mm long, monomorphic; primary shoots 5–8 mm wide, branches arising by lateral-intercalary branching. Stems without lamellae or paraphyllia, but with clusters of hyaline paraphyses within the leaf axils; reddish-brown, in primary shoots to 600 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 4 to 6 layers, cortical cell walls strongly and continuously thickened, constricting the cell lumen in middle cortical layers, reddish-brown, outer layer with thinner walls than inner cortical cell layers, free external wall with limited thickening, all cortical cells smaller than medulla cells; medulla cell walls without secondary thickening except those beneath the cortex, on whose walls thickening tapers over 2 or 3 tiers toward the stem centre, primary walls hyaline. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots contiguous to imbricate, succubously inserted and subtransversely orientated, broadly elliptic-ovate, 2560–5300 µm long × 2250–4650 µm wide, dorsal margin straight, ventral margin ampliate; dorsal margin entire, apex and ventral margins bearing 0–9 triangular teeth, comprised of 2–7 cells, up to four cells broad at base and capped by a triangular apical cell; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows

leaf-free. Marginal leaf cells quadrate to short rectangular 18–50  $\mu\text{m}$  long  $\times$  11–22  $\mu\text{m}$  wide, long axis parallel to leaf margin, walls with coarse quadrate to bulging trigones but not continuously thickened; medial leaf cells quadrate to polyhedral, 30–61  $\mu\text{m}$  long  $\times$  23–37  $\mu\text{m}$  wide, walls unpigmented, with convex trigones, medial thickenings absent; cells in leaf base long rectangular, 44–76  $\mu\text{m}$  long  $\times$  15–25  $\mu\text{m}$  wide, walls with bulging or cordate trigones, often attenuated along longitudinal walls, and rare weak medial thickening. Cell surfaces smooth. Oil-bodies 4–7 per cell, ovoid to ellipsoid, granular. Underleaves absent. Asexual reproduction absent.

Diocious. Androecia intercalary on shoots that continue vegetative growth, in fascicles of up to five or six branches produced at the apex of vegetative shoots by *Frullania*-type branching at the base of the leading male branch; lateral- and ventral-intercalary branches not associated with male branches; bracts in 4–8 pairs, imbricate, bract-lobe reduced and much smaller than adjacent leaves, margin entire, with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts unornamented. Gynoecia at apices of shoots; bracts broadly elliptic-ovate with an ampliate base, to 6000  $\mu\text{m}$  long, larger than subtending leaves; margins entire or with a few small triangular teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts with or without fertilisation. Perianth campanulate, to 6000  $\mu\text{m}$  long  $\times$  4500  $\mu\text{m}$  wide at mouth, dorsal and ventral keels not winged or with a low wing at the base of the dorsal keel only, laterally compressed but with a weakly inflated base, lateral walls plane; labia rounded, entire. Fig. 8.

**Recognition:** *Plagiochila gregaria* can be recognized by its relatively large stature, imbricate asymmetrically ovate leaves with an ampliate base, whose margins are entire or with a few triangular teeth around the apex; stolons originating by lateral-intercalary branching; female plants have broad mouthed perianths whose labia are entire; and male plants have gregarious male branches originating by *Frullania*-type branches in a cluster at the shoot apex. *Plagiochila gregaria* is also unique among Australasian *Plagiochila* in its production of clusters of paraphyses in the extreme axils of the leaves on vegetative shoots.

*Plagiochila gregaria* could be confused with *P. strombifolia*, but *P. strombifolia* has long spinose-ciliate teeth scattered around the leaf apex and along the ventral leaf margin; the perianth of *P. strombifolia* has labia with spinose-dentate teeth.

*Plagiochila gregaria* could be confused with *P. deltoidea*, but *P. deltoidea* has stolons originating by ventral-intercalary branching, and teeth distributed around the leaf apex and along the ventral leaf margin; the perianths of *P. deltoidea* have labia with prominent lacinate-dentate teeth; and the male branches are produced in single intercalary serial sequence, rather than clustered at the shoot apex by virtue of *Frullania*-type branching.

*Plagiochila gregaria* could be confused with *P. fragmentissima*, for characters differentiating these two species see the recognition section of *P. fragmentissima* above.

**Distribution and Ecology:** *Plagiochila gregaria* is endemic to New Zealand, where it occurs from Te Pahi in the Far North of the North Island to Rakiura in the south. *Plagiochila gregaria* is an inhabitant of rainforests, within which it grows as an epiphyte on tree trunks or as a lithophyte on exposed rocks. Perhaps the best-known population of *P. gregaria* occurs on Rangitoto Island within the Hauraki Gulf near Auckland, where *P. gregaria* forms extensive colonies on basalt, with *Plagiochila kirkii* Steph. and *P. trispicata* Colenso, in addition to other liverworts. *Plagiochila gregaria* is often encountered as a lithophyte, for example at Te Pahi *P. gregaria* grew on gabbro boulders in a streambed, and at Mataraua grew on andesite bedrock alongside a stream. *Plagiochila gregaria* may also be encountered as a trunk epiphyte in, for example, in *Syzygium maire*-*Weinmannia silvicola* dominated forest on alluvial terrace at Tutamoe.

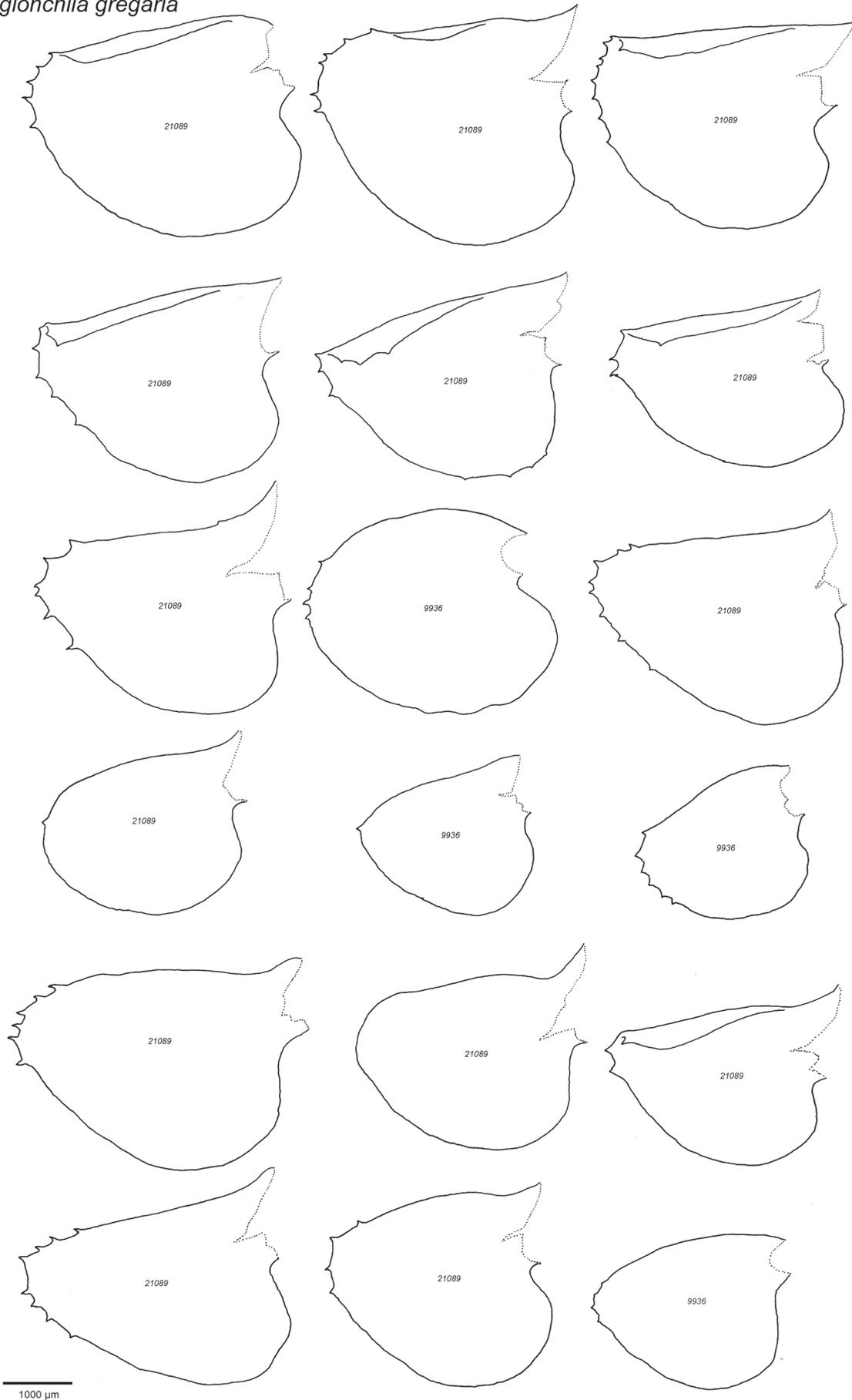
*Plagiochila gregaria* has been reported from Tasmania, but these records are based on misidentifications of other species including *P. fragmentissima*.

**Representative specimens examined: New Zealand:** A. Cunningham (FH 00284126 as *P. olivaceo-atra* Taylor ms); A. Cunningham, comm. Dr Hewitt Watson Feb 1844 (FH 00284125); **North Island:** Te Pahi, North Cape, Mokaikai Scenic Reserve, Whiriwhiri Stream, 34°24'54"S 173°01'36"E, 80 m, 25 Feb 2011, P.J. de Lange 9936 (AK 323588); SE corner of Waipoua Forest, just N of Tutamoe, 35°38'S 173°38'E, 540 m, 9 Feb 1995, J.J. Engel 21089 (F 1141554); Rangitoto Island, Lava Caves, 36°47'26"S 174°51'49"E, 120 m, 29 Dec 2009, P.J. de Lange 8302 (AK 308902); Coromandel Peninsula, Coromandel, Feb 1948, J. Langridge (AK 163906); New Zealand, R. Cunningham, comm. Dr K.R. Greville 1843 (FH 00284117); near Auckland, 1895, T.F. Cheeseman (G 026168); **Rakiura (Stewart Island):** 1909, L. Cockayne 8255 (AK 18666).

Representative misidentified specimens:

*Plagiochila strombifolia*

*Plagiochila gregaria*



**Fig 8.** *Plagiochila gregaria* leaves, from P.J. de Lange 9936 (AK 323588) and J.J. Engel 21089 (F 1141554).

Van Diemen's Land, *Gunn* (FH 00284115 – this specimen is male, the male branches are intercalary, short, not circinate. The two patches are glued onto the card, prohibiting access to stolon branching origin, but the plants are a good match with *P. strombifolia*).

*Plagiochila fragmentissima*

(?) New Zealand: *Allan Cunningham*, comm. Dr Hewitt Watson Feb. 1844 (FH 00284116); Tasmania: Manuka Road, Warra Long-term ecological research site, 43°06'S 146°41'E, 140 m, 17 May 2005, *J. Jarman* & *G. Kantvilas* (HO 531518).

*Plagiochila fasciculata*

New Zealand: Nelson Land District, Reefton, Victoria Range, Klondyke Spur track, 750 m, 28 Dec 2006, *D. Glenny* 9911 (HO 546689).

***Plagiochila gigantea*** Lindenb., *Species Hepaticarum* 2-4: 115 (1840) *nom. nov. pro Jungermannia gigantea* Hook.

Basionym: *Jungermannia gigantea* Hook., *Musci Exotici* 1: 93 (1818) *nom. illeg.*

*Type citation*: Hab. In sinu Dusky bay dicto, apud Novam Zeelandiam. *D. Menzies*, 1791.

*Type*: New Zealand, Dusky Bay, 1791, *Mr Menzies*, as *Jungermannia gigantea* Hooker (FH 00458016! E!d).

=*Plagiochila suborbiculata* Colenso, *Transactions and Proceedings of the New Zealand Institute* 19: 282 (1887)

*Type citation*: Dry hilly forests near Norsewood, County of Waipawa; 1886; *W.C.*

*Type*: New Zealand near Norsewood, County of Waipawa, 1886: *W. Colenso a.1357* (lectotype designated here: BM! isolectotype: G 00115851!)

**Notes**: The isotype of *P. gigantea* in E comprises two sheets, one labeled No. 29, which contains several perianth and sporophyte bearing shoot systems. These correspond with *Plagiochila gigantea* in current usage.

On the other sheet is a single shoot annotated 'Hook.' and two shoots 'In Novae Zelandia Menzies 1824'. The second is *P. gigantea*, the first corresponds with *P. intertexta*.

**Etymology**: giant, referencing the impressive stature of large plants.

**Description**: Plants with regularly branched, erect dendroid leafy shoots comprising repeated monopodial units of a basal stolon and upper leafy sector, stolons arising from within the leafy sector near its base by lateral-intercalary branching and immediately ascendant; forming tall turfs; dark-green, shoot systems to 200 mm long, dimorphic; primary shoots 5–8 mm wide, branches arising by *Frullania*-type branching. Stems without lamellae, paraphyllia, or paraphyses, reddish-brown, in primary shoots to 1500 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 5 to 7 layers, cortical cell walls strongly and continuously thickened, constricting the cell lumen in middle cortical layers, reddish-brown, outer layer cells quadrate, with walls thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls without secondary thickening except those beneath the cortex, on whose walls thickening tapers over 2 or 3 tiers toward the stem centre, primary walls hyaline. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots remote, succubously inserted and orientated, broadly elliptic, 2450–4350 µm long × 2510–3450 µm wide, dorsal margin shallowly curved, apex rounded, ventral margin ampliate; dorsal margin entire along basal two thirds, outer third, apex and ventral margins bearing 35–60 spinose teeth, comprised of 2–5 cells, up to three cells broad at base but uniseriate above, cells above base elongate, thick-walled, capped by a long triangular apical cell with an acute apex; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, not attaining dorsal stem midline, and not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells rectangular 20–31 µm long × 9–25 µm wide, long axis parallel to leaf margin, walls with continuous and even golden-brown pigmented thickening, cell ends rounded, free external wall slightly thicker than internal walls, thickening present in outermost two tiers of leaf cells only; medial leaf cells hexagonal to polyhedral, 28–52 µm long × 21–36 µm wide, walls yellow-brown pigmented, with triangular trigones, medial thickenings absent; cells in leaf base long rectangular, 46–88 µm long × 21–32 µm wide, walls continuously but unevenly thickened, yellow-brown pigmented. Cell surfaces smooth. Oil-bodies 2–6 per cell, ovoid to ellipsoid, finely botryoidal. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, in fascicles of up to three branches produced at the apex of vegetative shoots by *Frullania*-type branching at the base of the leading male branch;

lateral- and ventral-intercalary branches not associated with male branches; bracts in 3–6 pairs, imbricate, bract-lobe reduced and much smaller than adjacent leaves, margin dentate, with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts unornamented. Gynoecia at apices of shoots; bracts broadly elliptic to triangular-ovate with an ampliate base, to 4000  $\mu\text{m}$  long, larger than subtending leaves; margins with 60–70 spinose teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations absent, rarely with a single lateral intercalary innovation produced below the female bracts. Perianth long cylindrical, to 8000  $\mu\text{m}$  long  $\times$  1800  $\mu\text{m}$  wide at mouth, dorsal and ventral keels not winged, laterally compressed but with a weakly inflated base, lateral walls plane; labia rounded, with around 15 long spinose teeth each. Fig. 1.

**Recognition:** *Plagiochila gigantea* can be recognized by the dendroid shoots with flabellate branching by *Frullania*-type mode and monopodial replication of shoot systems resulting in stacking of three or more tiers of umbrella-like spreading branches. The leaves are elliptic-ovate and bear numerous spinose teeth on their margins, and the cells of the teeth and leaf margin have thickened, golden-brown-pigmented cell walls.

*Plagiochila gigantea* could be confused with *P. baileyana*, but the shoot systems of *P. baileyana* are procumbent, not erect, and the leaves are obovate, not elliptic-ovate (Fig. 1).

*Plagiochila gigantea* could be confused with *P. ramosissima* which also has a dendroid growth habit, but vegetative branching in *P. ramosissima* is by lateral-intercalary mode, not *Frullania*-type, and the leaves bear triangular teeth and do not have a border formed by cells with heavily thickened and pigmented cell walls.

**Distribution and Ecology:** *Plagiochila gigantea* is endemic to New Zealand, where it is widely distributed in cool hyperhumid forests throughout the three main islands. *Plagiochila gigantea* grows on leaf litter, soil, humus, and decaying logs on the forest floor where it contributes, with several other bryophyte giants, to some of the tallest, most extensive, and species-rich forest floor liverwort dominated bryophyte communities on earth. *Plagiochila gigantea* grows mixed with *Schistochila appendiculata* and *S. nobilis*, *Lepidozia microphylla*, *L. pendulina* and *L. spinosissima*, *Trichocolea hatcheri*, *Plagiochila ramosissima*, *Heteroscyphus ciliatus*, and the mosses *Dendrologotrichum dendroides*, *Dicranoloma robusta*, and *D. billardiarei*.

One specimen of *Plagiochila gigantea* collected by Max Fleisher in 1903 bears the locality 'Fern Tree, Tasmania', which is on the eastern flank of Mt Wellington near Hobart. This specimen is a copious, large plant from a readily accessible site close to major centre of population, yet Fleisher's collection is the only record of *P. gigantea* from Australia. A couple of points suggest this record may be in error. Firstly, though potential habitat remains at Fern Tree and elsewhere in Tasmania, *P. gigantea* has not been recollected in Tasmania. It is unlikely that such a large and conspicuous bryophyte would escape detection, or be neglected given its supposed restriction to New Zealand. Secondly, Fleisher collected around the Derwent River in early April 1903 before his ship departed for New Zealand, travelling from Hobart to Taranaki, where Fleisher also collected. It is possible that Fleisher mixed up some of his localities, and I reject *P. gigantea* from the Australian flora until material of undeniable provenance is obtained.

(?)Australia: Tasmania: Hobart, Mt. Wellington, Ferntree, 42°55'S 147°16'E, 15 Apr 1903, *M. Fleischer B2100* (CANB 302308).

**Representative specimens examined: New Zealand: North Island:** Te Apiti, Hawkes Bay, 3 May 1899, *T.W.N. Beckett 240* (NSW); **South Island:** Nelson Land District, Victoria Range, Klondyke Spur track, 750 m, 28 Dec 2006, *D. Glenny 9909* (HO 546692); Shenandoah Valley 1 km N of Shenandoah Saddle, 32 km SSW of Murchison, 42°01'S 172°14'E, 680 m, 3 Feb 1993, *H. Streimann 51236* (CANB 9306686); Victoria Range, near Tobins Creek crossing with State Highway 7, 42°17'30"S 172°03'38"E, 530 m, 19 Jan 2007, *L.H. Cave 680* (HO 549611); Haast Pass, 44°06.59'S 169°21.12'E, 562 m, 28 Nov 2002, *A.J. Downing* (HO 525111); near Riverton, Pourakino River, near Pourakino Picnic Area at Bridge 1908, 46°14'29"S 167°57'29"E, 20 m, 7 Dec 2010, *L.H. Cave 1354* (HO 571523); Catlins State Forest Park, Wisp track, 46°24'52"S 169°26'46"E, 160 m, 13 Dec 2008, *L.H. Cave 784* (HO 553072); Otago, Catlins, Thisbe Stream, Thisbe Valley track, 46°25'S 169°25'E, 13 Dec 2008, *H.M. Jolly & J. Milne* (MEL 2335938); **Rakiura (Stewart Island):** Sep 1942, *Miss Thompson* (NSW).

### *Plagiochila* sect. *Austrocaules* M.A.M. Renner section nov.

Diagnosis: Stolons originating by ventral-intercalary branching. Shoot systems modular with a basal stoloniferous section and upper leafy sector, replicated sympodially from basally produced stolons. Leafy shoot systems monomorphic. Vegetative branching exclusively lateral-intercalary. Teeth on leaves variable, spinose dentate to triangular. Underleaves absent or vestigial. Subfloral innovations lateral-intercalary. Androecial branching lateral- or ventral-intercalary. Androecia spicate or lax, intercalary, often in series, male bracts entire.

Type species: *Plagiochila deltoidea* Lindenb.

**Etymology:** *Austro* – southern, *caules* stems, in reference to both the southern distribution of this lineage but also the ventral-intercalary stolon origin which, when stems are viewed in transverse section, issue from the stem at a position equivalent to the southern compass point.

= *Plagiochila* sect. *Hodgsoniae* J.J.Engel et G.L.Merr., *Nova Hedwigia* 96: 403 (2013) ‘*Hodgsonia*’, *nom. inval.*

Type: *Plagiochila deltoidea* Lindenb.

= *Plagiochila* sect. *Deltoideae* E.A.Hodgs., *Trans. & Proc. Roy. Soc. New Zealand* 73: 271 (1944) *nom. inval.*

Type: *Plagiochila deltoidea* Lindenb.

**Notes:** Section *Deltoideae* was placed in synonymy with *Plagiochila* sect. *Duriae* by Groth *et al.* (2004), on the basis of a misidentified specimen of *P. ramosissima*.

Two Australasian species belong to *Plagiochila* sect. *Austrocaules*, *P. ratkowskiana* Inoue, and *P. deltoidea* Lindenb. Several other species belonging to this section occur in Malesia and Oceania, including the *P. gymnoclada* complex and at least one species described as a variety of *P. blepharophora*, a member of *Plagiochila* sect. *Cucullatae*, see below, given that ventral intercalary stolon branching is confined to this lineage within *Plagiochila*.

Putative ventral-intercalary branches were used to support the recognition of the genus *Szweykowskia* (Gradstein and Reiner-Drehwald 1995) based on *P. cucullifolia*, which had been previously treated as its own subgenus by Inoue (1984). However in this species the vegetative branching is not ventral-intercalary (Heinrichs *et al.* 2002, 2003). Nor in species of sect. *Austrocaules* are vegetative branches ventral intercalary, only stolon branches issue by this mode. Vegetative ventral-intercalary branching is confined to *Dinckleria*, *Pseudolophocolea* and the *Chiastocaulon* lineage.

### ***Plagiochila ratkowskiana*** Inoue, *Brunonia* 3: 141 (1980)

*Type citation:* Tasmania, Mt. Wedge, ca. 1000 m, leg. A. V. Ratkowsky no. 78/59 (TNS; duplicate in hb. Ratkowsky)

*Type:* Tasmania, South West, Mt Wedge, 42°51'S 146°18'E, 5 Mar 1978, A. V. Ratkowsky H1567 (78/59) (holo: TNS, iso: HO 49815!)

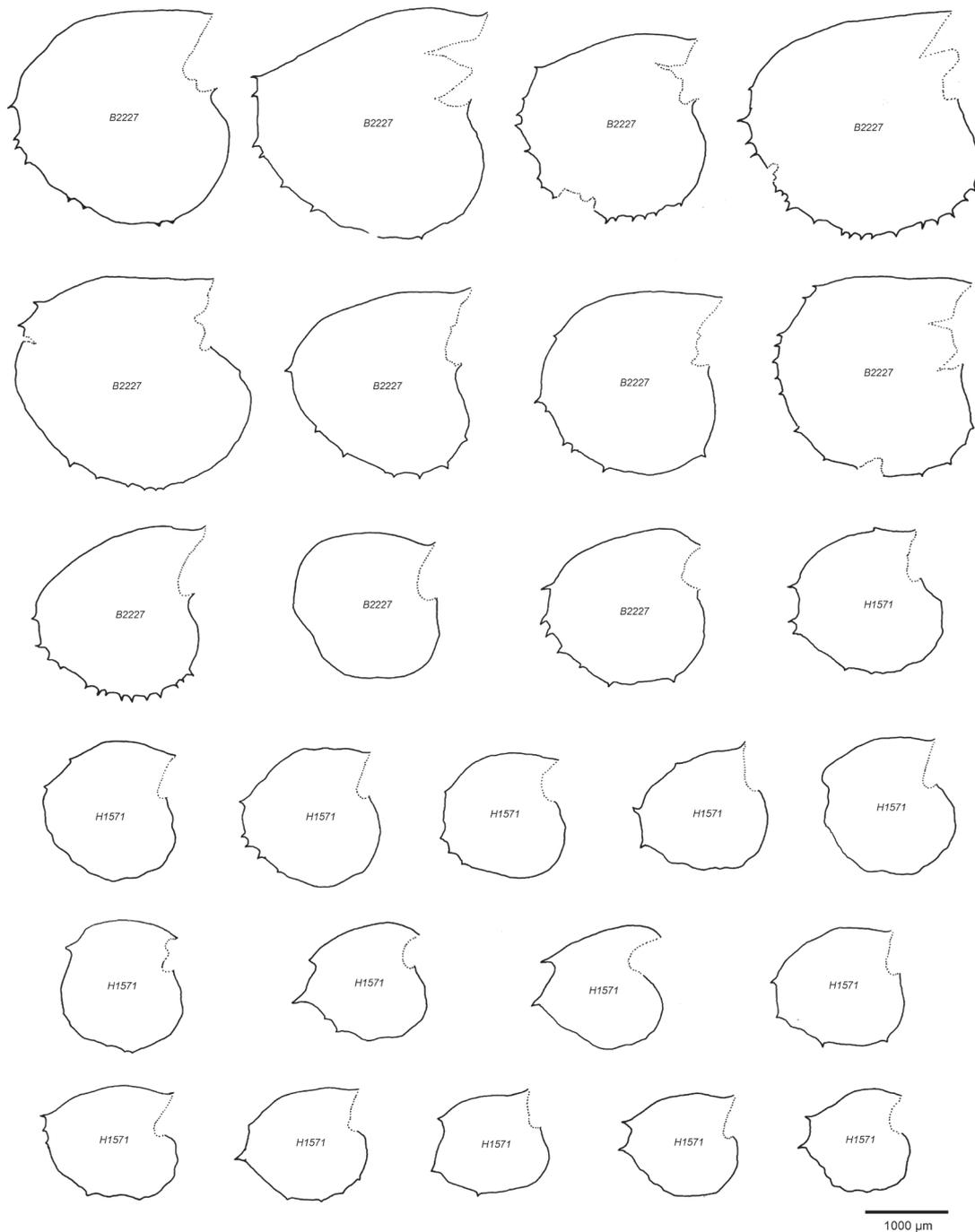
**Etymology:** for A.V. Ratkowsky, Tasmanian bryologist and collector of the type.

**Description:** Plants with irregularly branched, erect leafy shoots arising from a creeping basal stolon, stolons arising from other stolons and from leafy shoots by ventral-intercalary branching; forming interwoven mats; mid-green to light green, shoot systems to 40 mm long, monomorphic; shoots 3–5.5 mm wide, branches arising by lateral-intercalary branching. Stems without lamellae, paraphyllia, or paraphyses, reddish-brown, in primary shoots to 400 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 3 layers, cortical cell walls strongly and continuously thickened, reddish-brown fading to yellow on the innermost cortical cell walls, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls beneath with walls thickened but tapering, other walls with distinct triangular trigones and weak continuous thickening over some walls, walls faint yellow pigmented. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots imbricate, succubously inserted and orientated, broadly ovate to rotund, 1340–3070 µm long × 1340–3090 µm wide, dorsal margin shallowly curved, usually inrolled, ventral margin ampliate; dorsal margin entire, apex and ventral margins bearing 0–19 triangular teeth, comprised of 2–6 cells, two cells broad at base, uniseriate above and capped by a triangular apical cell; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular 24–41 µm long × 14–28 µm wide, long axis parallel or perpendicular to leaf margin, walls with coarse quadrate to bulging trigones but not continuously thickened, free external wall of each cell with a single low wave-shaped thickening projecting into the cell lumen; medial leaf cells quadrate to polyhedral, 26–44 µm long × 25–38 µm wide, walls faint yellow pigmented, with bulging cordate trigones, medial thickenings absent; cells in leaf base long polyhedral, 34–62 µm long × 21–38 µm wide, walls with bulging nodular to knot-like trigones, medial thickening absent, trigones not confluent. Cell surfaces smooth. Oil-bodies 3–5 per cell, large, botryoidal (fide *Jarman* HO 548184). Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, produced singly, never in fascicles, occasional branching within male branches by lateral- or ventral-intercalary branching may give rise to vegetative shoots or another male branch, *Frullania*-type branches not associated with male branches; bracts in

15 or more pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves but variable in size and exhibiting regular fluctuation in size from small to large to small along the shoot, margin entire, with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts unornamented. Gynoecia at apices of shoots; bracts broadly elliptic-ovate, to 4000  $\mu\text{m}$  long, larger than subtending leaves; dorsal margin inrolled; margins with around 20 dentate teeth, larger on ampliate base; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts with or without fertilisation. Perianth campanulate, about 2500  $\mu\text{m}$  long  $\times$  2100  $\mu\text{m}$  wide at mouth, dorsal keel without a wing, or with a low wing extending from the base to near the middle of the keel, entire, ventral keel not winged, laterally compressed but with a weakly inflated base, lateral walls plane; labia rounded, with numerous ciliate teeth comprised uniseriate rows of short rectangular cells. Fig. 9.

*Plagiochila ratkowskiana*



**Fig 9.** *Plagiochila ratkowskiana* leaves, from J.S. Whinray B2227 (MEL 2354417A) and A.V. Ratkowsky H1571 (CANB 8409926).

**Notes:** *Plagiochila ratkowskiana* was incorrectly synonymized with *P. fragmentissima* by me in Renner *et al.* (2017), when I overlooked the fact that my *Plagiochila aff. gregaria* was actually *P. fragmentissima*, and misinterpreted the figures and description in the protologue of *P. fragmentissima* (Inoue and Schuster 1971) and *P. ratkowskiana* (Inoue 1980).

**Recognition:** *Plagiochila ratkowskiana* can be recognized by the combination of stolon production by ventral-intercalary branching; vegetative leafy shoots originating by lateral-intercalary branching, the monomorphic leafy shoots, and the transversely orientated, rotund leaves whose margins bear up to ten, occasionally more, small triangular teeth (Fig. 9). Male plants are distinctive in their intercalary male branches bearing imbricate male bracts that have entire margins, with androecia produced in close series along a shoot, separated by short intervals of vegetative growth, and the occasional presence of androecial innovation by ventral-intercalary branching. Also distinctive in the relatively (apparently) large leaf cells which impart a distinctive texture to the dried plants, the broad cnemis, and the usually sparingly toothed leaf lobe margins. Depending on exposure *P. ratkowskiana* can vary from forming short, tight turfs whose shoots bear leaves with at most two teeth near the apex, or tall, openly branched mats whose shoots bear leaves with numerous small spinose-dentate teeth along the postal margin. Female bracts and perianth mouths mirror the variation observed in leaf margins.

*Plagiochila ratkowskiana* could be confused with *Cryptoplagiochila radiculosa* (as in HO 577295), but *C. radiculosa* has ovate leaves with a distinct bilobed apex, rather than subrotund leaves with margins entire or with scattered triangular teeth. The perianths of *C. radiculosa* bear several triangular teeth at their apex and have a basal shoot calyptra, whereas the perianths of *P. ratkowskiana* bear numerous small, short, spinose teeth on the labia and do not have a basal shoot-calyptra.

*Plagiochila ratkowskiana* could be confused with *Plagiochila fragmentissima*, but *P. fragmentissima* has asymmetrically ovate leaves, produces stolons by lateral-intercalary branching, and has triangular teeth on the perianth labia.

*Plagiochila ratkowskiana* could be confused with *P. deltoidea*, but *P. deltoidea* has asymmetrically ovate leaves with many sharp triangular teeth distributed around the apex and ventral margin, and perianth labia with large dentate teeth.

**Distribution and Ecology:** *Plagiochila ratkowskiana* is endemic to Australia and occurs in Tasmania and on Macquarie Island. In Tasmania *Plagiochila ratkowskiana* is a common liverwort, and grows as a lithophyte or epiphyte in forests, grasslands and herbfields between sea level and more than 1000 m elevation. In forest *P. ratkowskiana* may grow as a trunk or branch epiphyte on a range of tree species, including *Nothofagus* and *Acacia*, with a wide range of other bryophytes including *Cheilolejeunea* spp, *Cryptoplagiochila radiculosa*, *Dinckleria pleurata*, *Frullania* spp, *P. strombifolia*, *Macromitrium* spp, *Orthotrichum* spp, *Zygodon* spp. On rocks *P. ratkowskiana* may form low or tall turfs depending on exposure, and may form pure or mixed turfs, the latter with a wide range of bryophytes including *Dinckleria pleurata*, *Frullania*, *Lepicolea scolopendra*, *Macromitrium*, *Metzgeria*, *Radula multiamentula*, and *Syzygiella*. In alpine habitats *P. ratkowskiana* may occur on soil, or on exposed granite.

**Representative specimens examined: Australia: Tasmania:** Flinders: Cape Barren Island, Furneaux Group, Bass Straits. About 480 m at 81.25 degrees from Mount Munro's summit, 40°22'11.6"S 148°07'22.1"E, 548 m, 11 Feb 20117, *J.S. Whinray B2227* (MEL 2354417A); West Coast, Whyte-Pieman Rivers junction, Pieman River State Reserve, 41°39'S 145°05'E, 20 m, 8 Feb 1995, *A. Moscal 26610D* (HO 577100); Quoin Mountain, near Kempton, 42°33'S 147°16'E, 15 Mar 1980, *A.V. Ratkowsky H1575* (HO 49889); Mt Wellington, South Boughs, west of South Trig, 42°55'S 147°13'E, 7 Oct 1979, *A.V. Ratkowsky H1565* (HO 49870); Mt Wellington, organ pipes, 42°54'S 147°14'E, 31 Jan 1980, *A.V. Ratkowsky H1571* (CANB 8409926); Mt Wellington, summit plateau, 42°54'S 147°14'E, 20 Mar 1980, *A.V. Ratkowsky H1573* (HO 49892); Mt Cullen, near summit, 42°50'S 146°10'E, 700 m, 4 Mar 1978, *A.V. Ratkowsky* (HO 304464); South West National Park, southern slopes of Hermit Hill, 42°50'S 146°07'E, 380 m, 14 Jun 2008, *J. Jarman s.n.* (HO 548184); Freycinet National Park, Mt Freycinet, among rocks at summit, 42°13'S 148°18'E, 620 m, 12 Jul 2003, *K. Felton* (HO 525836); Arthur-Pieman Conservation Area, Mt Edith summit, 41°27'04"S 145°00'10"E, 760 m, 3 Feb 2015, *L.H. Cave 2626* (HO 576896); Mt Puzzler Forest Reserve, Meadstone Falls, in the gorge of St Pauls River, 41°45'S 148°05'E, 400 m, 1 Aug 1999, *K. Felton* (HO 501780); South West National Park, Maxwell Ridge, 43°30'E 146°43'E, 1030 m, 28 Feb 1999, *K. Felton* (HO 445255); Mt Wellington, Organ Pipes track, 42°54'S 147°14'E, 31 Jan 1980, *A.V. Ratkowsky* (HO 49868); Mt Wellington, near The Wires, 42°53'S 147°14'E, 7 Apr 1982, *A.V. Ratkowsky* (HO 66968); Central Highlands, Wild Dog Plains, 41°50'S 146°32'E, 1170 m, 18 Feb 1992, *A. Moscal 22822* (HO 302300); Mt Wellington, The Wires, 7 Apr 1982, *A.V. Ratkowsky* (HO 304355); Organ Pipes Directissimo, 42°54'S 147°14'E, 28 Feb 1980, *A.V. Ratkowsky H1566* (HO 304356); Mt Wellington, South Trig Directissimo, 42°55'S 147°14'E, 12 Apr 1982, *A.V. Ratkowsky H1779* (HO 304357); Kempston Quoin, 42°33'S 147°16'E, 15 Mar 1980, *A.V. Ratkowsky* (HO 304358); Adamsons Peak, above hut, 43°21'S 146°51'E, 2 Mar 1980,

A.V. Ratkowsky (HO 304359); Organ Pipes, on rocks, 42°54'S 147°14'E, 31 Jan 1980, A.V. Ratkowsky (HO 304360); Upper Collins Bonnet, 42°53'S 147°09'E, 2 Feb 1980, A.V. Ratkowsky H1576 (HO 304361); Mt Rufus, 42°08'S 146°06'E, 10 Mar 1979, A.V. Ratkowsky (HO 304362); Mt Rufus circuit, 42°08'S 146°06'E, 11 Nov 1978, A.V. Ratkowsky (HO 304363); Mt Wellington, The Wires, 42°53'S 147°14'E, 1050 m, 29 Sep 1979, A.V. Ratkowsky H1574 (HO 304364); Adamsons Falls, 43°22'S 146°51'E, 1 Mar 1980, A.V. Ratkowsky (HO 304365); Mt Wellington, Wires, 42°53'E 147°14'E, 20 Dec 1979, A.V. Ratkowsky H1572 (HO 304366); Hartz Mountain, 43°15'S 146°46'E, 1 May 1982, A.V. Ratkowsky H1780 (HO 304367); Mt Eliza below summit, 42°58'S 146°24'E, 17 Apr 1982, A.V. Ratkowsky H1778 (HO 304368); Organ Pipes, 42°54'S 147°14'E, 6 Mar 1980, A.V. Ratkowsky H1577 (HO 304370); Anthony Road, western Tasmania, 41°50'30"S 145°37'30"E, 590 m, 11 May 1991, J. Jarman s.n. (HO584301); South West, Mount Mangana, South Bruny Range, 43°22'S 147°17'E, 571 m, 27 Apr 1993, A. Moscal 25245 (HO 577298); North West, Minnow River, 41°29'S 146°19'E, 280 m, A. Moscal 16221 (HO 577300); East Coast, Douglas River, 41°47'S 148°14'E, 20 m, 7 May 1990, A. Moscal 19620 (HO 577301); Mt Field, Lake Rayner, 42°40'S 146°39'E, 1030 m, 12 Apr 1992, A. Moscal 23390 (HO 132892); East Coast, East Coast, Mount Clark, Tasman Peninsula, 43°06'S 147°46'E, 480 m, 30 Mar 1998, A. Moscal 29629 (HO 577422); Mt. Field, Mt. Mawson, 42°42'S 146°35'E, 1085 m, 11 Apr 1992, A. Moscal 23272 (HO 577302); Midlands, Breasted Sugarloaf, 42°12'S 147°53'E, 630 m, 8 Dec 1991, A. Moscal 22149 (HO 577303); South West, Mount Mangana, South Bruny Range, 43°22'S 147°17'E, 560 m, 27 Apr 1993, A. Moscal 25048 (HO 577117); East Coast, Mt Maria, Maria Island National Park, 42°37'S 148°06'E, 630 m, 24 April 1995, A. Moscal 27088B (HO 577110); **Macquarie Island**: 300 m east of Prion Lake, 54°35'S 158°54'E, 200 m, 12 Nov 1979, R.D. Seppelt 6381 (HO 577615); Pyramid Lake, 54°39'S 158°52'E, 230 m, 4 Dec 1981, R.D. Seppelt 12081 (HO 577616).

***Plagiochila deltoidea*** Lindenb., Species Hepaticarum 5: 132 (1843)

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

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

*Type*: New Zealand, Dusky Bay, without collector (lectotype designated by Inoue and Schuster (1971): STR! isolectotype: herb. Lindenberg 914, W! )

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

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

*Type*: New Zealand, Wood Creek, DVK, 10 Feb. 1887, W. Colenso a.1342 (lectotype designated here: WELT-H007775!)

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

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

*Type*: n.v.

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

*Type citation*: New Zealand, ubique communis.

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

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

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

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

=*Plagiochila deltoidea* var. *densa* J.J.Engel & G.L.Merr., Nova Hedwigia 92: 506 (2010) *syn nov.*

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

*Type*: n.v.

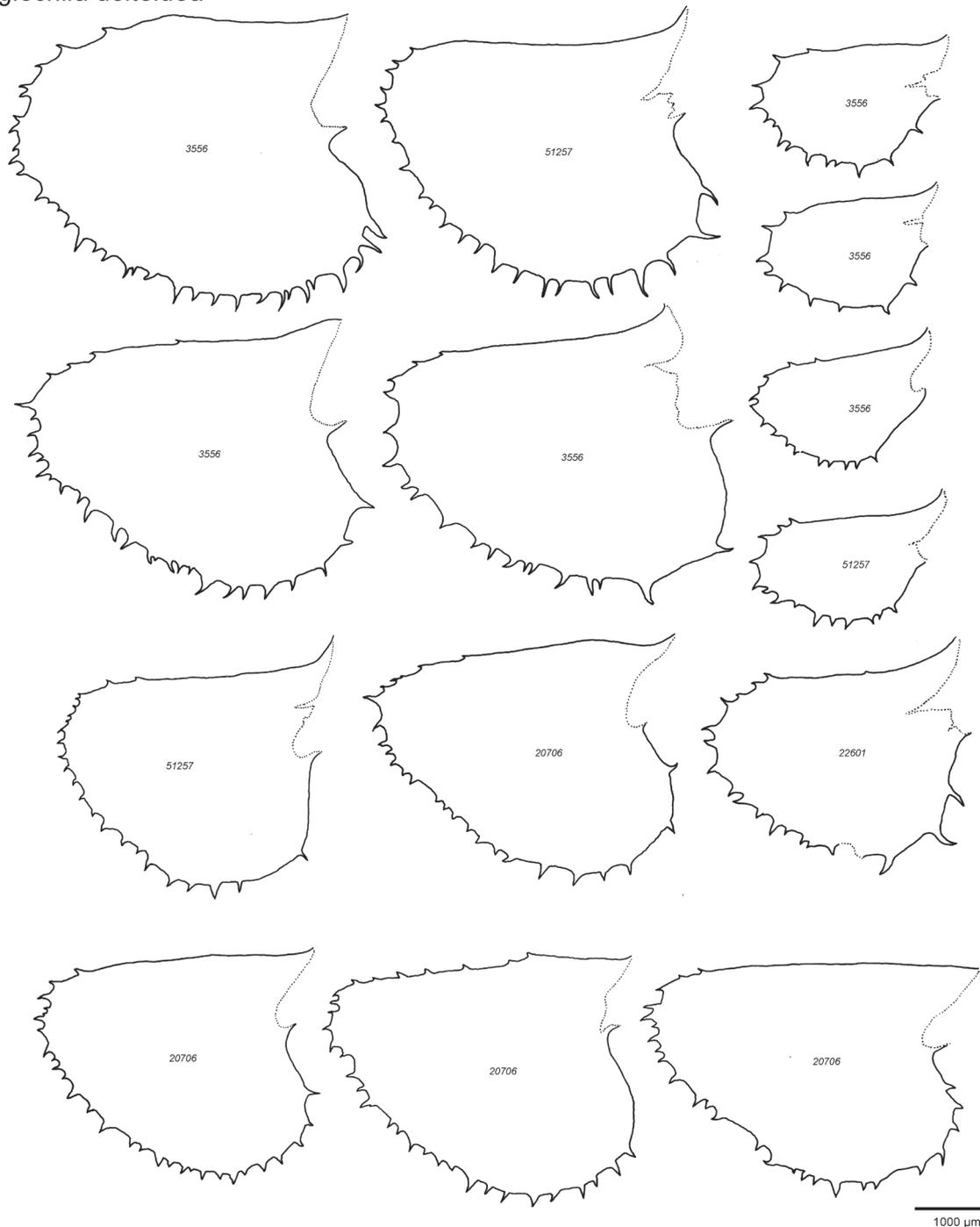
**Etymology:** possibly in reference to the deltoid leaf shape.

**Description:** Plants forming long pendulous turfs or short pendants of sparingly branched leafy shoots arising from a sharply differentiated creeping, branched, system of basal stolons bearing highly reduced leaves; leafy shoots mid-green to bronze-green in life, light brown in herbarium, to 100 mm long and 2677–4651  $\mu\text{m}$  wide, leafy shoots monomorphic, stature reduced at base close to stolons; flagellae absent. Branching within stolons predominantly ventral-intercalary, rarely lateral-intercalary, always giving rise to other stolons; within leafy sectors by lateral- and ventral-intercalary branching, giving rise to leafy shoots only. Stems on stolons and primary shoots in leaf sectors reddish-brown, to 280  $\mu\text{m}$  diameter, transversely elliptic, surfaces smooth; cortical cells in 4 layers, cortical much smaller than medullar, with strong continuous reddish-brown thickenings on cell walls constricting cell lumina, except in a wedge of unpigmented cell walls from the ventral merophyte, medullar cell walls with small triangular trigones at cell junctions otherwise without thickening, pale yellow pigmented; stems on leafy shoot similar without the ventral wedge of unpigmented walls and with outer walls within the medulla layer with thin continuous thickening. Rhizoids on stolons, arising in loose fascicles from the base of leaves, also scattered along the lateral and ventral stem surfaces. Leaves on leafy shoots imbricate, obliquely orientated, postically secund, deltoid, 1794–2965  $\mu\text{m}$  long  $\times$  1614–2803  $\mu\text{m}$  wide, transversely oriented when dry, succubously orientated when wet, dorsal margin straight, strongly recurved when dry, entire or with 1 or 2 small teeth; apex broadly rounded, postical margin broadly ampliate toward base; with 7–24 narrow triangular teeth of varying size and spacing distributed from around the apex, rarely on the outer part of the dorsal margin, to the base, though teeth on the straight, basal part of the postical margin rare; teeth narrow-triangular (1–)2–9(–10) cells wide and 3–10(–20) cell tiers high, uniseriate for 2–5 cells, upper cells rectangular, capped by a single acute cell; insertion J-shaped, oblique, recurved at ventral end but not decurrent, not attaining ventral stem midline, leaving two cortical cell rows leaf-free, dorsally decurrent and attaining the dorsal stem midline, but stem visible between leaves. Marginal cells quadrate to rectangular, 8.1–11.3  $\mu\text{m}$  long  $\times$  6.7–9.6  $\mu\text{m}$  wide, rectangular cells have long axis parallel with margin, free external wall heavily thickened, thickening convex, bulging into cell lumen medially, not sharply differentiated from medial cells; cells in median leaf isodiametric to elliptic 8.3–23.9  $\mu\text{m}$  long  $\times$  8.3–17.2  $\mu\text{m}$  wide, walls with discrete convex to nodular trigones, medial wall thickenings rare, thickenings above and below trigones along junction of transverse walls with free dorsal and ventral exterior walls absent, transition to basal cells more or less abrupt, particularly dorsally where isodiametric medial cells and rectangular cells are juxtaposed, medially and ventrally transitional cells have progressively coarser trigones and longer lengths relative to width; cells in leaf base rectangular to long rectangular, 22.2–67.4(–86.2)  $\mu\text{m}$  long  $\times$  10.5–18.8  $\mu\text{m}$  wide, trigones bulging, discrete or confluent with adjacent medial thickenings, 1 or 2 bulging medial wall thickenings present, occasionally confluent with each other and adjacent trigones; leaves on stolons remote to contiguous, appressed, ovate, unlobed but with triangular teeth. Cell surfaces smooth and unornamented. Oil-bodies not observed. Underleaves vestigial, amorphous aggregations of several cells, produced consistently on leafy sectors. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, solitary, growth of androecial branch positively geotropic, inclined downward from leafy shoot, becoming negatively geotropic at transition back to vegetative growth; repeated transition between androecia and vegetative shoots results in oscillating shoots; androecial bracts in 4–11 pairs, bract lobes orbicular, entire, margins weakly recurved toward ventral base, transversely orientated, obliquely spreading; connate across the dorsal stem surface or not, fused with the preceding bract or not; ventral leaf-free strip present, underleaves present throughout spike, small, ciliate, disc distinct; antheridia 1 per bract, stalk biseriate. Gynoecia at apices of leafy shoots; bracts elliptic-obovate, smaller than preceding leaves, 1696–3334  $\mu\text{m}$  long  $\times$  1188–2268  $\mu\text{m}$  wide; base truncate; median base inflated forming a prominent pocket; dorsal margin not reflexed, bearing 1–3 small spinose dentate teeth 2–4 cells broad at their base and 2–6 cells high, capped by a uniseriate row of 2–4 cells; apex and ventral margin lacinate, bearing 10–16 lacerate teeth, 3–14 cells broad at their base and up to 30 tiers high, radiating, more or less straight to weakly curved, separated by narrow to broad U-shaped sinus, rarely V-shaped; bract cells as for leaf cells; cell surfaces smooth and unornamented; female bracteole when present bifid, closely pressed against the prominent, rounded, protruding ventral perianth keel; gynoecial disc bearing about 10 archegonia. Subfloral innovations by lateral-intercalary branching from the antico-ventral end of the leaf insertion line, two or more present, rarely ventral-intercalary subfloral innovations are produced subsequent to lateral innovations; additional lateral-intercalary branches from the base of the subfloral innovation may be present; production of subfloral innovations seems curtailed by fertilisation of the gynoecium, in sporophyte-bearing plants a single innovation may subtend the perianth; in contrast, proliferation of subfloral innovations and repeated pulses of synchronous gynoecium production by each shoot may result in a flabellate shoot system in female plants whose gynoecia are not fertilised. Perianth campanulate when immature and unfertilised, elliptic-oblong, 2738–3548  $\mu\text{m}$  long  $\times$  2113–2660  $\mu\text{m}$  wide at mouth, drooping, with prominent wing on basal half of dorsal and ventral keels, dorsal keel curved at base and longer than ventral; laterally compressed

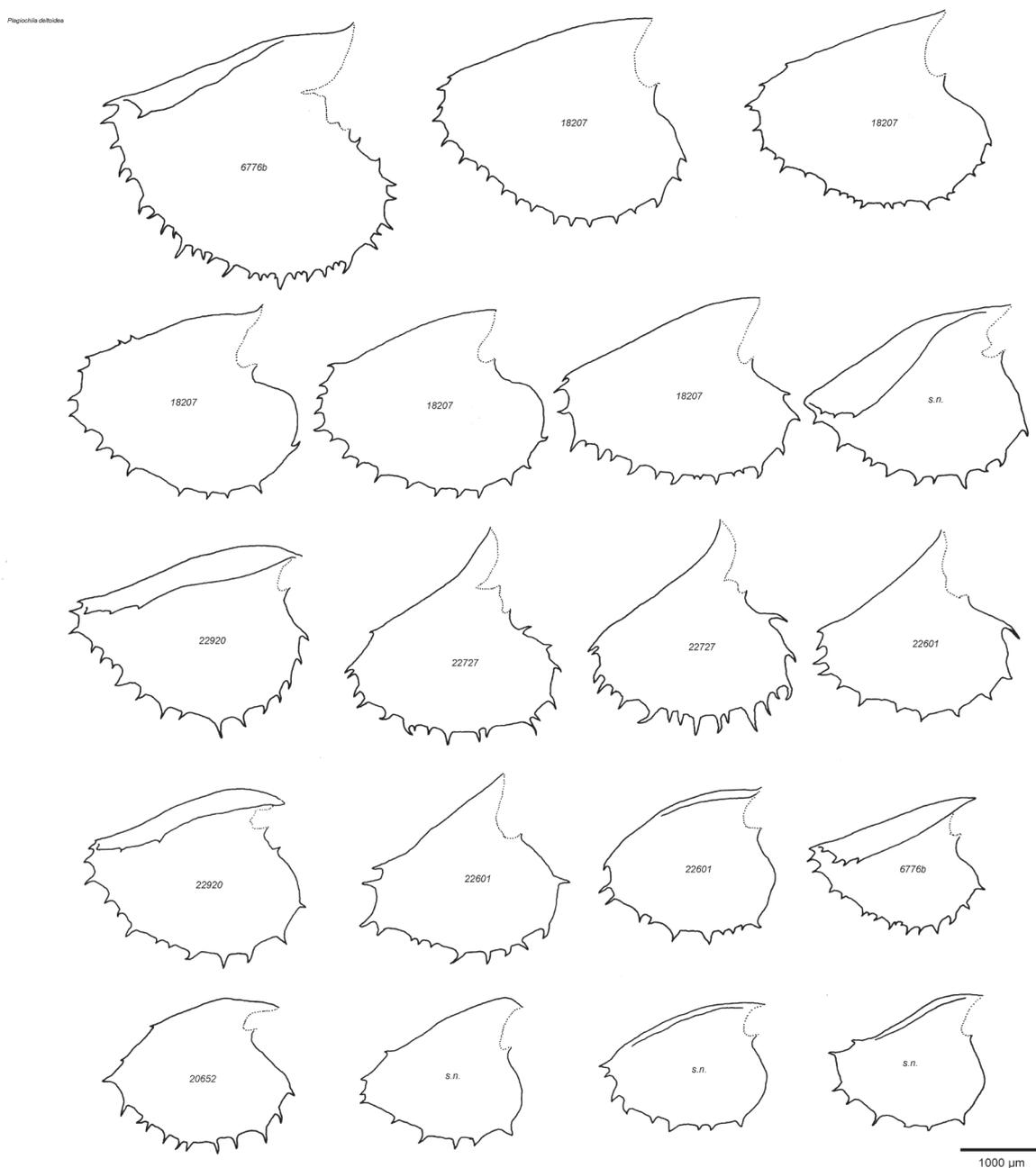
except near base, lateral walls plane; mouth bilabiate, labia curved, each with 11–22(–27) spinose-ciliate teeth, uniseriate in upper half, biseriate in lower half and 3–4 cells wide at base; cells of perianth walls as for female bracts. Fertilised perianth with coelocaula precursor, calyptral perigynium present, archegonia elevated on surface around base. Sporophytes shortly exerted or not, capsule short ellipsoidal, 1.2–1.5 times longer than wide; valves 5 or 6 stratose, epidermal layer cells 9.6–12.8  $\mu\text{m}$  deep, inner layers cells 5.2–7.9  $\mu\text{m}$  deep; inner layer cells elongate, tapering, haphazardly arranged, with 5–9 brown-pigmented semiannular bands on inner cell wall, confluent along the upright cell walls. Spores 11.5–14.3  $\mu\text{m}$  diameter, 2-celled when released from dehisced capsule, with stout echinate ornamentation. Figs 10–12.

*Plagiochila deltoidea*

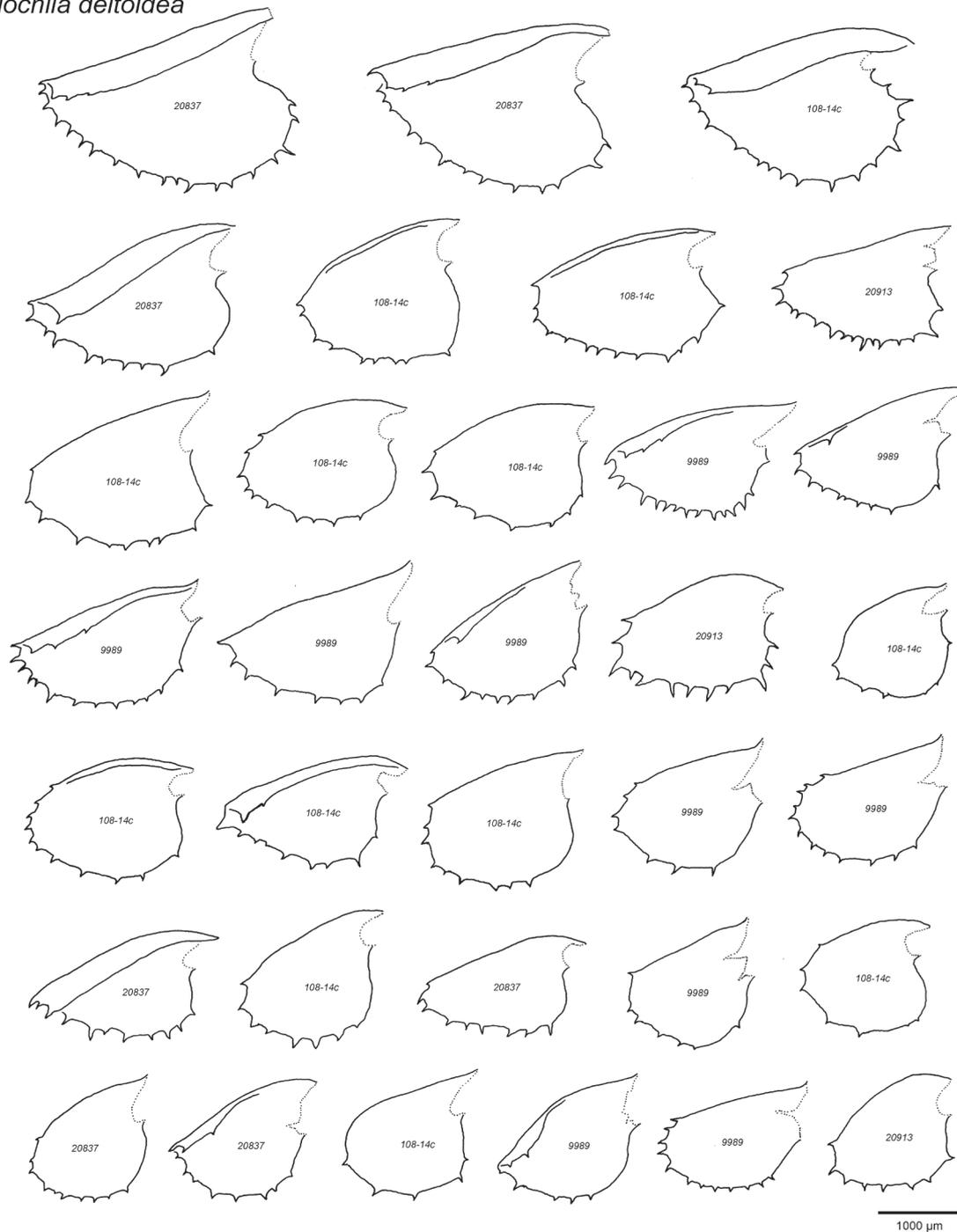


**Fig 10.** *Plagiochila deltoidea* leaves, from individuals corresponding with the type of *Plagiochila axillaris*, J.A. Curnow 3556 (CANB 9408642), J.J. Engel 20706 (F 1141750), J.J. Engel 22601 (F 1141724) and H. Streimann 51257 (CANB 9306707).

**Notes:** Besides the collection of *Monoclea forsteri* Hook. on Cook's second voyage, the first deliberate bryophyte collections from New Zealand were made by Archibald Menzies, surgeon on the H.M.S. *Discovery* which anchored at Dusky Bay from 2 to 22 November 1791 (Engel and Glenn 2008). Many new species were subsequently described from Menzies' collections. *Plagiochila deltoidea* Lindenb. was based on an unlikely assemblage of collections from Dusky Bay, Tasmania (collected by Fraser), and Barbados (Lindenberg 1843). Lindenberg made two observations. Firstly he compared *P. deltoidea* with *P. corrugata* (Nees) Nees & Mont., *P. renitens* (Nees) Lindenb., and *P. retrospectans* Lindenb., and gave distinguishing features for each. Secondly, he noted that the specimen from Van Diemen's Land (Tasmania) in herb. Hooker had leaves with minute denticulate teeth, and commented that another plant from Van Diemen's Land collected by Labillardière and held under the name *P. ramosissima* (Hook.) Lindenb. in herb. Montagne, had smaller stature, leaves less evidently secund, and leaf form approaching *P. ramosissima* and *P. abietina* (Nees) Nees & Mont. but differing in the widely spaced branches.



**Fig 11.** *Plagiochila deltoidea* leaves, from individuals corresponding with the type of *Plagiochila deltoidea*, M.A.M. Renner 6776b (NSW 899342), J.J. Engel 18207 (F 1141063), J.J. Engel 20652 (F 1141748); J.J. Engel 22601 (F 1141724), J.J. Engel 22727 (F 1141080), J.J. Engel 22920 (F 1140885), and J.E. Braggins s.n. (AK 287128).

*Plagiochila deltoidea*

**Fig 12.** *Plagiochila deltoidea* leaves, from individuals corresponding with a smaller unnamed northern coastal form, J.J. Engel 20837 (F 1141749), J.J. Engel 20913 (F 1141788), R.E. Beever & J.E. Beever 108-14c (AK 298125), and P.J. de Lange 9989 & M.A.M. Renner (AK 327793).

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

*Plagiochila deltoidea* was not listed by Hooker and Taylor (1844) probably because they had neither seen specimens nor Lindenberg's publication. Mitten (1860) listed *P. deltoidea* in Hooker's Flora of Tasmania, citing the collection by Labillardière from Van Diemen's Land as the type element, in contrast to Gottsche *et al.* (1845).

Bastow (1887) followed Mitten, again citing the very fine large plant collected by Labillardière. Stephani (1906) reported *P. deltoidea* for Tasmania, and eastern Australia, again citing the collection by Labillardière, and others by Weymouth and von Müller. He stated that *P. deltoidea* was probably not in New Zealand, where it had been confused with a plant Stephani described as *P. howeana* Steph. Stephani did not identify specific gatherings in the protologue of *P. howeana* but stated, somewhat dismissively, ‘New Zealand, ubique communis’.

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

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

For Australia, Inoue (1986) noted that *Plagiochila deltoidea* was reportedly rare on the Australian mainland, even though it had ‘long been known’ from Tasmania (Inoue 1986). Only one specimen was cited by Inoue (1986) from mainland Australia, collected at Gloucester Tops by Heinar Streimann. McCarthy (2006) accepted *P. deltoidea* for all eastern states and territories based on determinations on specimens in Australian herbaria.

So (2001) broadened the circumscription of *P. deltoidea* to include plants with terminal *Frullania*-type vegetative branching and toothed male bracts when she placed *Plagiochila hartziana* Pearson, with a Tasmanian type, into synonymy of *P. deltoidea*. Engel and Merrill (2010) made no mention of this synonymy when they designated the male plants in the New Zealand material collected by Menzies and held in Vienna (W) as the lectotype of *P. deltoidea*. The identity of *P. deltoidea* in New Zealand had been well established, and was ‘no longer in question’ at the time of Engel and Merrill’s study (Engel and Merrill 2010 p. 505). As circumscribed by Engel and Merrill (2010) *Plagiochila deltoidea* was distinct among Australasian species in its entire male bract lobes, usually solitary male branches, complete absence of terminal branching, and triangular teeth on the leaf margins and perianth mouth, making the species relatively easy to identify in both herbarium and field.

*Plagiochila deltoidea* var. *densa* was described for plants with smaller median leaf cells and densely areolate leaves, but these characters are variable within the *P. deltoidea* complex, particularly leaf cell size.

A recent molecular study (Renner *et al.* 2017a) resolved *P. deltoidea* as circumscribed by So (2001) polyphyletic, with one lineage in sect. *Austrocaules* (incorrectly called sect. *Fragmentissimae* (Inoue & R.M.Schust.) R.M.Schust.), the other in sect. *Belangerianae* Carl, among species of the *P. fasciculata* Lindenb. complex. Individuals of the latter corresponded with *P. hartziana*.

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

*Plagiochila deltoidea* and *P. strombifolia* have been confused from the time *P. deltoidea* was first described. Differences between the two species were elucidated by Inoue and Schuster (1971), who concluded that the species were easily separated by 1) the more numerous narrow-based, usually shorter, fine, sometimes aciculate marginal teeth possessing an elongated terminal cell in *P. strombifolia*; 2) leaves longer than wide in *P. strombifolia* (Fig. 27); 3) the basal leaf cells more elongate in *P. deltoidea*; 4) the homogeneous oil-bodies of *P. strombifolia*; and 5) male branching by *Frullania*-type branches in *P. strombifolia*. All five of these characters successfully separate these two species, in addition to the presence of ventral-intercalary stolon branching in *P. deltoidea* versus lateral-intercalary stolon production in *P. strombifolia*.

**Variation:** Within *P. deltoidea* there is variation in the stature of male plants. Most male plants are smaller than female plants, but some collections (e.g. F 1140885 and F 1141063) are of male plants as large and robust as females. Paraphyllia may occur on the dorsal stem surface preceding gynoeceium formation, as in AK 349209. Female bracts exhibit variation in size and dentition that may cause confusion. Usually leaves and bracts increase in size toward the gynoeceium, so that the female bracts are the largest ‘leaves’ on the shoot. In some instances though, the female bracts closest to the gynoeceium are around half the area of the previous leaf pair, which are the largest. The dentition of these half-sized bracts is particularly coarse, thus their overall appearance is rather different from normal bracts. Variation in bract stature can be observed within individuals. There is also variation in the size and number of teeth on perianth labia, with one specimen (F 1141748) having as many as 28 narrow triangular teeth on each labium. More typical specimens have fewer, larger teeth that are often curved.

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

Leaf cell size is variable within *Plagiochila deltoidea*, and was the basis for the recognition of *P. deltoidea* var. *densa* J.J.Engel & G.L.Merr., whose medial cells are smaller than the typical variety. My counts of cell size did not recover the same range of variation within *P. deltoidea* as reported by Engel and Merrill (2010a). This may be due to different interpretations of ‘medial’, which may have resulted in measurements made closer to or further from the leaf apex than in Engel and Merrill (2010a), but I measured 270 medial leaf cells from 16 specimens and on such a sample a generalizable distinction, if such exists, should have manifested. It did not.

**Distribution and Ecology:** *Plagiochila deltoidea* is endemic to New Zealand, where it occurs from the Auckland Region south through the middle and lower North Island, and throughout the South Island. *Plagiochila deltoidea* grows in *Nothofagus* forests and podocarp-broadleaf forests, within which it occupies a wide variety of microsites, including tree trunks, tree branches, soil on banks of mossy streamsides, raised areas on the forest floor, and within bryophyte turfs on steep slopes.

*Plagiochila deltoidea* has been widely reported from Tasmania, all reports are based on misidentifications of other species, primarily *P. strombifolia*, but also *P. fasciculata* and *P. hartziiana*.

Inoue (1986) reported one specimen of *P. deltoidea* from mainland Australia, collected from the Gloucester Tops (*Streimann 1547*); this specimen has both *Frullania*-type vegetative branching and stolons originating by lateral-intercalary branching which, together with leaf shape and dentition including the strong U-shaped stem insertion line and decurrent wing on the ventral stem insertion, make this plant *P. fasciculata*.

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

The second point is no easier, except that if the specimen in STR is not part of the original material then it is ineligible to serve as a lectotype. In herb. Lindenberg in Vienna there are two specimens from Dusky Bay bearing Hooker numbers 47 and 54 respectively, which were likely collected by Menzies in 1791 (Engel and Merrill 2010a). These comprise part of the original material and indicate that Dusky Bay plants were stored as different specimens, of which 54 includes male and 47 female plants. Was the single sterile shoot in STR derived from one of these specimens or another portion of the Dusky Bay material of *P. deltoidea*? Article 9.3(2)

of the Melbourne code (McNeill *et al.* 2012) makes clear that all duplicates of syntype specimens are part of the original material, even if they were not seen by the describing author. Lindenberg did not cite a collector of New Zealand material, only the locality ‘Dusky Bay’. Both Inoue and Schuster (1971) and Engel and Merrill (2010a) inferred that their respective lectotypes were collected by Menzies. The STR specimen bears the same evidence as those in W for supporting its inclusion within the original material.

Engel and Merrill (2010a) made no mention of Inoue and Schuster’s (1971) lectotypification, except to note that ‘until now the species has not been evaluated with reference to the original material studied by Lindenberg (1839-1843)’ (Engel and Merrill 2010a p. 505). This statement implies, but does not directly assert, that Inoue and Schuster’s (1971) lectotypification should not be accepted because the specimen in STR is not an isosyntype.

There are few early collecting events at Dusky Bay. Subsequent to Menzies in 1791, Lyall collected at Dusky Bay between 1847 and 1851 when he served as surgeon Naturalist on *HMS Acheron* (Engel and Glennly 2008). This implies that only Menzies’ gatherings were available from Dusky Bay when *P. deltoidea* was described; they were widely distributed by Hooker. The replication of locality information, absence of collector, proximity, and content (specimens in W and STR contain the same entity) are all consistent with the STR specimen being a duplicate from one of the W specimens or another portion of the original material. It is difficult to envisage how the specimen from Dusky Bay in STR is not part of the original material, if specimens from Dusky Bay in herb. Lindenberg in W are.

If both the STR and W specimens are part of the original material of *P. deltoidea* (Article 9.3) and Inoue and Schuster’s statement “in herb. Lindenberg” is considered a negligible error then Inoue and Schuster’s (1971) lectotypification must be followed (Article 9.19), because their lectotypification was clear and direct (Article 7.10). There is no provision for rejecting a lectotype because another better, more representative, or ideal specimen is available. Indeed, the nomenclatural type is not necessarily the most typical or representative element of a taxon (Article 7.2). However, despite perceived or real issues with the lectotypifications, application of the name *P. deltoidea* will not change regardless of which lectotype is accepted, because both STRAS and W specimens contain the same entity, whose agreement with the protologue (Article 9.19b) was already established by Engel and Merrill (2010a).

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

I have not seen the lectotype of *P. howeana* designated by Inoue and Schuster (1971). However, in Genève there are two syntypes of *P. howeana*: Nova Zelandia, ins. merid. Waimate (Canterbury) damp bush, May 1901, T.W.N. Beckett, ex herb. Levier 2792, (G 00121950!); and Nova Zelandia, ins. merid. Waimate (Canterbury) damp bush, May 1898, T.W.N. Beckett, ex herb. Levier 1183, (G 00121967!), both contain plants with large, succubously inserted, sparsely and evenly toothed leaves with a low decurrent wing on the ventral stem insertion; and male branches terminal and single. Critical features described by Stephani included the large leaf size, 4 mm long, the ampliate leaf base, and the coarsely toothed perianth mouth. Whether the syntypes in G match the protologue better than the lectotype designated by Inoue and Schuster (1971) is an issue that should be addressed on the basis of a simultaneous and critical appraisal of all relevant syntype material.

**Representative specimens examined: New Zealand: North Island:** Te Pahi, Radar Bush, 34°28'03"S 173°51'15"E, 160 m, 19 Sep. 2011, *P.J. de Lange 9989 & M.A.M. Renner* (AK 327793); Radar Bush, WSW of Cape Reinga, S of Mt Te Pahi, 34°28'S 172°46'E, 100 m, 6 Feb. 1995, *J.J. Engel 20837* (F 1141749); Northern edge of Herekino Forest S of quarry, Kiwanis Reserve, junction of Okahu Stream and unnamed stream, c 5 miles S of Kaitaia, 35°10'S 173°16'E, 60-80 m, 7 Feb. 1995, *J.J. Engel 20913* (F 1141788); Waima Forest, Hauturu Highpoint Track in vicinity of summit area of Hauturu Trig, off Waiotemarama Track, 650-680 m, 35°31'S 173°28'E, 23 Feb. 1997, *J.J. Engel 22601* (F 1141724); Lake Waikaremoana, 10 Feb 1936, *E.A. Hodgson* (NSW); Whirinaki Forest Park, Waterfall Loop track near Whirinaki River, SSW of Minginui, 38°41'S 176°43'E, 380 m, 30 Jan 1995, *J.J. Engel 20706* (F 1141750); Urewera National Park, crest trail from Highway 38 towards Whakataka summit, N of northern extremity of Lake Waikaremoana, 38°42'S 177°03'E, 930-1030 m, 29 Jan 1995, *J.J. Engel 20652* (F 1141748); Urewera National Park, Panekiri Range, summit area of Pukenui in vicinity of Punekiri Bluff, S of Lake Waikaremoana, 38°47'S 177°04'E, 1180 m, 24 Mar 1997, *J.J. Engel 23325* (F 1141064); Urewera National Park, Huiarau Range, summit area of Te Rangaakapua, 38°33'S 177°13'E, 1265-1320 m, 25 Mar 1997, *J.J. Engel 23428* (F 1141729); Tongariro National Park, Central Plateau, Ruapehu, Mangawhero River catchment, Ohakune Mountain Road, 1048 m, 23 Nov 2013, *M.A.M. Renner 6780* (NSW 899341); *ibid*, *M.A.M. Renner 6776b* (NSW 899342); Tongariro National Park, Mt Ruapehu, Ohakune Mountain Road, lower

end of Mangawhero Track on east side of road, 39°24'02"S 175°25'16"E, 650 m, 23 Nov 2013, *J.E. Braggins* 13/234D (AK 349209); **South Island:** North West Nelson Ecological Region, Arthur Ecological District, start of track to Harwoods Hole, 40°56'37"S 172°53'22"E, 740 m, 30 Oct 2004, *J.E. Braggins* 04/092A (AK 290693); Richmond Ecological Reserve, Pelorus Ecological District, Brown River Reserve on SH6 north of Rai Valley township, 41°12'37"S 173°34'46"E, 60 m, 28 Oct. 2004, *J.E. Braggins* 04/055C (AK 290978); Shenandoah Valley, 1 km N of Shenandoah Saddle, 32 km SSW of Murchison, 42°01'S 172°14'E, 680 m, 3 Feb. 1993, *H. Streimann* 51257 (CANB 9306707); North Westland Ecological Region, Blackball Ecological District, Sewell Peak, in *Nothofagus* forest near top of road to first peak, 42°24'32"S 171°20'24"E, 780 m, 6 Dec 2000, *J.E. Braggins s.n.* (AK 287128); Nova Zelandia, ins. merid. Westland, Kelly's Range, Bruce's Creek, 30 Jan 1903, *T.W.N. Beckett*, det. F. Stephani n.4348 (M); Nelson Province, Nelson Lakes National Park, off Lakehead Track near junction with southern end of Loop Track, NE of Lake Rotoiti, SSE of St. Arnaud, 41°49'S 172°51'E, 630 m, 1 Mar 1997, *J.J. Engel* 22727 (F 1141080); Waimate (Canterbury) damp bush, May 1901, *T.W.N. Beckett*, ex herb. Levier 2792 (G 0012195, remaining syntype of *P. howeana*); Waimate (Canterbury) damp bush, May 1898, *T.W.N. Beckett*, ex herb. Levier 1183 (G 00121967, remaining syntype of *P. howeana*); Arthurs Pass National Park, Bridal Veil Track, E side of Bealey River and just N of town of Arthur's Pass, 42°56'S 171°33'E, 760–825 m, 7 Mar 1997, *J.J. Engel* 22920 (F 1140885); Mt Cook National Park, Governors Bush, SW of town of Mt Cook, 43°44'S 170°05'E, 760–800 m, 1 Jan 1983, *J.J. Engel* 18207 (F 1141063); Limestone Cavern track, upper reaches of a tributary of Pig Creek, 10 km NW of Monowai Power House, 45°45'S 167°30'E, 335 m, 18 Nov. 1990, *J.A. Curnow* 3556 (CANB 9408642). **Chatham Islands:** Rekohu, Alfred Preece farm, east of Rangaika Reserve, 44°04'04"S 176°25'00"W, 6 Jan 2007, *R.E. Beever & J.E. Beever* 108-14c (AK 298125).

Representative misidentified Australian specimens examined:

*Plagiochila fasciculata*

New South Wales: Gloucester Tops, 42 km WSW of Gloucester, 32°04'S 151°36'E, 25 Jan 1975, *H. Streimann* 1547 (CANB 56709); Tasmania: Derby, 41°09'S 147°48'E, 330 m, 13 Nov 1913, *W.A. Weymouth* 1550 (NSW 763464); Tasman Peninsula, Wellard River, 42°56'S 147°52'E, 6 Feb 1899, *W.A. Weymouth* 828 (NSW 763467); Mt Wellington, Deep Creek, 42°56'S 147°14'E, 26 Dec 1887; *W.A. Weymouth*, (HO 87668); Arthur Land District, along Serpentine River less than 0.5 km below Serpentine Dam of Lake Pedder, 300 m, 42°46'23"S 145°58'45"E, 5 Dec 2007, *J.R. Shevock* 31417 (HO 566199); North West, Black Bluff, Winter Brook, 920 m, 41°27'S 145°58'E, 3 May 1999, *A. Moscal* 30549 (HO 577102).

*Plagiochila strombifolia*

Victoria: Coast Range Road, 18 km SSE of Bendoc, 37°17'S 148°58'E, 900 m, 10 Apr 1986, *J.A. Curnow* 775 (CANB 781856); Tasmania: Tasman Peninsula, Wellard Rivulet, 42°56'S 147°52'E, 6 Feb. 1899, *W.A. Weymouth* 828 (CANB 781854); Mt Victoria, Una forest, plateau, 2000 ft, 41°23'S 147°50'E, 8 Nov 1913, *W.A. Weymouth* 1566 (HO 87671, CANB 781855); West Coast, Strahan, 42°09'S 145°19'E, 21 Oct 1893, *W.A. Weymouth* 175 (HO 87663); Mt Wellington, Deep Creek track, 42°56'S 147°14'E, 23 Jan 1899, *W.A. Weymouth* 543/4 (HO 87669); Central Highlands, Netherby Plain, 9 km south of Waratah, 41°32'S 145°33'E, 17 Dec 1986, *A. Moscal* 13674 (HO 103118); Mt Wellington, Long Creek, 480 m, 42°56'S 147°14'E, 23 Jan 1899, *W.A. Weymouth* 317 (HO 305121).

*Plagiochila baylisii* Inoue & R.M.Schust.

Tasmania: Deadmans Bay, 15 m, 43°32'S 146°30'E, 21 Jan 1987, *A. Moscal* 14263 (CANB 781853).

*Plagiochila retrospectans*

Tasmania: East Coast, Tatnells Creek, 3.5 km east of Taranna, 43°03'S 147°55'E, 21 Jan 1999, *A. Moscal* 30304 (HO 577101).

*Plagiochila circinalis* (Lehm. & Lindenb.) Lindenb.

Tasmania: South West, Huon River, 1.25 SSE of Scotts Peak Dam, 290 m, 43°02'S 146°18'E, 17 Feb 1996, *A. Moscal* 28144A (HO 577097).

**Notes on other species of sect. *Austrocales***

***Plagiochila vitilevuana* (Schiffn.) M.A.M.Renner comb. et stat. nov.**

Basionym: *Plagiochila blepharophora* var. *vitilevuana* Schiffn., Forschungsreise S.M.S. "Gazelle". 4, Botanik: 6 (1889) [1890]

*Type citation:* Fidji-insulae, Vitilevu, Reva superior in silva Montana (30. 11. 75) c. perianth.

*Type:* Fidji-Insula, Vitilevu, Obere Rewa, 30 Nov 1875, Gazellen Exped. *Dr Naumann*, (FH!)

**Notes:** Inoue (1981) placed *Plagiochila blepharophora* var. *vitilevuana* in synonymy of *P. vitiensis*, however the plant in the type of *P. blepharophora* var. *vitilevuana* has stolons originating by ventral-intercalary branching. As this character is confined to *Plagiochila* sect. *Austrocaules* the plant belongs here, not in sect. *Cucullatae* alongside *P. vitiensis* and *P. blepharophora*, species with lateral-intercalary stolon branching. Because the retention of *P. blepharophora* var. *vitilevuana* at that rank renders *P. blepharophora* polyphyletic, I propose a new combination at species rank here.

***Plagiochila praecipua* M.A.M.Renner nom. nov.**

Basionym: *Plagiochila gymnoclada* var. *major* Schiffn., Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien. Mathematisch-Naturwissenschaftliche Klasse 70: 166 (1900)

*Type citation:* Sumatra occid. in monte Singalang, in silvis primaevae ad latus austro-orient. ad arbores. Regio nubium, alt. 2360 m s. m. – 25 7. 1894 (pl. male) (No. 840). Ibidem: Alt. 2400 m s. m. – 25 7. 1894 (c. per. et male) (No. 841).

*Type:* Sumatra occid. in monte Singalang, in silvis primaevae ad latus austro-orient. ad arbores, regio nubium, 2360 m, 25 Jul 1894, V. Schiffner *Iter Indicum 1893/94 No. 840*, ex Herb Delessert (lectotype designated by Inoue (1984): G 00128882!)

A new combination for *P. gymnoclada* var. *major* at species rank is blocked by *Plagiochila major* S.W.Arnell. Illustrated Moss Flora of Fennoscandia. I. Hepaticae: 162. 1956.

**Etymology:** chief, in reference to the varietal epithet of the basionym.

**Notes:** The plant in the lectotype specimen of *P. gymnoclada* var. *major* has stolons originating by ventral-intercalary branching, so it is also member of this lineage. Another variety, *P. gymnoclada* var. *longifolia* Schiffn. has stolons originating by lateral-intercalary branching, suggesting these two varieties of *P. gymnoclada* belong to different sections, and making the species *P. gymnoclada* polyphyletic as currently circumscribed. The polyphyly of *P. gymnoclada* is resolved in part here by the proposal of new combinations for Schiffner's varieties at species level.

***Plagiochila schiffneriana* M.A.M.Renner nom. nov.**

Basionym: *Plagiochila gymnoclada* var. *longifolia* Schiffn., Die Hepaticae der Flora von Buitenzorg: 119 (1900)

*Type citation:* n.v.

*Type:* Java, Prov. Preanger, in decliv. austral. montis Pangerango: in silvis primaevae supra locum dictum "Tjiburrum", region nubium, ad arbores, 1690 m, 2 May 1894, V. Schiffner *Iter Indicum 1893/1894 No. 839* (G 00128879!)

A new combination at species rank for *P. gymnoclada* var. *longifolia* is blocked by *Plagiochila longifolia* Steph., Species Hepaticarum 6: 178 (1921).

**Etymology:** dedicated to Austrian Bryologist Victor Felix Schiffner (1862–1944), collector of the type and author of the replaced basionym.

**Notes:** The plant in this type specimen has stolons originating by lateral-intercalary branching, so is not a member of sect. *Austrocaules* but its exact affinities are unclear.

***Plagiochila* sect. *Arrectae* Carl, Ann. Bryol. Suppl. 2: 52 (1931)**

*Type species:* *Plagiochila arrecta* Gottsche (= *P. bifaria* (Sw.) Lindenb.)

One species of sect. *Arrectae* occurs in Australasia, *P. spinulosa*, which was long known in New Zealand by the name *Plagiochila caducifolia* Inoue & R.M.Schust. (Renner *et al.* 2017b).

***Plagiochila spinulosa* (Dicks.) Dumort., Recueil d'Observations sur les Jungermanniacées: 15 (1835)**

Basionym: *Jungermannia spinulosa* Dicks. Fasciculus Plantarum Cryptogamicarum Britanniae 2: 14 (1790)

*Type citation:* Scotland "in alpibus Scotiis". Wales. Snowdon.

*Type:* n.v.

=*Plagiochila caducifolia* Inoue et R.M.Schust., Journal of the Hattori Botanical Laboratory 34: 71 (1971)

*Type citation:* New Zealand: South Island: Fiordland Natl. Park, trail from Eglinton-Hollyford Divide to Lake Howden, in *Nothofagus menziesii* forest, RMS 51964 (MASS; duplicate in TNS).

*Type: n.v.*

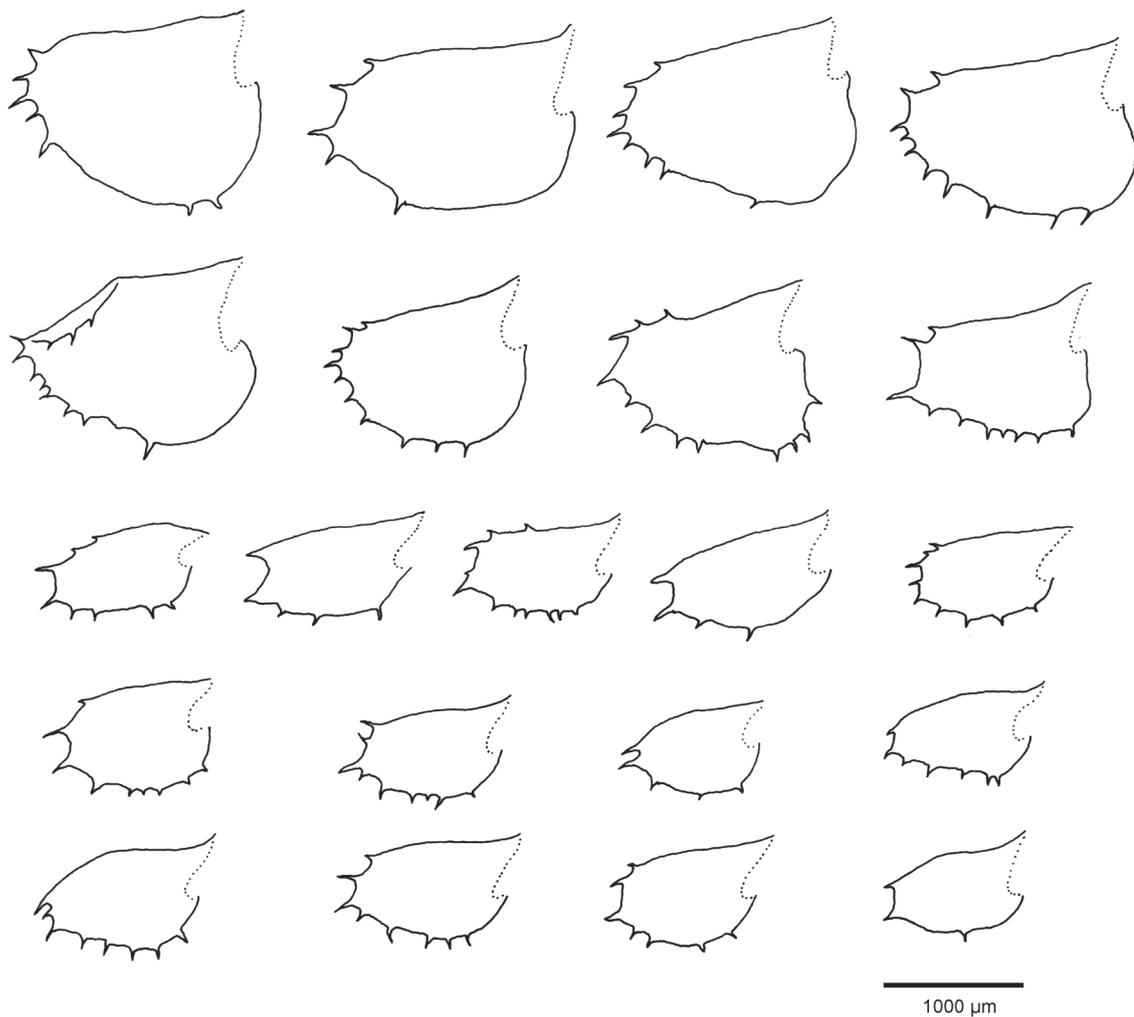
**Etymology:** in reference to the teeth on the leaf margin.

Description [from New Zealand material]: Plants with branched sprawling leafy shoots forming loose, untidy, predominantly pure turfs; bronze-green to dull tan, shoot systems without fixed hierarchical structure, while stolons and leafy shoots are sharply differentiated they are completely intermixed; leafy shoots to 50 mm long, dimorphic, stature reduced at base close to stolons; flagellae absent; primary shoots 1510–2536  $\mu\text{m}$  wide, secondary shoots smaller. Branching within stolons and leafy shoots exclusively lateral-intercalary. Stems of stolons and primary shoots in leaf sectors reddish-brown, to 220  $\mu\text{m}$  diameter, transversely elliptic, surfaces smooth; cortical cells in 2 layers dorsally and ventrally, cortical cells smaller than medullar, with continuous brown thickenings on cell walls, medullar cell walls brown-pigmented, with small concave trigones at cell junctions and thin continuous thickening on medial walls. Rhizoids on stolons scattered, produced from lateral and ventral merophytes. Leaves on leafy shoots remote to contiguous, obliquely orientated, ovate to deltoid, 775–1940  $\mu\text{m}$  long  $\times$  486–1515  $\mu\text{m}$  wide, dorsal margin shallowly curved or in large leaves straight, entire; when dry antical and postical margin in-rolled along the long axis; two teeth prominent at the leaf apex, both 5–8 cells broad at base, narrow triangular, straight, uniseriate in upper part for around four cells, capped by a single acicular, hyaline cell; ventral margin straight or weakly curved in outer third, broadly curved and ampliate in basal two thirds, with 1–12 teeth on postical margin, variable in stature, from two or three cells only with a hyaline acicular apical cell hyaline up to 33  $\mu\text{m}$  long, to four cells broad at the base and 7 or 8 cells long, uniseriate for most of the length, spacing between teeth fairly regular; insertion J-shaped, oblique, decurrent dorsally, with a low wing of tissue extending down the stem; slightly recurved at ventral end, not attaining ventral stem midline leaving, variably along a shoot, one to three cortical cell rows leaf-free, attaining the dorsal stem midline, stem visible between leaves. Marginal cells quadrate to rectangular, 14.8–16.7  $\mu\text{m}$  long  $\times$  8.0–13.1  $\mu\text{m}$  wide; cells in median portion more or less isodiametric to elliptic, 16.2–21.8  $\mu\text{m}$  long  $\times$  11.5–16.9  $\mu\text{m}$  wide, walls with discrete cordate to convex trigones, medial wall thickenings absent; cells in leaf base rectangular to long rectangular, 31.5–42.0  $\mu\text{m}$  long  $\times$  10.5–12.9  $\mu\text{m}$  wide, trigones bulging, low medial wall thickenings present, occasionally confluent with adjacent trigones; leaves on stolons bifid, weakly spreading, ovate. Cell surfaces striolate in basal cells, typically pronounced on smaller leaves and faint on large leaves, grading to faintly papillose on medial cell surfaces. Oil-bodies (4)5–7(8) per cell, tan pigmented, ovoid, granular, arranged in a loose submarginal ring. Underleaves absent or present, narrow triangular up to four cells broad at base and six cell tiers high. Asexual reproduction by caducous leaves that fragment in entirety. Sexual reproductive structures not seen. Fig. 13.

**Recognition:** In New Zealand, *Plagiochila spinulosa* can be recognised by the combination of 1) caducous leaves which fragment from the stem in their entirety, 2) leaves with a bifid apex and smaller spinulose teeth on the margin, particularly the postical margin, 3) exclusively lateral-intercalary branching, 4) the striolate-papillose leaf cell surface, particularly on the basal leaf cells (Renner *et al.* 2017b). The decurrent wing of leaf tissue extending to the dorsal stem mid-line is an unusual feature among Australasian species.

*Plagiochila spinulosa* could be confused with species of the *P. fasciculata* Lindenb. complex, but differs from all in its lack of terminal *Frullania*-type vegetative branching. *Frullania*-type vegetative branches occur within shoot systems of all species of the *P. fasciculata* complex, either as the dominant branching mode or mixed with lateral-intercalary branching. *Plagiochila spinulosa* is also similar to *P. incurvicolla* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees, but again the latter possesses vegetative *Frullania*-type branches, though these occur infrequently, with lateral-intercalary vegetative branching dominant in this species. No species of the *P. fasciculata* complex nor *P. incurvicolla* have the conspicuously striolate-papillose ornamentation on the basal leaf cell surfaces.

**Distribution and Ecology:** In New Zealand *Plagiochila spinulosa* has been collected at a range of locations in the North and South Island from the Waima Forest in Northland, to Western Nelson and Fiordland in the South Island, in a variety of habitats including low windswept broadleaf forest, tall *Nothofagus* dominated forest, and alpine herbfield. Contrary to statements in Renner *et al.* (2017b) that *P. spinulosa* is restricted in New Zealand to the South Island, it is also known, by one collection, from Northland in the North Island. On the Thousand Acre Plateau, near Matiri, *P. spinulosa* formed a small mass within a sheltered hollow in a steep slope dominated by *Dracophyllum filifolium* Hook.f., *Chionochloa pallens* Zotov, *Oreobolus* R.Br., and *Donatia* J.R.Forst. & G.Forst., and at Bridal Veil Falls and Rainbow skifield, *P. spinulosa* grew as a lithophyte on cliff faces. *Plagiochila spinulosa* is accepted as indigenous to New Zealand despite the striking disjunction in its populations, for reasons outlined in Renner *et al.* (2017b).

*Plagiochila spinulosa*

**Fig 13.** *Plagiochila spinulosa* leaves, all from J.J. Engel 27071B & M.J. von Konrat (F C0311977F).

Specimens examined: **New Zealand: North Island:** Northland, Waima Forest, Hauturu Highpoint track, in vicinity of Hauturu Trig, 35°31'S 173°28'E, 650–680 m, 23 Feb 1997, J.J. Engel 22616 (F 1142109); **South Island:** North West Nelson, upper Burgoo Stream, 41°02'55"S 172°31'08"E, 10 Feb 1988, E.A. Brown 88/144c (AK 327235); North West Nelson, near Salisbury Lodge, rock shelter, 41°10'47"S 172°39'39"E, 1100 m, 4 Feb 1988, E.A. Brown 88/81a (AK 316654); Western Nelson Province, Kahurangi National Park, Matiri Range, Thousand Acres Plateau, 41°37.5'S 172°17.0'E, 1100–1200 m, 22 Feb. 2006, J.J. Engel 27071B & M.J. von Konrat (F C0311977F); Nelson Province, St Arnaud Range, Rainbow skifield just below ski tow area, E of S end of Lake Rotoiti, S of St Arnaud, 41°53'S 172°51'E, 1210 m, 2 Mar 1997, J.J. Engel 22807 (F 1141636); Westland Province, Arthurs Pass National Park, Bridal Veil Track, E side of Bealey River and just N of town of Arthurs Pass, 42°56'S 171°33'E, 760–825 m, 7 Mar 1997, J.J. Engel 22932 (F 1141635); Tributary of Siberia River, opposite Hut, 2500 ft, 17 Jan 1976, J. Child 2889, BM; Routeburn region, Feb 1978, F.J. Newhook (AK 316756); Southland, Fiordland National Park, Moraine Creek, track north of Moraine Creek west of Hollyford River, 44°44'S 168°05'E, 610 m, 16 Mar 1997, J.J. Engel 23234 (F 1141587).

***Plagiochila* sect. *Deflexifoliae*** Carl, Ann. Bryol. Suppl. 2: 139 (1931)

Type: *Plagiochila deflexifolia* Steph. [= *Plagiochila circinalis* (Lehm. & Lindenb.) Lehm.]

Four species of *Plagiochila* sect. *Deflexifolia* occur in southern temperate Australasia, and currently no other species are known to belong to this section. The species of this section have monomorphic shoot systems, exclusively lateral-intercalary vegetative branching, and long, ligulate perianths. Two species have dense paraphyllia on their dorsal stem surfaces.

***Plagiochila circinalis*** (Lehm. & Lindenb.) Lehm. & Lindenb., Species Hepaticarum 5: 124 (1843)

Basionym: *Jungermannia circinalis* Lehm. & Lindenb., Novarum et Minus Cognitarum Stirpium Pugillus 4: 64 (1832)

*Type citation:* in Nova Hollandia.

Type: Nova Hollandia, Fraser, 'Gottsche ipse dedit' ex herb. Stephani (G 026593!) 'Original of Lehmann oda Lindenb., auf Kurt Sprengel's herba (G 026589!) Nova Hollandia, 'Lehm. dedit' (G!) Nova Hollandia, 'Lindenb. dedit, aus Meissner's Herba (G 026587!)

=*Plagiochila decurvifolia* Steph., Bulletin de l'Herbier Boissier, sér. 2 4: 780 (1904) = Species Hepaticarum 2: 457 (1904)

*Type citation:* Tasmania (Oldfield); New Zealand (Kirk, Beckett, Dall)

Type: Tasmania, Oldfield, ex herb. Kew sub *P. retrospectans*, (lectotype designated by Bonner (1962): G 00064159!)

=*Plagiochila deflexifolia* Steph., Species Hepaticarum 6: 145 (1918)

*Type citation:* Tasmania (Weymouth legit)

Type: Australia: Tasmania, Weymouth 1168c (lectotype designated by Bonner (1962): G 00112959! isolectotype: HO 87697!)

=*Plagiochila circinalis* f. *deflexifolia* (Steph.) Inoue et R.M.Schust., Journal of the Hattori Botanical Laboratory 34: 129 (1971)

=*Plagiochila hemicardia* (Hook.f. & Taylor) Taylor & Hook.f. ex Gottsche, Lindenb. et Nees, Synopsis Hepaticarum 5: 626 (1847)

Basionym: *Jungermannia hemicardia* Hook.f. & Taylor, London Journal of Botany 3: 371 (1844)

*Type citation:* Campbell's Island.

Type: New Zealand: Campbell Island, Voyage of H.M. Discovery Ships Erebus and Terror (FH 00284127!)

=*Plagiochila pigmentata* E.A.Hodgs., Records of the Dominion Museum 4: 119 (1962)

*Type citation:* New Zealand, Stewart Island, leg. W.Martin, in hb. Hodgson n.11113

Type: *n.v.*

=*Plagiochila circinalis* f. *pigmentata* (E.A.Hodgs.) Inoue & R.M.Schust., Journal of the Hattori Botanical Laboratory 34: 129 (1971)

=*Plagiochila circinalis* var. *subsimplax* Lindenb., Species Hepaticarum 5: 125 (1843)

*Type citation:* Nova Hollandia, a Fraserso lecta (Herb. Hookeri) ; ... in herb. Willdenow.

Type: *n.v.*

**Notes:** The type of *Plagiochila decurvifolia* comprises several very long shoots, up to 12 cm long, and is fertile, bearing mature perianths and sporophytes. The plant is the same as that in the type of *P. deflexifolia*, but the dentition on the leaf margins is less frequent. All branching in the type of *P. decurvifolia* is lateral-intercalary. Engel and Smith-Merrill (2010a) proposed the same specimen as lectotype of *P. decurvifolia* as did Bonner (1962).

The type of *Plagiochila deflexifolia* has closely spaced (densely imbricate) leaves with strongly recurved margins, an outline that descends to below shoot level at the outer part of the cnemis, whose outline is evenly curved, sinuous postical leaf margin, a decurrent dorsal insertion, and small triangular teeth sometimes. There are no teeth on the dorsal margin at the stem insertion line, but there are several small spinose teeth on the postical margin and at the apex. The leaf cell walls have large nodular trigones. This form is common in Tasmania. The type of *Plagiochila hemicardia* has stolons of lateral-intercalary origin, lateral-intercalary vegetative branching (two seen – no terminal vegetative branches), and aspect agreeing with *P. circinalis*.

**Etymology:** referencing the circinate male branches.

**Description:** Plants with irregularly branched, erect to spreading leafy shoots arising from a creeping basal stolon, stolons arising from other stolons and from leafy shoots by lateral-intercalary branching; forming turfs or short wefts; bronze-green, shoot systems to 70 mm long, monomorphic; shoots 3–4 mm wide, branches arising by lateral-intercalary branching. Stems without lamellae, paraphyllia, or paraphyses; reddish-brown,

in primary shoots to 450 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, reddish-brown fading to yellow on the innermost cortical cell walls, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls beneath with walls thickened but tapering, other walls with distinct triangular trigones and weak continuous thickening over some walls, walls faint yellow pigmented. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots closely imbricate, succubously inserted and transversely orientated, broadly ovate to triangular ovate rotund, 1200–2900 µm long × 1150–2530 µm wide, dorsal margin shallowly curved, usually inrolled, ventral margin ampliate, sometimes undulate; dorsal margin entire or with a few scattered triangular teeth, apex and ventral margins entire or with bearing 0–23 triangular teeth, comprised of 2–6 cells, two cells broad at base, capped by a short triangular cell; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with large strongly nodulose, block-like trigones but not continuously thickened; medial leaf cells quadrate to polyhedral, 15–30 µm long × 15–40 µm wide, walls faint yellow pigmented, with large strongly nodulose, block-like trigones, medial thickenings absent; cells in leaf base long polyhedral, 24–40 µm long × 18–21 µm wide, walls with large strongly nodulose, block-like trigones, medial thickening absent, trigones not confluent. Cell surfaces smooth. Oil-bodies 4–6 per cell, spherical to ellipsoidal, coarsely botryoidal. Underleaves absent. Asexual reproduction absent.

Diocious. Androecia intercalary on short determinate circinate and ventrally secund shoots arising by *Frullania*-type branching, produced singly or in pairs scattered along leafy shoots or in two or more pairs at the shoot apex, never in fascicles, branching within male branches absent, ventral-intercalary and *Frullania*-type branches not associated with male branches; bracts in 5–9 pairs, hyaline, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin entire, with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts unornamented. Gynoecia at apices of shoots; bracts broadly elliptic-ovate, to 4000 µm long and 3100 µm wide, larger than subtending leaves; dorsal margin inrolled, ventral margin sometimes undulate; margins entire or with up to 20 small triangular teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts with or without fertilisation. Perianth oblong, about 4000 µm long and 2500 µm wide at mouth, dorsal and ventral keels with a low wing extending from the base to near the middle of the keel, entire, laterally compressed but with an inflated base, lateral walls plane; labia truncate, with numerous ciliate-dentate teeth comprised uniseriate rows of short rectangular cells. Fig. 14.

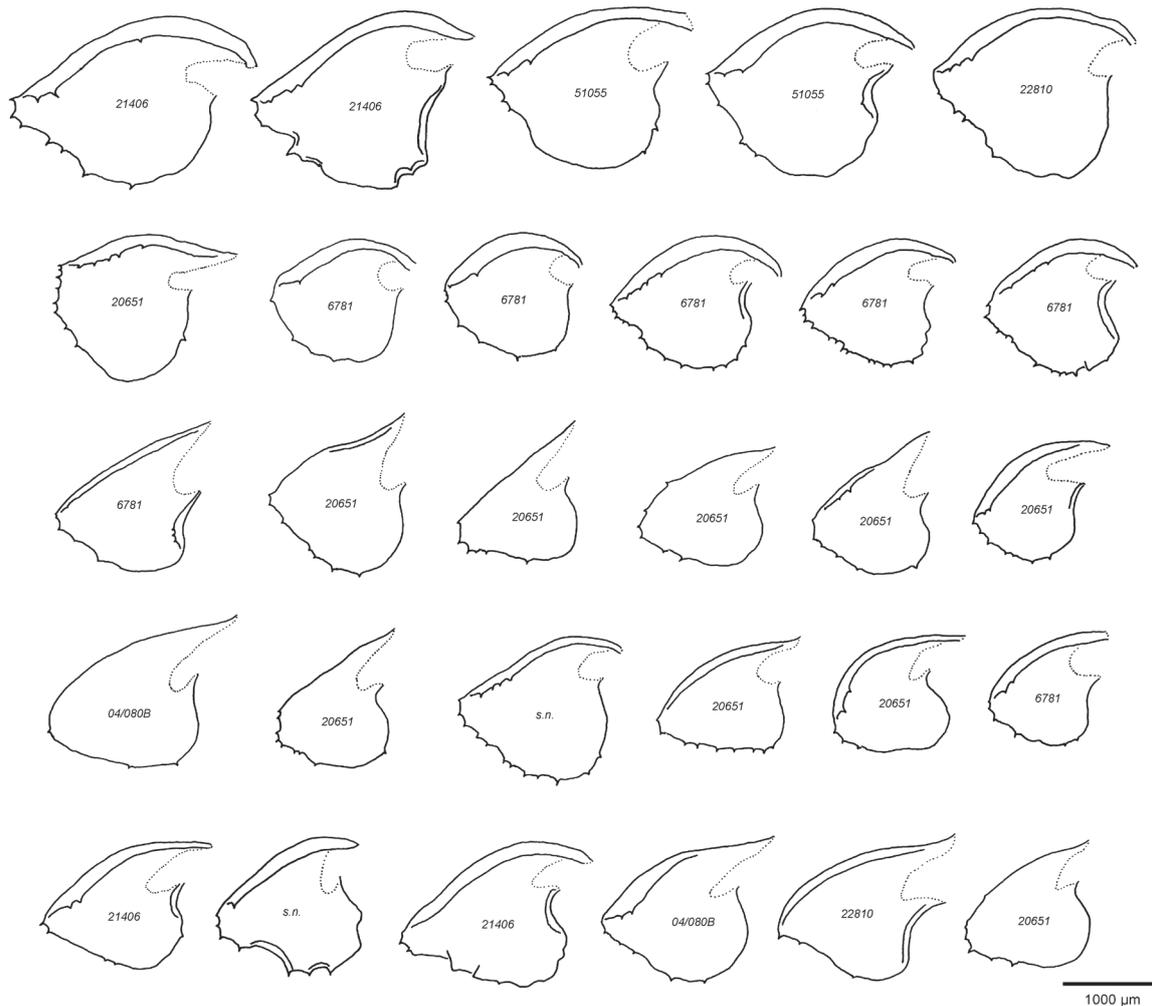
**Recognition:** *Plagiochila circinalis* can be recognized by the combination of imbricate transversely oriented leaves with margins often undulate and either entire or dentate with low triangular teeth, the deep ampliate base, and the tightly inrolled dorsal leaf margin forming a distinct cnemis (Fig. 14); the lateral intercalary stolon origin; the lateral-intercalary vegetative branching; male plants have circinate male branches; female plants have oblong perianths with spinose-dentate mouth.

*Plagiochila circinalis* could be confused with *P. retrospectans* and *P. fuscella*, but *P. retrospectans* and *P. fuscella* both have numerous small triangular teeth comprised of two or three cells around its leaf margin, and the leaves are not tightly inrolled along their dorsal margin. Occasionally *P. fuscella* has entire leaves, in which case it can be distinguished by the thickened cell walls in the marginal leaf cells.

*Plagiochila circinalis* could be confused with *P. baylisii*, but *P. baylisii* has several small sharp triangular teeth at the base of the dorsal leaf margin, often has two teeth prominent at the leaf apex, and has both *Frullania*-type and lateral-intercalary vegetative branching, perianths of *P. baylisii* have a large paraphyllum attached to their dorsal side, and the male branches are straight, not circinate.

*Plagiochila circinalis* could be confused with *P. hartziana*, but *P. hartziana* has two or three teeth at the leaf apex, and no other teeth around the margin of its ovate leaves; the plants are a shiny warm bronze or dark brown colour, vegetative branches are produced by *Frullania*-type and lateral-intercalary branching, and male branches are not circinate.

**Distribution and Ecology:** *Plagiochila circinalis* occurs in Australia and New Zealand. In Australian *P. circinalis* is confined to higher elevation forests in the Great Dividing Range of Victoria. *Plagiochila circinalis* is widespread and common in Tasmania. In New Zealand, *Plagiochila circinalis* is widespread in all three main islands, and on the subantarctic islands. Throughout its distribution *P. circinalis* is an epiphyte on tree trunks, branches, and twigs, or a lithophyte on bedrock and large boulders in forests and alpine shrublands, where it grows in a wide range of forest types and on many different tree and shrubs including species of Mimosaceae, Nothofagaceae, Podocarpaceae, Lauraceae, Atherospermaceae, and with a range of other bryophyte species.

*Plagiochila circinalis*

**Fig 14.** *Plagiochila circinalis* leaves, from J.J. Engel 22810 (F 1141095), J.J. Engel 21406 (F 1141268), J.J. Engel 20651 (F 1141269), M.A.M. Renner 6781 (NSW 903564), H. Streimann 51055 (CANB 9304386), J.E. Braggins s.n. (AK 287614), and J.E. Braggins 04/080B (AK 290529)

A range of specimens from Papua New Guinea have been identified as *P. circinalis* but in every case the identification has been based on error. No genuine specimens of *P. circinalis* are known from Papua New Guinea.

**Representative specimens examined:** **Australia:** **Victoria:** East Gippsland, Errinundra National Park, Mt Ellery, summit area, 37°23'39"S 148°46'47"E, 998 m, 4 Mar 2011, M.A.M. Renner 5199 & E.A. Brown (NSW 893123, MEL 2365550); Eastern Highlands, Mt Boobyalla, c. 1 km from Road 4, 37°42'S 145°42'E, 1100 m, 5 Dec 1992, A.W. Thies 1585 (MEL 242731); **Tasmania:** Midlands, First Falls, Holwell Gorge, c 13 km SW of Beaconsfield, 41°16'38"S 146°45'57"E, 220 m, 28 Feb 1995, P.C. Jobson 3415 (MEL 2293031); Mount Laperouse, Oldfield (G 00113101, G 00113102, G 00113103); SW National Park, Mt Anne, NE ridge 1 km N of summit, 41°56'10"S 146°25'E, 1100 m, 18 Feb 1989, J.R. Croft 10196 & M.M. Richardson (CANB 8904421); Hartz Mountains National Park, 0.5 km from Waratah Lookout downhill along road, 43°11'S 146°46'E, 760 m, 25 Nov 1988, R.W. Purdie 3484A (CANB 9102958); **New Zealand:** leg Dall, (G 00113104); 1891, T. Kirk (G 00113106); **North Island:** Near boundary of Gisbourne and South Auckland Province, Urewera National Park, crest trail from Highway 38 towards Whakataka summit, N of northern extremity of Lake Waikaremoana, 38°42'S 177°03'E, 930-1030 m, 29 Jan 1995, J.J. Engel 20651 (F 1141269); Tongariro National Park, Central Plateau, Ruapehu, Mangawhero River catchment, Ohakune Mountain Road, 39°20'22"S 175°29'01"E, 1048 m, 23 Nov 2013, M.A.M. Renner 6781 (NSW 903564); Kaimanawa Ecological Region and District, Maungaorangi, vicinity of enclosure plot at Oamaru site, 39°05'44"S 176°11'13"E, 1340 m, 27 Nov 2000, J.E. Braggins s.n. (AK 286464); Hawkes Bay, Te Apiti, May 1899, T.W.N. Beckett, ex herb. Levier 1925, (G 00113105); Kaimanawa Ecological Region and District, Kaweka Range, Venison Tops, north end deer exclusion plot site, 39°15'S 176°19'24"E, 1420 m, 4 Jun 2000, J.E. Braggins s.n. (AK 287614); **South Island:** North-west Nelson Ecological

Region, Arthur Ecological District, start of track to Harwoods Hole, 40°56'37"S 172°53'22"E, 740 m, 30 Oct 2004, *J.E. Braggins 04/080B* (AK 290529); Flora Saddle-Mt Arthur Hut track, North West Nelson Forest Reserve, 25 km SSW of Motueka, 41°11'S 172°44'E, 950 m, 29 Jan 1993, *H. Streimann 51055* (CANB 9304386); Nelson Province, Nelson Lakes National Park, Pinchgut Track, W of southern sector of Lake Rotoiti, SSW of St Arnaud, 41°50'S 172°48'E, 1280–1390 m, 19 Feb 1995, *J.J. Engel 21406* (F 1141268); Nelson Province, St Arnaud Range, Rainbow Skifield just below ski tow area, E of S end of Lake Rotoiti, S of St Arnaud, 41°53'S 172°51'E, 1210 m, 2 Mar 1997, *J.J. Engel 22810* (F 1141095); Bealey River, *T.W.N. Beckett* (G 00113107); Rough Gully, Bealey River, May 1889, *T.W.N. Beckett*, ex herb. Levier 722 (G 00113026); Westland, Lake at top of Kelley's Range, 11 May 1889, *T.W.N. Beckett* (G 00113108); Arthur's Pass National Park, Bealey River, off Bealey Valley track, 42°55'S 171°33'E, 830–850 m, 8 Jan 1982, *J.J. Engel 18467* (F 1173544).

NSW 903564.

Representative misidentified specimens examined

Family uncertain

West Irian, Carstensz Mountains, Carstensz Meadow, western side, 3600 m, 10 Dec 1971, *G. Hope CGE H1* (CANB 307237).

*Plagiochila* sp. indet.

West Irian, Carstensz Mountains, Carstensz Meadow, western side, 3580 m, 18 Dec 1971, *G. Hope CGE H5* (CANB 307241);

*Plagiochila hartziana*

Tasmania, old Pipeline track, 42°57'S 147°13'E, 16 Mar 1980, *A. V. Ratkowsky* (HO 304334).

***Plagiochila circumdentata*** Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 778 (1904) = Species Hepaticarum 2: 456 (1904)

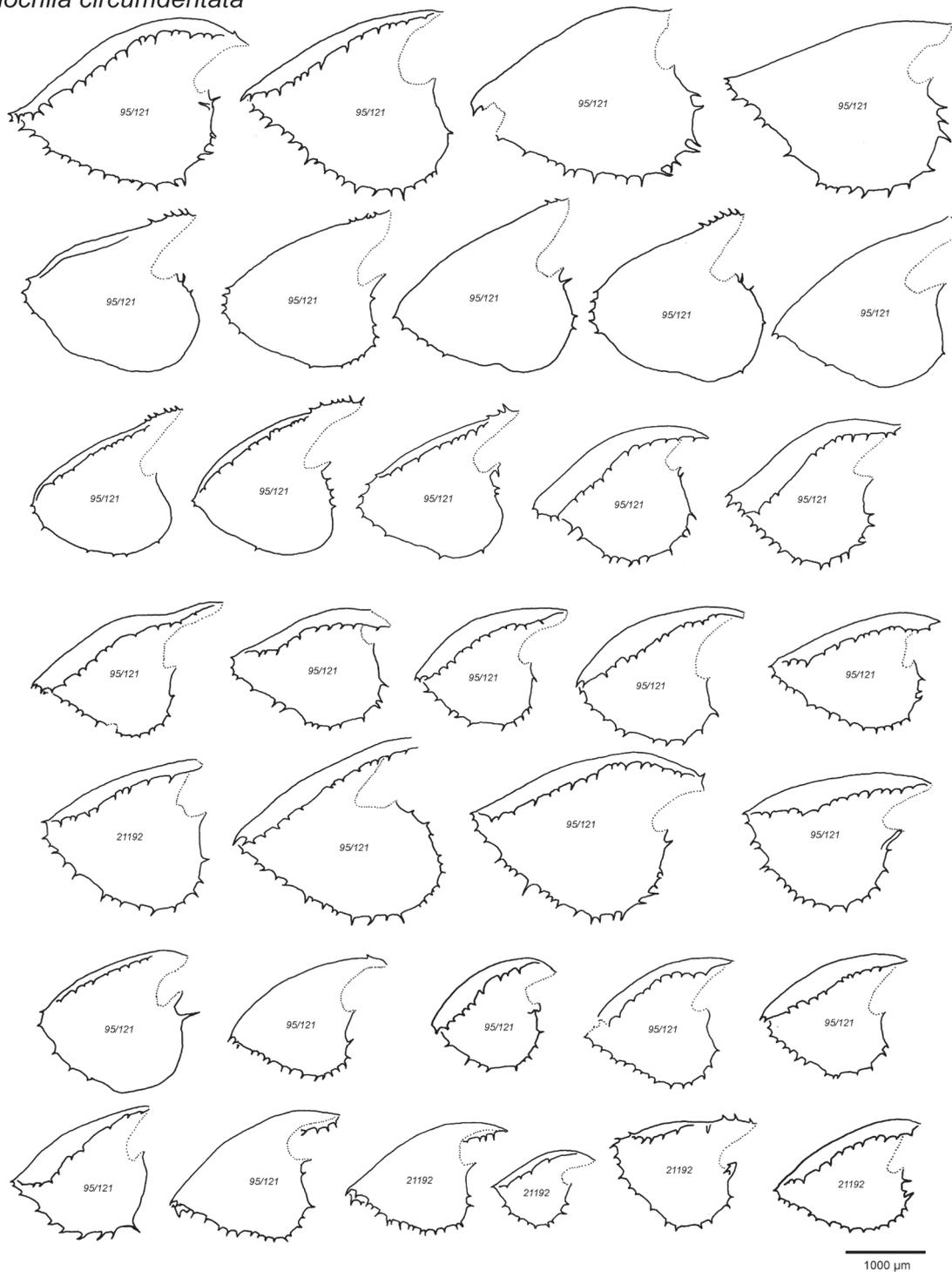
*Type citation:* New Zealand (Beckett)

*Type:* New Zealand, ins. merid., Waimate (Canterbury) on rocks by side of stream, 1 May 1901, *T.W.N. Beckett* 254, (lectotype designated by Bonner (1962): G 00283132!)

**Notes:** The type is a mixed collection of male and female shoots.

**Etymology:** referencing the teeth distributed on all leaf margins.

**Description:** Plants with irregularly branched, erect to spreading leafy shoots arising from a creeping basal stolon, stolons arising from other stolons and from leafy shoots by lateral-intercalary branching; forming turfs; bronze-green, shoot systems to 70 mm long, monomorphic; shoots 4–6 mm wide, branches arising by lateral-intercalary branching. Stems with paraphyllia and short lamellae on their dorsal surface only, single triangular teeth or longer aggregations of two or three triangular teeth, acute, numerous and closely packed among the leaves; paraphyses absent; stem reddish-brown, in primary shoots to 600 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, reddish-brown fading to yellow on the innermost cortical cell walls, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls beneath with walls thickened but tapering, other walls with distinct triangular trigones and weak continuous thickening over some walls, walls faint yellow pigmented. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots imbricate, succubously inserted and orientated, triangular ovate, 1050–2780 µm long × 1010–2100 µm wide, dorsal margin straight, ventral margin ampliate; dorsal margin, apex, and ventral margin all bearing short, acute teeth, 15–45 in total, teeth two or three cells broad at base, uniseriate above, comprised rectangular cells, capped by a slightly longer cell with a narrow apex; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with nodulose trigones but not continuously thickened; medial leaf cells hexagonal to polyhedral, 20–38 µm long × 15–33 µm wide, walls faint yellow pigmented, with nodulose trigones, medial thickenings absent; cells in leaf base long polyhedral, 30–60 µm long × 20–30 µm wide, walls with large nodulose trigones, medial thickening absent, trigones not confluent. Cell surfaces smooth. Oil-bodies 2–6 per cell, ellipsoidal, botryoidal. Underleaves absent. Asexual reproduction absent.

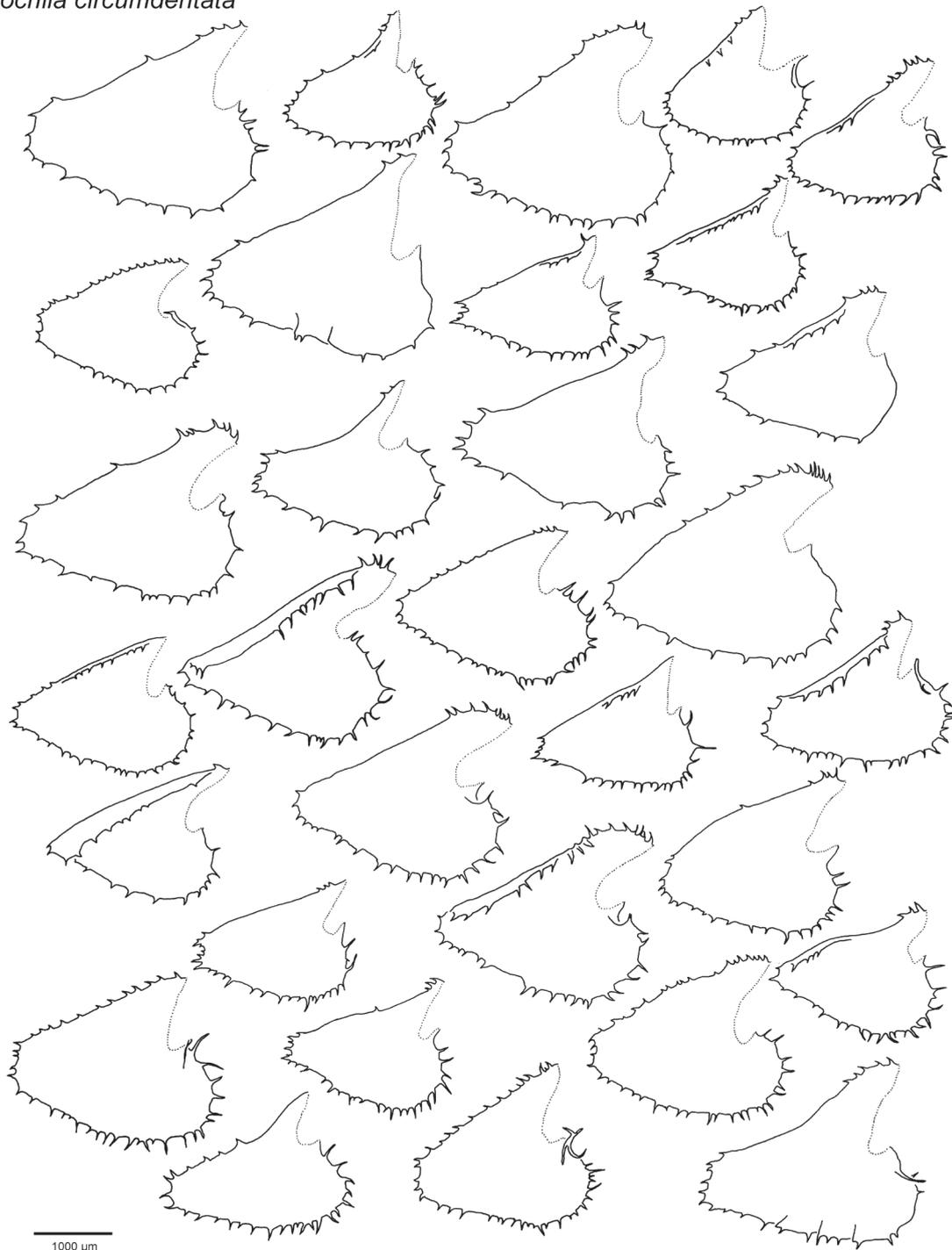
*Plagiochila circumdentata*

**Fig 15.** *Plagiochila circumdentata* leaves, from J.E. Braggins 95/121 (AK 255132) and J.J. Engel 21192 (F 1141079).

Dioicous. Androecia intercalary on shoots that continue vegetative growth arising by *Frullania*-type branching, produced singly or in loose fascicles of three at shoot apex, branching within male branches by *Frullania*-type branching, lateral- and ventral-intercalary branches not associated with male branches; bracts in 5–20 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin entire or with a few small triangular teeth, with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts with scattered paraphyllia. Gynoecia at apices of shoots; bracts broadly elliptic-ovate, to 3200  $\mu\text{m}$  long and 2100  $\mu\text{m}$  wide, larger than subtending leaves; dorsal margin inrolled, ventral margin ampliate; margins spinose-dentate; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts with or without fertilisation. Perianth oblong, about 6000  $\mu\text{m}$  long and 2500  $\mu\text{m}$  wide at mouth, dorsal keel usually with a low wing extending from the base

to near the middle of the keel, entire, laterally compressed but with an inflated base, lateral walls plane; labia truncate, with numerous small teeth comprised uniseriate rows of short rectangular cells. Figs 15, 16.

*Plagiochila circumdentata*



**Fig 16.** *Plagiochila circumdentata* leaves, all from *J.E. Braggins 01/691* (AK 309826).

**Recognition:** *Plagiochila circumdentata* can be recognized by the combination of asymmetrically triangular-ovate leaves with many sharp, spinose-dentate teeth distributed all around the leaf margin, from the base of the dorsal margin next to the stem, to the top of the ventral margin, again next to the stem (Figs 15, 16); the lateral-intercalary stolon origin, and vegetative branching by lateral-intercalary branching only.

*Plagiochila circumdentata* could be confused with *P. baylisii*, but *P. baylisii* has two prominent teeth at the leaf apex, a few teeth at the base of the dorsal leaf margin, and often no or few teeth elsewhere on the leaf margin.

**Distribution and Ecology:** *Plagiochila circumdentata* is endemic to New Zealand, where it occurs in the North and South Islands, between 200 and 1200 m elevation in a wide variety of forest types, and alpine tussock, often as a lithophyte on bedrock and large boulders in association with waterways, but also on rock associated with cliffs and bluffs, and occasionally as an epiphyte on or at the base of the trunks of small or large trees including *Brachyglottis eleagnifolia* and *Nothofagus* spp. At the type locality *P. circumdentata* still grows on large boulders at the side of the stream.

**Variation:** As circumscribed here *Plagiochila circumdentata* exhibits variation in the shape and dentition of leaves and male bracts, whose significance has not been resolved. Leaves may be more or less entire, with a few short triangular teeth scattered around the margin and at the dorsal base, in plants with leaves so armed the leaves tend toward the rotund end of a spectrum of leaf shape variation from rotund to ovate-triangular and have the aspect of *P. circinalis*. At the ovate-triangular end of this spectrum leaves are typically armed with numerous long spinose-ciliate teeth, that are particularly long on the margin of the ampliate leaf base, and particularly closely spaced at the dorsal end of the leaf insertion line and have the aspect of *P. annotina*. In ovate-triangular leaves the dorsal leaf margin may be entire between its base and the apex.

Engel and Merrill (2010a) described *P. circumdentata* var. *carinata* J.J.Engel & G.L.Merr. for plants with deltoid-ovate leaves with a distinctly ampliate base and margins typically sharply ciliate-dentate especially at the extreme dorsal and ventral base (Fig. 16). Plants with this leaf morphology also have entire male bracts. *Plagiochila circumdentata* var. *circumdentata* by contrast has leaves ovate to subreniform, with a less distinctly ampliate leaf base and leaf margins more sparsely and distantly toothed to subentire (Fig. 15), male bracts have a weakly toothed apex.

It is certainly the case that individuals agreeing with the alternate morphologies above can be observed, and the existence of correlated patterns of variation in leaf shape and dentition is without doubt. It is also the case that when placed alongside one another individuals of the two varieties are strikingly different, to the extent that it is tempting to attribute to each species status. However, at the type locality where *P. circumdentata* can still be found in quantity on rocks, individuals exhibit variation in leaf shape and dentition within patches and a continuum in leaf shape and dentition can be observed in a sample across several individuals. In other contexts variation appears less variable and plants from high elevation sites in both the North and South Islands in AK all share a morphology corresponding with *P. circumdentata* var. *carinata*. Although automated methods for species delimitation suggested the existence of phylogenetic structure within *P. circumdentata*, the three individuals included in the study of Renner *et al.* (2017a) are not congruent in relationships defined by molecular data and morphology. The range of material studied has been insufficient to draw satisfactory conclusions regarding the circumscription of *P. circumdentata*, and the molecular data so far investigated may also be insufficiently informative within this system. I therefore agree with Engel and Merrill (2010) that the recognition of two varieties within *P. circumdentata* is warranted, but urge that more detailed investigation incorporating more extensive sampling be conducted on this species.

*Plagiochila circinalis*, another member of sect. *Deflexifoliae*, also expresses variation in leaf dentition and to a lesser degree leaf shape.

**Representative specimens examined: New Zealand: North Island:** Egmont Ecological Region and District, Mt. Taranaki, Egmont National Park, track to skifield from top Pembroke Road, 39°18'28"S 174°05'40"E, 1200 m, 26 Nov 2001, J.E. Braggins 01/691 (AK 309826); Urewera, Maungapohatu, 4600 ft, Dec 1953, A.P. Druce 969B, ex herb. Delessert (G); Wellington Province, Tree Trunk Gorge, west bank of Tongariro River, eastern border of Tongariro National Park, boundary of Kaimanawa State Forest Park, 39°09'S 175°48'E, 700 m, 15 Feb 1995, J.J. Engel 21192 (F 1141079); Kaimanawa Ecological Region and District, Tongariro River, upstream margin, west bank of Tree Trunk Gorge, 39°10'S 175°48'E, 700 m, 15 Feb 1995, J.E. Braggins 95/121 (AK 255132); **South Island:** Nelson District, valley of the Oparawa River, on track between logging road bridge at mouth of Narya Creek and Moria Gate limestone arch, 41°09'S 172°11'E, 230 m, 17 Dec 1984, A.J. Fife 7057 (F 1096446); Canterbury Province, Arthur's Pass National Park, Bealey River, off Bealey Valley track, 42°55'S 171°33'E, 830–850 m, 8 Jan 1982, J.J. Engel 18474 (F 1141073); Westland Province: Westland National Park, Franz Josef Glacier Valley, Roberts Point, SW of Mt. Gunn, 43°26'S 170°11'E, 620–670 m, 24 Dec 1982, J.J. Engel 18114 (F 1141059); Ngakawau Ecological District, Stockton mine area, upper Deep Stream, 41°42'52"S 171°50'31"E, 850 m, 6 Dec 2006, J.E. Braggins 06/284C (AK 302377); Westland National Park, west side of Waiho River Valley between car park for track to glacier and Franz Josef Glacier, 43°26'S 170°10'E, 250 m, 23 Dec 1982, J.J. Engel 18042 (F 1141066); Westland National Park, Franz Josef Glacier Valley, Roberts Point, SW of Mt Gunn, 43°26'S 170°11'E, 620–670 m, 24 Dec 1982, J.J. Engel 18101 (F 1141060); Mt. Cook National Park, east facing slope of Mt. Wakefield, just below Wakefield Falls, 43°42'S 170°09'E, 870 m, 31 Dec 1982, J.J. Engel 18170 (F 1141058).

*Plagiochila circumdentata* var. *carinata* J.J.Engel & G.L.Merr. Nova Hedwigia 91: 511. 2010.

Type citation: New Zealand, South Is., Otago Prov., Mt Aspiring Natl. Park, Blue Valley Track, above Blue River just N of confluence with Makarora River, 430–480 m, *Engel 21897* (F); isotype: (CHR)

*Type: n.v.*

Representative misidentified specimens examined

*Plagiochila baylisii*

Australia: Tasmania: Hillend (Burnie-Zeehan Railway Line) near Zeehan, West Coast, 42°53'S 145°20'E, Apr 1900, *P.H. Weymouth* comm. *W.W. Weymouth 939* (HO 87831).

***Plagiochila kirkii*** Mitt. ex Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 775 (1904) = Species Hepaticarum 2: 453 (1904)

*Type citation:* New Zealand, Great Barrier Island (Kirk).

*Type:* New Zealand, Great Barrier Island, *Kirk*, ex herb. Mitten, (lectotype designated by Bonner (1962): G 00115852!)

=*Plagiochila bazzanioides* J.J.Engel & G.L.Merr., Novon 9: 29 (1999) *syn. nov.*

*Type citation:* New Zealand. North Island: North Auckland Province, Rangitoto Island, immediately E of Auckland, 50–160 m, 4 Feb. 1995, *Engel 20769* (holotype, F; isotype, CHR)

*Type:* New Zealand. North Island: North Auckland Province, Rangitoto Island, immediately E of Auckland, 50–160 m, 4 Feb. 1995, *J.J. Engel 20769*, (holotype: F 1136402! isotype: CHR)

**Notes:** The details of Stephani's protologue of *P. kirkii* agree with the plant represented in the Kirk specimen from Great Barrier ex herb. Mitten in G, in particular the fuscous colour, the decurved falcate-trigonal leaves with an emarginated or bidentate apex, an ampliate base bearing long and spinose teeth, and spinulose margins elsewhere. Stephani commented on the *P. kirkii* type packet 'pulchra species', and it is not possible to disagree with this assessment.

*Plagiochila bazzanioides* was described by Engel and Merrill (1999) based on plants collected from the 600 year old basaltic volcanic island of Rangitoto within New Zealand's Hauraki Gulf, where the species is a common lithophyte on basalt in moist, shaded situations, often in association with *P. gregaria*. *Plagiochila bazzanioides* differed from all other New Zealand species in the combination of toothed paraphyllia on the dorsal stem surface, the ventrally decurved, falcate and narrowly channeled leaves bearing unique slender, claw-like teeth uniseriate for up to 6 cells, particularly well developed along the interior leaf margin.

In their revision of Tasmanian and New Zealand Plagiochilaceae Inoue and Schuster (1971) commented that within *P. annotina* there was considerable variation in the density and stature of marginal teeth on leaves of different specimens, and noted that the type of *Plagiochila kirkii* had denser and longer teeth around the ampliate margin than the type of *P. annotina*, and that 'the more frequent, typical form of *P. annotina* is identical with the type specimen of *P. kirkii*' (Inoue and Schuster 1971 p. 143). This seems to hold true in the northern half of the North Island, where *P. kirkii* has been collected more often than *P. annotina*. The type of *Plagiochila kirkii* bears toothed, lamellate paraphyllia on the dorsal stem surface between the leaf insertion lines, and has ventrally decurved, falcate and narrowly channelled leaves bearing slender, claw-like teeth that are uniseriate for up to 6 cells on the interior lobe margin. In these characters it differs from *P. annotina*, and is identical with the plant represented in the type of *P. bazzanioides*.

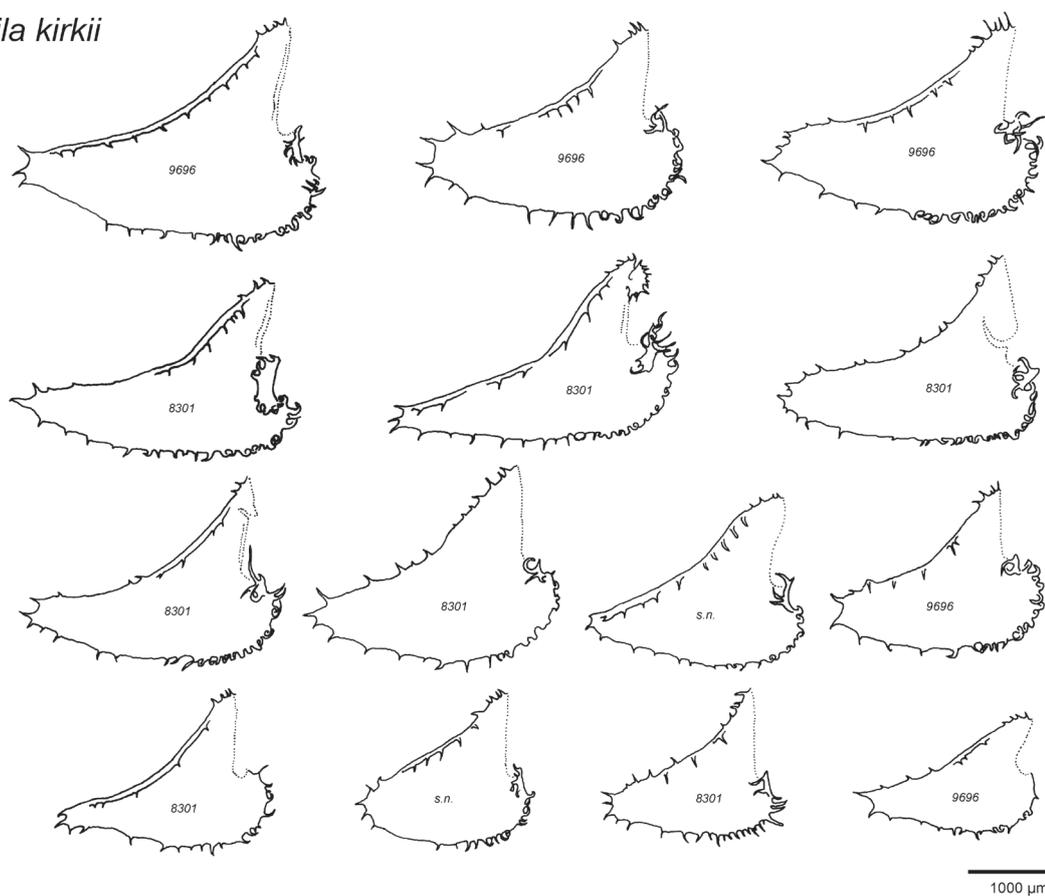
**Etymology:** for Thomas Kirk (1828–1898), who collected on Great Barrier in 1867, later becoming curator at Auckland Museum (1868–1874).

**Description:** Plants with irregularly branched, erect to spreading leafy shoots arising from a creeping basal stolon, stolons arising from other stolons and from leafy shoots by lateral-intercalary branching; forming turfs to short wefts; olive green to brown-green in life to almost black in herbarium, shoot systems to 70 mm long, monomorphic; shoots 4–6 mm wide, branches arising by lateral-intercalary branching. Stems with paraphyllia and short lamellae on their dorsal surface adjacent to the dorsal leaf base, single triangular teeth or longer aggregations of two or three triangular teeth, acute, closely packed among the leaves; paraphyses absent; stem reddish-brown, in primary shoots to 600 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, reddish-brown fading to yellow on the innermost cortical cell walls, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls beneath with walls thickened but tapering, other walls with distinct triangular trigones and weak continuous thickening over some walls, walls faint yellow pigmented. Rhizoids scattered, on stolons arising from the lateral merophytes

at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots imbricate, succubously inserted and orientated, narrowly triangular ovate, falcate, ventrally secund, 1730–3000  $\mu\text{m}$  long  $\times$  860–1760  $\mu\text{m}$  wide, dorsal margin arched, ventral margin straight in outer half and weakly ampliate at base, dorsal margin, apex, and ventral margin all bearing acute teeth, 24–48 in total, teeth one or two cells broad at base, uniseriate above, comprised rectangular to long rectangular cells, capped by a cell with a narrow apex, teeth on the ampliate base longer and hooked; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with nodulose trigones but not continuously thickened; medial leaf cells hexagonal, 30–36  $\mu\text{m}$  long  $\times$  20–29  $\mu\text{m}$  wide, walls faint yellow pigmented, with nodulose trigones, medial thickenings absent; cells in leaf base long polyhedral, walls with large nodulose trigones, medial thickening absent, trigones not confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth produced singly, in pairs or in loose fascicles of three at shoot apex, branching within male branches by *Frullania*-type branching, lateral- and ventral-intercalary branches not associated with male branches; bracts in 5–20 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin entire or with small triangular teeth, with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts with scattered paraphyllia. Gynoecia at apices of shoots; bracts triangular-ovate, to 3500  $\mu\text{m}$  long and 2000  $\mu\text{m}$  wide, larger than subtending leaves; dorsal margin inrolled, ventral margin ampliate; margins spinose-dentate; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts with or without fertilisation. Perianth oblong, about 6000  $\mu\text{m}$  long and 2500  $\mu\text{m}$  wide at mouth, dorsal and ventral keels without a wing, laterally compressed but with an inflated base, lateral walls plane; labia truncate, with numerous spinose-ciliate teeth comprised uniseriate rows of short rectangular cells. Fig. 17.

*Plagiochila kirkii*



**Fig 17.** *Plagiochila kirkii* leaves, from P.J. de Lange 8301 (AK 308901), P.J. de Lange 9696, et al. (AK 322361), J.E. Braggins s.n. (AK 257177).

**Recognition:** *Plagiochila kirkii* can be recognized by the combination of ventrally secund, narrowly-triangular leaves with numerous, with close-set curved teeth on the interior margin, and scattered teeth around the remainder of the margin (Fig. 17), the presence of paraphyllia on the dorsal stem surface among the leaves, the lateral-intercalary stolon origin, and lateral-intercalary vegetative branching. The leaf shape and dentition, in combination with the toothed linear paraphyllia on the dorsal stem surface and strong fuscous pigmentation, serve to differentiate *P. kirkii* from all other *Plagiochila* species.

*Plagiochila kirkii* could be confused with *P. annotina*, but *P. annotina* lacks the stem paraphyllia found in *P. kirkii*, and the teeth on the ventral margin of the leaf are straight, not hooked; the leaves of *P. annotina* are triangular with nearly straight dorsal and ventral margins in *P. annotina*, while in *P. kirkii* the leaves are falcate with a concave dorsal margin, and a convex ventral margin; *P. annotina* lacks the strong fuscous pigmentation characteristic of *P. kirkii* both in the field and herbarium.

*Plagiochila kirkii* could be confused with *P. circumdentata*, which share leaves toothed around nearly all margins and dorsal stem paraphyllia, but *P. kirkii* has narrow triangular leaves and is fuscous whereas *P. circumdentata* has rotund to ovate leaves and is bronze-green.

**Distribution and Ecology:** *Plagiochila kirkii* is endemic to New Zealand where, as far as is known, it is restricted to the north of the North Island and associated inshore and offshore islands, and on the Chatham Islands. In the north of the North Island *P. kirkii* grows in coastal forests, including coastal forests dominated by *Metrosideros excelsa* (pohutukawa) with *Pouteria costata* (tawapou), *Vitex lucens* (puriri) and *Dysoxylum spectabile* (kohekohe), while in the central North Island it was collected in forests dominated by podocarps and *Beilschmiedia*. *Plagiochila kirkii* grows as a lithophyte on gabbro at Te Pahi, and on basalt on Rangitoto Island, which is its best known locality, and on rocks on Mayor Island, but may also grow as an epiphyte on tree trunks, as at Kerikeri Falls.

**Specimens examined:** **New Zealand:** *Stephenson* ex herb. Stephani as *P. annotina* (BM); *Colenso* ex herb. Stephani as *P. annotina* (BM); **North Island:** Te Pahi Ecological Region and District, Te Pahi, North Cape, North Cape Scenic Reserve, 'Wasp Sting Bush', 34°24'31"S 173°02'11"E, 60 m, 24 Feb 2011, *P.J. de Lange* 9696, *J.R. Rolfe*, & *J. Collings* (AK 322361); Bay of Islands, 'From the trees at the entrance to the cave under the Keri Keri waterfall' Oct 1845, *Capt. Sir E. Home* (BM); Great Barrier Island, near New Zealand, *Hutton & Kirk* 317 (G 026081); Auckland Ecological Region, Rangitoto Ecological District, Rangitoto Island, Dyke area near Reservoir, west of track, 36°48'S 174°51'E, 180 m, 21 Jul 2001, *J.E. Braggins s.n.* (AK 257177); Auckland Ecological Region, Rangitoto Ecological District, Rangitoto Island, Lava Caves, 36°47'26"S 174°51'49"E, c. 120 m, 29 Dec 2009, *P.J. de Lange* 8301 (AK 308901); Tuhua (Mayor Island), Opuhi Spring, 37°16'56"S 176°14'39"E, 215 m, 29 Jan 2012, *P.J. de Lange* 10658 (AK 330946); Central North Island, Pureora State Forest, Waihaha, 38°39'06"S 175°39'58"E, 640 m, 25 May 1984, *J.E. Braggins* 84/118b (AK 321035); Whanganui River, Tawata, 39°04'S 175°03'E, May 1948, *E.H. Bunn Lloyd* 8 (AK 321071); **Chatham Islands:** Rekohu (Chatham Island), Tuku-a-Tamatea Nature Reserve, 44°04'S 176°36'W, 200 m, 13 Sep 2007, *P.J. de Lange* CH1126 & *P.B. Heenan* (AK 302345).

Misidentified specimens:

*Plagiochila annotina*

New Zealand, *Kirk*, ex herb. Stephani (G); Stewart Island, Half Moon Bay, Feb 1910, *B. Leland* & *E.W.B. Chase* (G) Greymouth, *Helms* ex herb. Stephani (G)

*Plagiochila ratkowskiana*

Tasmania, Mt La Perouse, ex herb. Stephani (G).

***Plagiochila microdictyon*** Mitt. in Hooker, *Flora Novae Zelandiae* 2: 131 (1854)

*Type citation:* Northern Island: Bay of Islands, with *P. prolifera*, amongst *Sendtnera attenuata*, *J.D.H.*

*Type:* New Zealand: Northern Island: Bay of Islands, amongst *Sendtnera attenuata* Mitten, *Dr J.D. Hooker* (BM!)

**Notes:** The type is a tiny female plant bearing denticulate female bracts. There are no teeth on the base of leaves, which spread weakly when dry, branching is lateral-intercalary, and stolons are lateral-intercalary in origin. I have seen less than five specimens of *Plagiochila microdictyon* during this study, including the type, and have not had opportunity to include the species in molecular phylogeny reconstruction. However, all specimens I have seen share the small stature, the evenly sized and closely spaced entire leaves with a sinuous ventral base, and this, in combination with the absence of terminal branching impart a distinctive aspect. Furthermore, male plants reported by Engel and Merrill (2010b) have no equivalent within the New Zealand flora and I am therefore satisfied that the recognition of *P. microdictyon* is warranted. I am also content that, on

the basis of similarity with *P. circinalis*, placement within sect. *Deflexifoliae* is appropriate, but advocate further work to corroborate both, and especially this second assertion.

**Etymology:** micro- small, dictyon – Greek, possibly ‘net’, but meaning unknown.

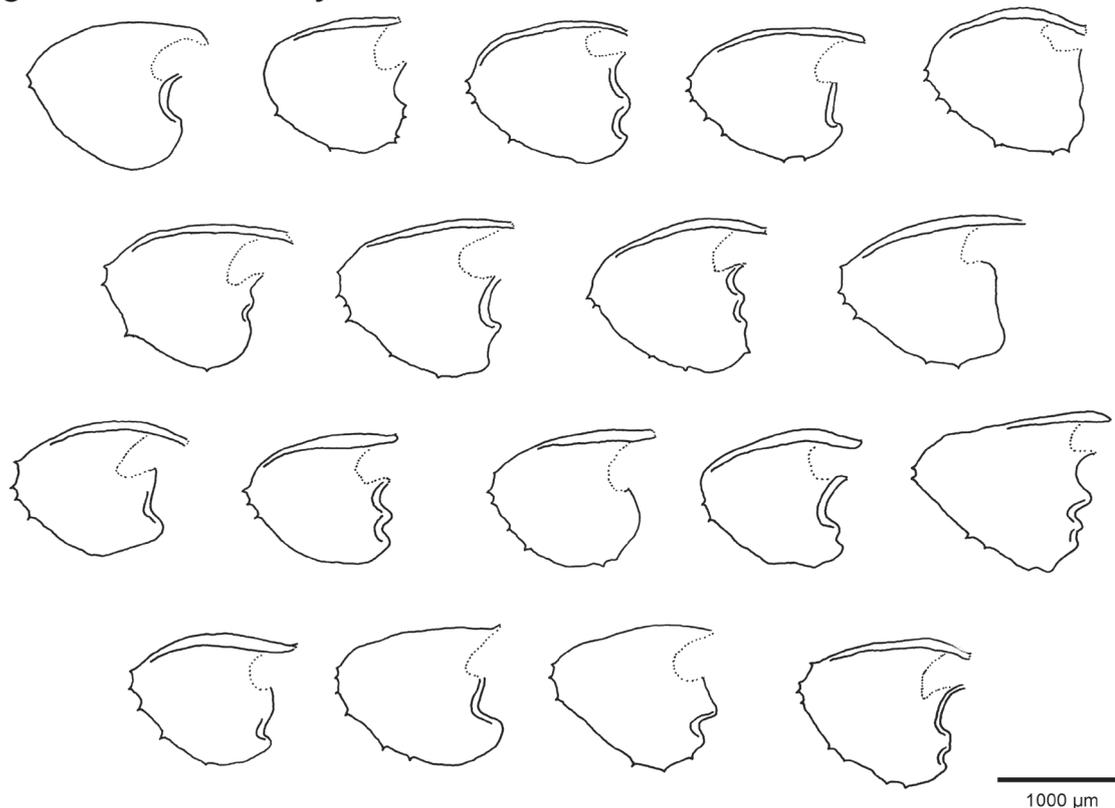
**Description** (adapted from Engel & Merrill 2010b): Plants with irregularly branched, erect to spreading leafy shoots arising from a creeping basal stolon, stolons arising from other stolons and from leafy shoots by lateral-intercalary branching; forming turfs to short wefts; olive green to brown-green in life to almost black in herbarium, shoot systems to 70 mm long, monomorphic; shoots 4–6 mm wide, branches arising by lateral-intercalary branching. Stems with paraphyllia and short lamellae on their dorsal surface adjacent to the dorsal leaf base, single triangular teeth or longer aggregations of two or three triangular teeth, acute, closely packed among the leaves; paraphyses absent; stem reddish-brown, in primary shoots to 600 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, reddish-brown fading to yellow on the innermost cortical cell walls, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls beneath with walls thickened but tapering, other walls with distinct triangular trigones and weak continuous thickening over some walls, walls faint yellow pigmented. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots imbricate, succubously inserted and orientated, narrowly triangular ovate, falcate, ventrally secund, 1730–3000 µm long × 860–1760 µm wide, dorsal margin arched, ventral margin straight in outer half and weakly ampliate at base, dorsal margin, apex, and ventral margin all bearing acute teeth, 24–48 in total, teeth one or two cells broad at base, uniseriate above, comprised of rectangular to long rectangular cells, capped by a cell with a narrow apex, teeth on the ampliate base longer and hooked; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with nodulose trigones but not continuously thickened; medial leaf cells hexagonal, 30–36 µm long × 20–29 µm wide, walls faint yellow pigmented, with nodulose trigones, medial thickenings absent; cells in leaf base long polyhedral, walls with large nodulose trigones, medial thickening absent, trigones not confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth produced singly, in pairs or in loose fascicles of three at shoot apex, branching within male branches by *Frullania*-type branching, lateral- and ventral-intercalary branches not associated with male branches; bracts in 5–20 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin entire or with small triangular teeth, with a dorsal pouch, antheridia 1 per bract, stalk biseriate; stem among bracts with scattered paraphyllia. Gynoecia at apices of shoots; bracts triangular-ovate, to 3500 µm long and 2000 µm wide, larger than subtending leaves; dorsal margin inrolled, ventral margin ampliate; margins spinose-dentate; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts with or without fertilisation. Perianth oblong, about 6000 µm long and 2500 µm wide at mouth, dorsal and ventral keels without a wing, laterally compressed but with an inflated base, lateral walls plane; labia truncate, with numerous spinose-ciliate teeth comprised of uniseriate rows of short rectangular cells. Fig. 18.

**Recognition:** *Plagiochila microdictyon* is outwardly similar to *Plagiochila circinalis* but differs by its smaller size and leaves forming a distinct tubular cnemis that runs along the stem surface such that the stem is visible between the two rows of leaves in dorsal view, whereas in *P. circinalis* the leaves conceal the stem surface in dorsal view (Engel & Merrill 2010b). Male plants of *Plagiochila microdictyon* and *P. circinalis* differ in their male branches, which are straight in *P. microdictyon*, but circinate in *P. circinalis*. The male bracts of *P. microdictyon* have toothed margins, whereas those of *P. circinalis* are entire. *Plagiochila microdictyon* also produces androecial innovations by lateral-intercalary branching, whereas *P. circinalis* androecial innovations arise by terminal *Frullania*-type branching.

**Distribution and Ecology:** *Plagiochila microdictyon* is endemic to New Zealand, where it is confined to the upper half of the North Island. The known specimens were all collected as epiphytes in wind-pruned cloud forest on ridges and summits, from a range of host species including *Coprosma grandifolia*, *Dracophyllum*, and *Quintinia* (Engel and Merrill 2010b). *Plagiochila microdictyon* has been recorded from Australia, but all reports are based on misidentifications of other species.

**Specimens examined: New Zealand, North Island:** Hauraki Gulf, Hauturu (Little Barrier Island) Hauturu summit ridge, 36°12'S 175°05'E, 13 Jun 1984, J.E. Braggins 84/185 (AK 320581); *ibid.*, J.E. Braggins 84/195b (AK 328753).

*Plagiochila microdictyon*

**Fig 18.** *Plagiochila microdictyon* leaves, all from *J.E. Braggins 84/185* (AK 320581).

Representative misidentified specimens

*Plagiochila retrospectans*

Tasmania, St Crispins Well, 42°55'S 147°12'E, ?*R.A. Bastow* (MEL 2058210).

*Plagiochila circinalis*

Tasmania, Adventure Bay, 43°22'S 147°20'E, Mar 1921, *L. Rodway* (HO 87642); Blue Tier, 41°13'S 147°57'E, Dec 1921, *L. Rodway* (HO 87643); Cradle Mountain, 41°41'S 145°57'E, Dec 1916, *L. Rodway* (HO 87640).

*Plagiochila hartziana*

Tasmania, Mt Wellington Plateau, 42°54'S 147°14'E, Jan 1915, *L. Rodway* (HO 87641).

***Plagiochila* sect. *Belangerianae*** Carl, Ann. Bryol. Suppl. 2: 117 (1931)

Type: *Plagiochila belangeriana* Lindenb. [= *Plagiochila arbuscula* (Brid. ex Lehm.) Lindenb.]

= *Plagiochila* sect. *Annotinae* Carl, Ann. Bryol. Suppl. 2: 143 (1931)

Type: *Plagiochila annotina* Lindenb.

= *Plagiochila* sect. *Mitteniae* J.J.Engel & G.L.Merr., Nova Hedwigia 96: 401 (2013)

Type: *Plagiochila stephensoniana* Mitt.

= *Plagiochila* subsect. *Obscurae* Inoue & R.M.Schust., J. Hattori Bot. Laboratory 34: 160 (1971)

Type: *Plagiochila obscura* Colenso [= *Plagiochila stephensoniana* Mitt.]

*Plagiochila* sect. *Belangeriana* may be a predominantly Australasian lineage, fourteen species occur here. However the distribution of one, *P. arbuscula*, extends into Malesia, and at least one other species belonging to this section occurs Malesia, and the full diversity and distribution of sect. *Belangerianae* remains unknown. All species have homogeneous or nearly homogeneous, few segmented smooth and hyaline oil-bodies (where

known), and most, but not all, produce *Frullania*-type vegetative branching to form pinnate or bipinnate shoot systems.

***Plagiochila incurvicolla*** (Hook.f. & Taylor) Hook.f. & Taylor ex Gottsche, Lindenb. & Nees, Synopsis Hepaticarum 5: 651 (1847)

Basionym: *Jungermannia incurvicolla* Hook.f. & Taylor, London Journal of Botany 3: 564 (1844)

*Type citation*: New Zealand.

*Type*: New Zealand, 1843, *J.D. Hooker*, Voyage of H.M. Discovery Ships Erebus and Terror (FH 00458018!)

Epitype (designated here): South Auckland, Tongariro National Park, Ruapehu, Mangawhero River, c 300 m above bridge on track to Waitonga Falls, 39°19'41"S 175°29'46"E, 900-1000 m, 25 Nov 2013, *M.A.M. Renner* 6796 (NSW 899787).

=*Plagiochila hatcheri* J.J.Engel & G.L.Merr., Journal of the Hattori Botanical Laboratory 87: 297 (1999)

*Type citation*: Holotype: New Zealand, Stewart Is., Ulva Is. in Paterson's Inlet, *Hatcher 1609* (F); isotype: (CHR)

*Type*: New Zealand, Stewart Is., Ulva Is. in Paterson's Inlet, *Hatcher 1609* (holotype: F 1136401! isotype: CHR)

=*Plagiochila quinquespina* Steph., Bulletin de l'Herbier Boissier, sér. 2, 3: 328 (1903) = Species Hepaticarum 2: 312 (1903)

=*Plagiochila lyallii* var. *quinquespina* (Steph.) Inoue & R.M.Schust., Journal of the Hattori Botanical Laboratory 34: 88 (1971)

*Type citation*: New Zealand, Stewart Island (Kirk).

*Type*: New Zealand, Stewart Island, *T. Kirk* 267, ex herb. Kirk (lectotype designated by Bonner (1962): G 00067673!)

=*Plagiochila lonchoscypha* Herzog, Transactions and Proceedings of the Royal Society of New Zealand 68: 42 (1938)

=*Plagiochila lyallii* var. *lonchoscypha* (Herzog) E.A.Hodgs., Transactions and Proceedings of the Royal Society of New Zealand 73: 284, 1944.

=*Plagiochila incurvicolla* var. *lonchoscypha* (Herzog) J.J.Engel & G.L.Merr., Nova Hedwigia 92: 504 (2010)

*Type citation*: New Zealand, Mt. Moehau, 2700ft, Coromandel, Auckland (n.8), 31 Dec. 1933

*Type*: n.v.

**Notes:** The type of *P. incurvicolla* in FH comprises a dense mat of stolons within which lateral-intercalary branching from the postical half of the lateral merophyte is frequent. Branches approach the ventral stem midline, or even cross it and in one case appeared to arise from it, but in all cases the branch base was round, not elliptic, and the cortical stem cells did not separate, as in ventral-intercalary branching in *P. deltoidea* and its allies, suggesting that the branch, despite its apparent position was lateral in origin. Arising from this dense network of stolons are 9 leafy shoots around 10 mm tall. All are sterile, two are broken, and only one of which bears a branch, of lateral-intercalary origin. The type is hardly sufficient to convey an adequate conception of most of the plant form, with the exception of leaf shape and dentition, and in these features the type plant is fairly distinctive. The leaves are elliptic-ovate, the dorsal margin is curved and entire. The apex and ventral margin bear 6-12 sharp, acicular teeth of varying stature with the largest around the apex, typically two of the teeth at the apex are larger than those on the antical margin. Further, the plants are nitid, and have a strong fuscous pigmentation, approaching black in a couple of the shoots.

The type of *P. hatcheri* is a much larger plant, the shoots are at least 30 mm long, and leaves are elliptic-ovate, with 5-12 teeth, again two teeth at the apex are larger, the leaves are remote, and with a strongly curved dorsal margin. Vegetative branching is only lateral-intercalary in the type of *P. hatcheri*, and no *Frullania*-type branches are present. There is size-correlated variation in leaf-shape, in that on larger primary shoots the leaves are deltoid, with an ampliate base that partially covers the stem. The dentition of these leaves is comparable with smaller leaves.

The type of *Plagiochila quinquespina* is typical *P. incurvicolla*. It is tall, with widely remote transversely inserted leaves, and lateral-intercalary branches. The plant is nitid, and warm brown colour. It is not *P. colensoi* because it lacks underleaves, and it does not have the leaf shape and dentition characteristic of that species.

**Etymology:** reference unclear.

**Description:** Plants with irregularly branched, erect leafy shoots arising from a creeping basal stolon, stolons arising from other stolons and from leafy shoots by lateral-intercalary branching; forming turfs; olive green to bronze-green in life to opaque light brown in herbarium, shoot systems to 40 mm long, monomorphic; shoots 2–3 mm wide, branches arising by lateral-intercalary branching, or rarely *Frullania*-type branching. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 300 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, reddish-brown fading to yellow on the innermost cortical cell walls, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls beneath with walls thickened but tapering, other walls with distinct triangular trigones and weak continuous thickening over some walls, walls faint yellow pigmented. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots remote to imbricate, succubously inserted and transversely orientated, spreading and postically secund, ovate, 995–1645 µm long × 720–1350 µm wide, dorsal margin curved, ventral margin curved in outer half and weakly ampliate at base, apex, and ventral margin bearing 5–15 spinose teeth, two at apex often larger, teeth radiating outward from leaf margin, straight, teeth one to four cells broad at base, uniseriate above, comprised rectangular to long rectangular cells, capped by a cell with a narrow apex; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with nodulose trigones but not continuously thickened; medial leaf cells hexagonal, 20–30 µm long × 17–25 µm wide, walls unpigmented, with triangular to bulging trigones, medial thickenings absent; cells in leaf base polyhedral, 40–50 µm long × 18–25 µm wide walls with triangular to bulging trigones, medial thickening absent, trigones not confluent. Cell surfaces smooth. Oil-bodies 4–7 per cell, homogeneous or with few transverse bars, smooth. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth produced singly, in pairs or in fascicles of three at shoot apex, branching within male branches by *Frullania*-type branching, lateral- and ventral-intercalary branches not associated with male branches; bracts in 5–15 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin with small triangular teeth, epistatic, antheridia 1 per bract, stalk biseriate; stem among bracts smooth. Gynoecia at apices of shoots; bracts oblong-ovate, to 1500 µm long and 1000 µm wide, larger than subtending leaves; dorsal margin inrolled, ventral margin not ampliate; margins spinose, including dorsal margin which bears short teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts with or without fertilisation. Perianth oblong, about 2000 µm long and 1000 µm wide at mouth, dorsal and ventral keels without a wing, laterally compressed but with an inflated base, lateral walls plane; labia rounded, with around 15 spinose-dentate teeth. Fig. 19.

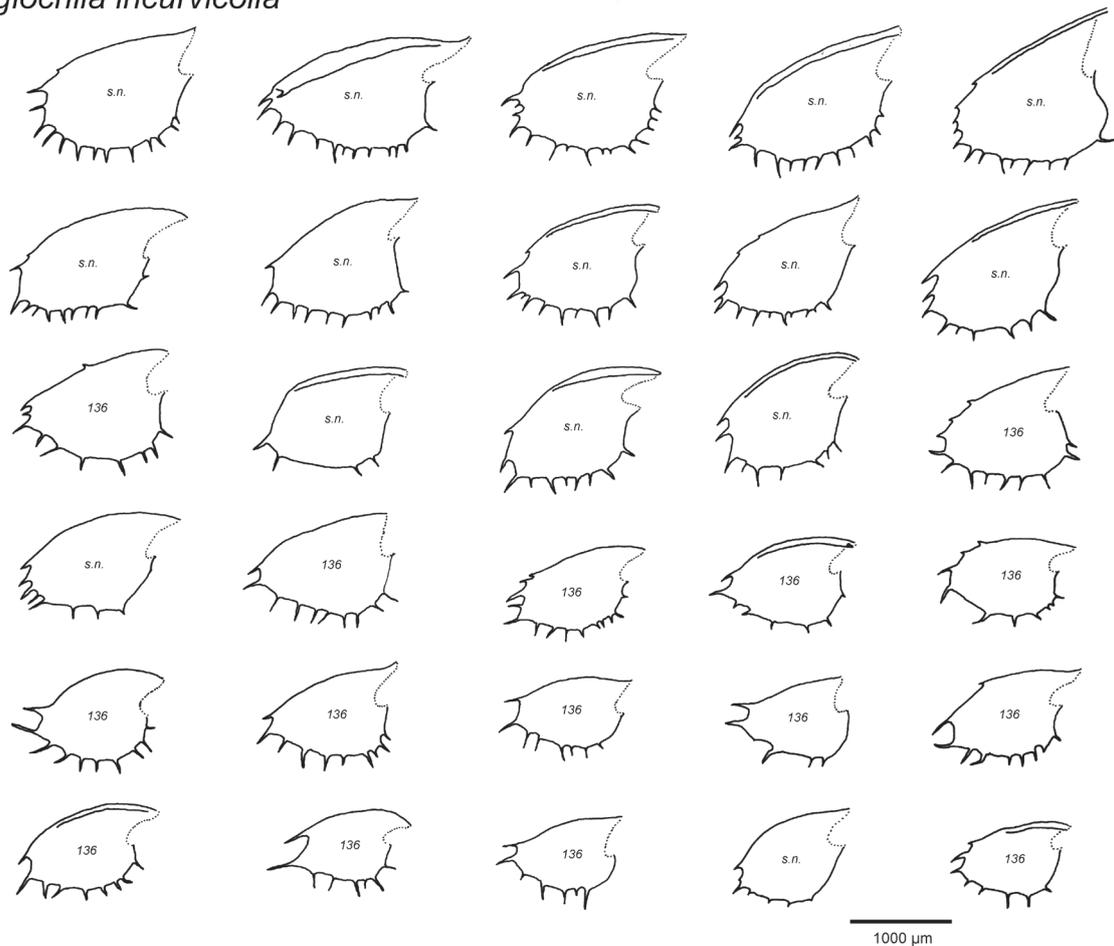
**Recognition:** *Plagiochila incurvicolla* can be recognized by the combination of ovate leaves with an inrolled entire dorsal margin, and outer and ventral margins armed with 5 to 15 sharp spinose-dentate teeth, the leaves contiguous to imbricate, nitid and often bronze-green or bronze, the vegetative branching is usually lateral-intercalary though sporadic *Frullania*-type branches are produced, and oil-bodies are homogeneous. The plants are often bronze- or brown-green and are characteristically nitid in herbarium material.

*Plagiochila incurvicolla* could be confused with *P. fasciculata* but *P. fasciculata* has leaves with a triangular-ovate outline, an obscurely truncate apex, and 13 to 23 triangular teeth on the leaf margin. The vegetative branching in *P. fasciculata* is usually *Frullania*-type.

*Plagiochila incurvicolla* could be confused with *P. colensoi*, but *P. colensoi* has vestigial underleaves on vegetative shoots, and pinnate shoot systems. Inoue and Schuster (1971) report that oil-bodies of *P. colensoi* are granular while those of *P. incurvicolla* are homogeneous.

*Plagiochila incurvicolla* could be confused with *P. fasciculata*, but *P. fasciculata* has ovate-triangular primary-shoot leaves often with a truncate apex and with 13–23 triangular teeth which are variable in size on the margins; and *Frullania*-type branching is the usual mode of vegetative branching. In contrast *P. incurvicolla* has primary shoot leaves with 5–15 sharp spinose teeth which are more or less the same size on the leaf margins; and lateral-intercalary branching is the usual mode of vegetative branching.

*Plagiochila incurvicolla* could be confused with *P. conturbata*, and indeed is very similar to it, however *P. conturbata* is a larger plant whose leafy shoots are up to 100 mm long, which forms turfs of loosely packed shoots, usually on exposed granite boulders in the Wet Tropics Bioregion of north-east Queensland. Please note that this comparison is the only one in which the use of geography as a component of species identification may be required.

*Plagiochila incurvicolla*

**Fig 19.** *Plagiochila incurvicolla* leaves, from M.A.M. Renner 136 (AK 255217) and J. Salter s.n. (AK 322871).

**Distribution and Ecology:** *Plagiochila incurvicolla* occurs in Tasmania and New Zealand. In Tasmania *P. incurvicolla* is widespread and common in cool hyperhumid forest habitats between sea level and around 900 m elevation, as a lithophyte on exposed bedrock or large boulders alongside watercourses, a corticole on fallen and decaying tree trunks and large branches, a humicole on humic soil, and an epiphyte on tree trunk bases and trunks, situations in which it grows with a wide range of other bryophyte species. In New Zealand *P. incurvicolla* inhabits the same diverse range of microsites in cool forests within the central mountain range of the North Island, and along the western side of the Southern Alps in the South Island. *Plagiochila incurvicolla* also occurs on Rakiura (Stewart Island) and on the subantarctic islands.

**Representative specimens examined:** **Australia: Tasmania:** Macquarie River, Jan 1836, Mr Rob. Ball, ex herb. Taylor as *Jungermannia aculeate* (FH 00284119); Mt Romulus, 41°41'S 145°44'E, 880 m, 24 Sep 1985, M.J. Brown 1317a (HO 312722); road to Corinna, 41°28'S 145°21'E, 360 m, 21 Nov 1989, J. Jarman (HO 572974); near Link Road turnoff, 41°34'S 145°41'E, 660 m, 25 May 2000, J. Jarman (HO 505282); Mt Puzzler Forest Reserve, 41°44'30"S 148°04'51"S, 434 m, 25 Jan 2014, T. Thekathyil 163 (HO 576864); East Coast, Sandspit River 8.5 km WNW of Cape Bernier, 42°43'S 147°50'E, 200 m, 30 Oct 1988, A. Moscal 16685 (HO 548783); Mt Wedge, 42°51'S 146°18'E, 24 Dec 1978, A.V. Ratkowsky H1594 (HO 304342); South West, Mt La Perouse, 43°30'S 146°45'E, A.F. Oldfield (MEL 1039440); Manuka Road, Warra Coupe, 43°06'S 146°41'E, 150 m, 30 Apr 2002, J. Jarman (HO 577543); Manuka Road, Warra Coupe, 43°06'S 146°41'E, 170 m, 25 Jan 2000, J. Jarman (HO 577568); Southwest National Park, Mt Norold summit, 43°15'S 146°15'E, 970 m, 24 Feb 1994, J. Jarman (HO 574184); East Coast, Mt Raoul, Cape Raoul State Reserve, 43°13'S 147°47'E, 380 m, 8 Apr 1993, A. Moscal 24930 (HO 548730); **New Zealand: North Island:** Coromandel Peninsula, Ridge NW of Mt Rowe, track to Mt Rowe, 37°02'16"S 175°40'19"E, 720 m, 14 Feb 2007, M.A.M. Renner 2600 (AK 299724); **South Island:** Nelson Province, Mt Richmond Forest Park, Aniseed Valley, SE of Richmond via Aniseed Valley Road off S.H.6, margins of Hackett Stream prior junction with Whispering Falls Track, 41°23'20"S 173°12'18"E, 220–270 m, 7 Feb 2007, J.J. Engel 28202 & M.J. von Konrat (F); Westland Province, Mt Aspiring National Park, Cross Creek, 1 km N of Haast Pass, 44°06'S 169°22'E, 510 m, 12 Mar 1997, J.J. Engel 23137 (F 1142133); Te Wae Wae

Ecological Region, Tuatapere Ecological District, Dean Forest, Deans Bush, end of Lillburn Monowai Road, 45°52'14"S 167°38'09"E, 130 m, 6 Dec 2010, *J. Salter* (AK 322871). **Rakiura (Stewart Island)**: Rakiura National Park, Pryse Peak, plateau area on western side of summit, South West Arm, 46°55'S 167°59'E, 330–340 m, 3 Mar 2003, *J.J. Engel 24668, M.J. von Konrat & J.E. Braggins* (F); Stewart Island, *Kirk 267* ex herb. Stephani as *P. bidens* (BM); Rakiura Ecological Region, Anglem Ecological District, Freshwater Valley, 500 m along track to Rocky Mountain from junction with track to North Arm, 46°52'S 167°56'E, 80 m, 9 Apr 2001, *M.A.M. Renner 136* (AK 255217).

***Plagiochila hartziana*** Pearson, Bulletin of Miscellaneous Information, Royal Gardens, Kew 1924: 72 (1924)

*Type citation*: None provided.

*Type*: Australia: Tasmania, Hartz Mountains, on rocky bank, Lake Perry, 43°13'S 146°45'E, 3,000 ft, 7 January 1908, *W.A. Weymouth 1553*, as *Plagiochila hartziana* n. sp. *Pears.* (lectotype designated here: HO 72734! isolectotypes: HO 87607! HO 87608! BM 000963555!)

=*Plagiochila virido-nigra* (E.A.Hodgs.) Inoue, The Bryologist 68: 218 (1965)

Basionym: *Syzygiella viridonigra* E.A.Hodgs. Records of the Dominion Museum 4: 120 (1962)

*Type citation*: n.v.

*Type*: New Zealand: Auckland Islands, Waterfall Inlet, 27 Nov 1943, *W.H. Dawbin*, herb. Hodgson no. 11871 (holotype: MPN 36945; isotypes: CHR 105305, TNS)

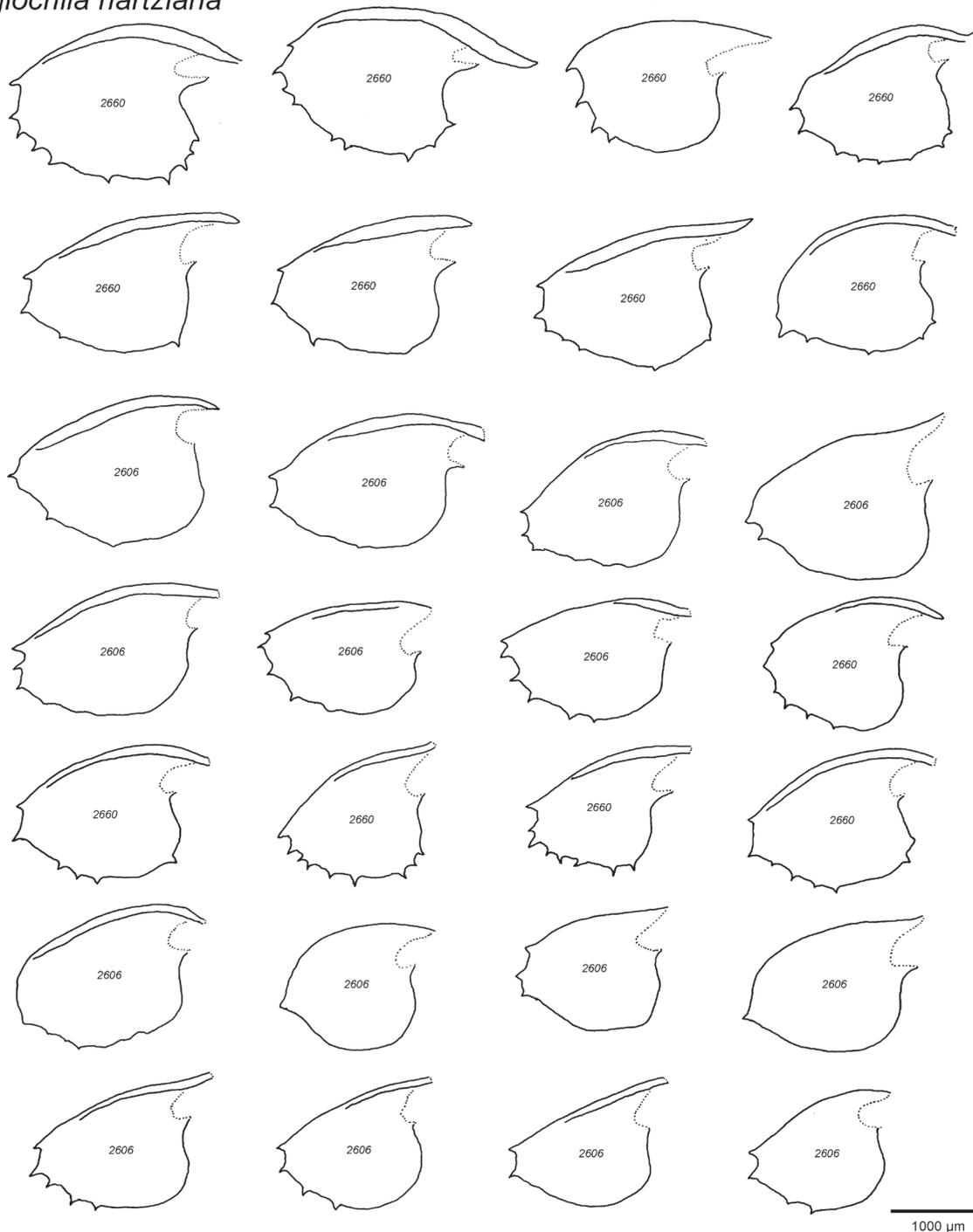
**Notes**: In the introduction to his paper, Pearson (1924) stated that 'Mr. W. A. Weymouth, of Hobart, Tasmania, who attained his eightieth birthday on the 24th of September last, sent me some time ago a rich collection of Tasmanian Hepatics to name with the intention of distributing sets from his extensive gatherings, for charitable purposes.' No specimens were cited by Pearson (1924) in his protologue for *P. hartziana*, but this did not stop So (2001) from identifying a holotype in HO. This is an error to be corrected (Article 9.9) so a lectotype for *P. hartziana* is proposed above. There is sufficient evidence, in the form of Pearson's statement regarding the source of the specimens studied and the presence of his annotation '*Plagiochila hartziana* Pearson n.sp.' on *Weymouth 1553*, to regard this as part of the original material of *P. hartziana*. There are three duplicates of *Weymouth 1553* in HO and one in BM, and one of the HO specimens is designated as the lectotype, the others are isolectotypes because, although derived from the same gathering, the multiple packets in HO are not clearly labeled as being part of the same specimen (Article 8.3). Presumably these duplicates were prepared by Weymouth for distribution to other herbaria, as stated by Pearson, but have never been sent. Even if So (2001) had identified *Weymouth 1553* in HO as lectotype, this can still be narrowed to a single specimen (Articles 8.3, 9.17, and 9.19). The lectotype of *Plagiochila hartziana* possesses occasional *Frullania*-type branches in addition to lateral-intercalary branches in leafy sectors. The stolons are of lateral-intercalary origin, from the ventral half of the lateral merophyte, and the plant is nitid. The New Zealand endemic *Plagiochila viridonigra* was synonymized with the Tasmanian *P. hartziana* by Engel *et al.* (2017).

**Etymology**: probably named for the Hartz Mountains from where the type gathering was made. The dedicative adjectival form is not often applied to geographical names, and this obscures the precise meaning, but this practice is not contrary to the code.

**Description**: Plants with irregularly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; forming loose turfs; to bronze-green, black-green, or nearly black, shoot systems to 80 mm long monomorphic or weakly dimorphic and 30 mm wide; shoots 3–4 mm wide, branches arising by lateral-intercalary or *Frullania*-type branches. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 400 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, reddish-brown fading to yellow on the innermost cortical cell walls, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls beneath with walls thickened but tapering, other walls with distinct triangular trigones and weak continuous thickening over some walls, walls faint yellow pigmented. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots remote to contiguous, succubously inserted and transversely orientated, spreading and postically secund when hydrated, often appressed to stem when dry, ovate, 1470–2190 µm long × 1330–1960 µm wide, dorsal margin curved, often inrolled, ventral margin curved in outer half and weakly ampliate at base, apex and ventral margin bearing 0–10 triangular teeth, often two or three teeth around the apex only, teeth one to four cells broad at base; leaf insertion J-shaped, recurved

at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with bulging trigones and with free external wall continuously thickened; medial leaf cells hexagonal, 18–30  $\mu\text{m}$  long  $\times$  16–23  $\mu\text{m}$  wide, walls unpigmented, with cordate to nodular trigones, medial thickenings absent; cells in leaf base elongated, walls with bulging trigones and medial thickening, trigones not confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction absent.

*Plagiochila hartziana*



**Fig 20.** *Plagiochila hartziana* leaves, from J.A. Curnow 2660 (CANB 8808028) and J.A. Curnow 2606 (CANB 8807975).

Dioicous. Androecia intercalary on shoots that continue vegetative growth, produced singly, in pairs, or in fascicles of three at shoot apex, branching within male branches by *Frullania*-type branching, lateral- and

ventral-intercalary branches not associated with male branches; bracts in 5–15 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin entire, epistatic, antheridia 1 per bract, stalk biseriate; stem among bracts smooth. Gynoecia at apices of shoots; bracts similar in size, shape and dentition to adjacent leaves; dorsal margin revolute, ventral margin not ampliate; margins entire or with 1–4 small triangular teeth around apex; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. One or two subfloral innovations produced by lateral-intercalary branching from between the female bracts and perianth with or without fertilisation. Perianth obovate, about 2000 µm long and 1000 µm wide at mouth, dorsal keel with a wing, ventral keel winged or not, laterally compressed but with an inflated base, lateral walls plane; labia rounded, with several large irregularly-spaced long triangular teeth. Fig. 20.

**Recognition:** *Plagiochila hartziana* can be recognized by the glossy, bronze-green to black shoots whose leaves usually have 2–4 low stature triangular teeth (occasionally more) around the apex, and otherwise entire margins, though some plants have teeth scattered along the ventral margin; vegetative branching by *Frullania*-type and lateral-intercalary modes; male plants in which the bract lobes are more or less entire with the free lobe small compared to the bucket; female plants in which the perianths have labia bearing a few broadly triangular teeth.

*Plagiochila hartziana* could be confused with *P. fasciculata*, but *P. fasciculata* has leaves whose apex and ventral margins are armed by 13 to 23 triangular teeth, and shoots that are dark green and not nitid.

*Plagiochila hartziana* could be confused with *P. strombifolia*, but *P. strombifolia* has leaves with spinose-ciliate teeth around the apex and on the ventral margin.

*Plagiochila hartziana* could be confused with *P. subfasciculata*, but *P. subfasciculata* has leaves whose apex and ventral margins are armed by three to sixteen teeth and shoots that are green to yellow green and not nitid.

*Plagiochila hartziana* has been largely overlooked in Tasmania and New Zealand. The three specimens included in Renner *et al.* (2017a) were all from Tasmania, and had been variously identified as *P. baileyana*, *P. incurvicolla*, and *P. strombifolia*.

**Distribution and Ecology:** *Plagiochila hartziana* is widely distributed on the West and South West coasts of Tasmania, where it grows in cool hyperhumid forests and scrubs, and in alpine herbfields between 50 and 1100 m elevation, often on soil and rock alongside streams and rivers, especially in association with waterfalls, but also on the forest floor and on tree trunk bases within forests as well. *Plagiochila hartziana* has been collected as an epiphyte on *Nothofagus cunninghamii* and *Arthrotaxis cupressoides*. It also colonises fallen and decaying wood, and may even grow on rocks under running water. In New Zealand *Plagiochila hartziana* has a more restricted distribution, and is currently known from Rakiura (Stewart) Island and the subantarctic Auckland Islands, in the same habitats as it occurs in Tasmania.

**Representative specimens examined:** **Australia: Tasmania:** Archer, (HO 87657); West Coast, Donaldson River, 41°09'S 145°05'E, 180 m, 13 Jan 2001, A. Moscal 31170C (HO 577147); North West, Winter Brook, 41°27'S 145°58'E, 860 m, 3 May 1999, A. Moscal 30575 (HO 577182); Central Highlands, Liffey River, 41°43'S 146°44'E, 840 m, 22 Apr 1989, A. Moscal 17695 (HO 577144); North West, River Forth, 41°44'S 146°03'E, 345 m, 5 Sep 1987, A. Moscal 14978 (HO 577485); Central Highlands, Below Lake Mackenzie Dam, H.E.C. Concession Area, 41°41'S 146°23'E, 1100 m, 12 Mar 2000, A. Moscal 30958 (HO 577433); Central Highlands, Drys Bluff, 41°42'S 146°49'E, 1150 m, 16 Dec 1989, A. Moscal 18490 (HO 577112); Central Highlands, Mt. Pillinger, 41°50'S 146°08'E, 1040 m, 29 Oct 1987, A. Moscal 14919 (HO 577058); West Coast, Montezuma Falls, 41°50'S 145°28'E, 320 m, 2 Feb 1997, A. Moscal 28987 (HO 577363); *ibid.*, A. Moscal 28990 (HO 577134); Central Highlands, Powena Creek, Great Pine Tier, 41°53'S 146°22'E, 1070 m, 15 Feb 1992, A. Moscal 22680 (HO 301763); Central Highlands, Lake Antimony, Great Pine Tier, 41°54'S 146°23'E, 1050 m, 14 Feb 1992, A. Moscal 22660 (HO 133892); Montezuma Falls, 7 km SW of Roseberry, 41°50'S 145°28'E, 480 m, 9 May 1997, H. Streimann 59579 (HO 501622); Mt Rufus Track, 42°07'S 146°08'E, 1000 m, 30 Dec 1982, A.M. Buchanan 1066 (HO 305929); Mt Field, Lady Barron Creek, 42°41'S 146°38'E, 980 m, 12 Mar 1992, A. Moscal 23127 (HO 301758); Mt Field National Park, Lady Barron Creek, 42°41'S 146°37'E, 1000 m, 7 Dec 1988, J.A. Curnow 2606 (CANB 8807975); Lake Belcher, 42°41'S 146°33'E, Apr 1921, L. Rodway (HO 85844); Mt Wellington, 42°53'S 147°15'E, Jan 1915, L. Rodway (HO 576900); South West, Junction Creek, 43°06'S 146°16'E, 240 m, 15 Feb 1996, A. Moscal 28048A (HO 577139); East Coast, Mill Creek, Fortescue Forest Reserve, 43°09'S 147°58'E, 80 m, 20 Nov 1998, A. Moscal 30098 (HO 577161); Mt Hartz track, 43°15'S 146°46'E, Dec 1914, L. Rodway (HO 85842); Summers Creek, Toms Bottom, 4 km WSW of Lune River, 43°27'S 146°52'E, 60 m, 10 Dec 1988, J.A. Curnow 2660 (CANB 8808028, HO318834); Mt Wellington, NW Bay River, 26 Mar 1980, A.V. Ratkowsky H1553 (CANB 8408762). **New Zealand: Rakiura (Stewart Island):** Rakiura National Park, Mt Rakeahua summit area, 46°56.4'S 167°52.5'E, 600–690 m, 2 Mar 2003, J.J. Engel 24581A, M.J. von Konrat & J.E. Braggins

(F); Rakiura National Park, Port Pegasus, at top of Belltopper Falls, North Arm, 30 m, 47°09'S 167°41'E, *J.J. Engel 24155, M.J. von Konrat, & J.E. Braggins* (F).

***Plagiochila conturbata*** Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 778 (1904) = Species Hepaticarum 2: 456 (1904)

*Type citation:* Queensland (Bailey).

*Type:* Australia, Queensland, Bellenden Ker District, 1889, *F.M. Bailey 627a* (lectotype designated by Bonner (1962): G 00064149!)

*Epitype* (designated here): Daintree National Park, Manjal Jimalji, track over summit, 16°23'10"S 145°17'31"E, 907 m, 19 May 2014, *M.A.M. Renner 6984 & T.C. Wilson* (NSW 880559)

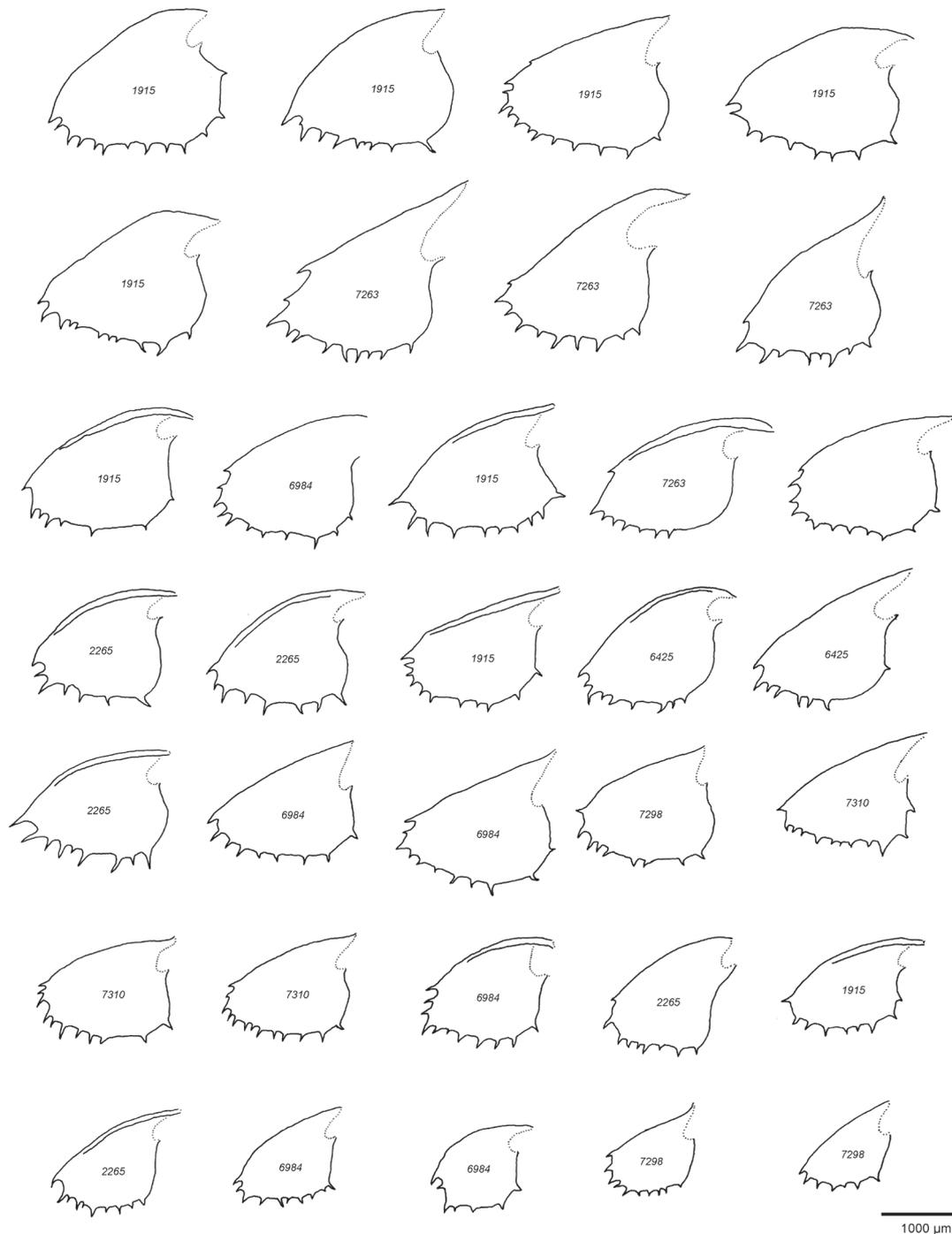
**Notes:** The lectotype of *P. conturbata* in G comprises a plant with shoots up to 5 cm long arising from a basal stolon proliferating by lateral-intercalary branches. Branching within the leafy shoot sectors is entirely lateral-intercalary, and many shoots have damaged apices, subtended by lateral intercalary branches. The leaf shape and dentition in the lectotype corresponds well with that illustrated by Inoue and Schuster (1971 Fig. 61: 2-3, 5) from the NY specimen labeled *Plagiochila baileyana* as discussed above under that species. The number on the lectotype may be a Bailey collection number, but it may also be a Brotherus herbarium number, as several other Bailey collections came to Stephani from this source.

**Etymology:** con- under, and turbatus- disordered, reference unclear.

**Description:** Plants with openly pinnately branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; forming loose turfs; green to bronze-green, shoot systems to 100 mm long, dimorphic and 30 mm wide; shoots 3–4 mm wide, branches arising by *Frullania*-type or lateral-intercalary branches. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 400 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, reddish-brown fading to yellow on the innermost cortical cell walls, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls beneath with walls thickened but tapering, other walls with distinct triangular trigones and weak continuous thickening over some walls, walls faint yellow pigmented. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots remote to contiguous, succubously inserted and orientated, spreading and postically secund when hydrated, often appressed to stem when dry, ovate, 1030–2070 µm long × 910–1600 µm wide, dorsal margin straight to shallowly curved, often inrolled, ventral margin curved in outer half and weakly ampliate at base, apex and ventral margin bearing 7–13 triangular to spinose teeth, teeth one to four cells broad at base, uniseriate above; leaves on secondary shoots 1100–1200 µm long × 750–800 µm wide, margins bearing 5–10 teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, 12–18 µm long × 8–14 µm wide, long axis parallel or perpendicular to leaf margin, walls with nodulose trigones confluent so that walls are more or less continuously thickened; medial leaf cells isodiametric, 13–23 µm long × 11–20 µm wide, walls unpigmented, with bulging trigones, medial thickenings occasional, trigones sometimes confluent; cells in leaf base oblong, 16–31 µm long × 11–19 µm wide walls with bulging to knot-like trigones, medial thickening present, trigones sometimes confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, produced singly at shoot apex, branching within male branches by *Frullania*-type branching, lateral- and ventral-intercalary branches not associated with male branches; bracts in 3–10 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margins with two or three triangular teeth, epistatic, antheridia not seen; stem among bracts smooth. Gynoecia at apices of shoots; bracts triangular-ovate, larger than subtending leaves; dorsal margin inrolled, ventral margin not ampliate; margins lacerate-dentate; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts. Perianth not seen. Fig. 21.

**Recognition:** *Plagiochila conturbata* can be recognized by the combination of ovate leaves with up to 13 teeth concentrated at the apex and outer half of the ventral margin, and *Frullania*-type vegetative branching. The shoots of *P. conturbata* are typically long, and sparingly branched, bronze to brown-green in colour, with remote to contiguous leaves that, in combination, give the plants a characteristic aspect in the field and herbarium.

*Plagiochila conturbata*

**Fig 21.** *Plagiochila conturbata* leaves, from M.A.M. Renner 1915 & E.A. Brown (NSW 980506), M.A.M. Renner 2265 & E.A. Brown (NSW 980505), M.A.M. Renner 6425, V.C. Linis & E.A. Brown (NSW 896964), M.A.M. Renner 6984 & T.C. Wilson (NSW 880559), M.A.M. Renner 7263 & L.J. Gray (NSW 849236), M.A.M. Renner 7298 & L.J. Gray (NSW 880471), M.A.M. Renner 6984 & T.C. Wilson (NSW 880559), and M.A.M. Renner 7310 & L.J. Gray (NSW 880457)

*Plagiochila conturbata* could be confused with *Plagiochila fasciculata* but *P. fasciculata* has leaves with an obscurely truncate apex and whose apex and ventral margins bear 13 to 23 triangular teeth.

*Plagiochila conturbata* could be confused with *P. incurvicolla*, but *P. incurvicolla* is a smaller plant with leafy shoots to 40 mm long, which forms densely-packed turfs in a variety of microsites in Tasmania and New Zealand.

**Distribution and Ecology:** *Plagiochila conturbata* is endemic to the Wet Tropics Bioregion of north-east Queensland, where it is confined to tropical montane rainforest habitats on higher elevation mountain tops,

above 900 m elevation. Within these forests *P. conturbata* is a common lithophyte on granite boulders and outcrops, but also grows as an epiphyte on tree trunk bases. *Plagiochila conturbata* may form extensive pure turfs, but often grows admixed with or in close proximity to *Plagiochila aenea* and *P. lamellata* in addition to a number of other bryophytes.

**Specimens examined: Australia: Queensland:** Cook, Track to Mt Finnegan, Mt Finnegan Range, Cedar Bay National Park, 39 km S of Cooktown, 15°49'S 145°16'E, 1000 m, 20 Oct 1995, *H. Streimann 57161* (CANB 9519304); Daintree National Park, Manjal Jimalji, track over summit, 16°23'10"S 145°17'31"E, 907 m, 19 May 2014, *M.A.M. Renner 6984* & *T.C. Wilson* (NSW 880559); Daintree National Park, Coast Range, Little Falls Creek catchment, immediately above Coral Fern patch on track to Manjal Jimalji from Karnak, ENE of spot height 1198, 16°23'43"S 145°17'57"E, 1030 m, 28 Mar 2012, *M.A.M. Renner 6374*, *V.C. Linis* & *E.A. Brown* (NSW 896825); Cook, Daintree National Park, Mount Lewis summit, 16°34'52"S 145°16'34"E, 1224 m, 27 Mar 2012, *M.A.M. Renner 6351*, *V.C. Linis* & *E.A. Brown* (NSW 896801); Cook, Mt Lewis National Park, Eastern flank of Mt Lewis summit, headwaters of stream flowing SW to Mt Lewis road, 16°34'53"S 145°16'38"E, 1200 m, 29 Aug 2014, *M.A.M. Renner 7263* & *L.J. Gray* (NSW 849236); Cook, Mount Bellenden Ker, 17°15'55"S 145°51'14"E, 1540 m, 7 Jul 2005, *M.A.M. Renner 1915* & *E.A. Brown* (NSW 980506); Cook, Mount Bellenden Ker, water supply stream at end of track to NE of communications precinct, 17°15'47"S 145°51'14"E, 1450 m, 8 Jul 2005, *M.A.M. Renner 1997* & *E.A. Brown* (NSW 980508); Mt Bellenden ker, centre peak area around Cable car, 17°16'S 145°51'E, 2 Nov 1981, *D.H. Vitt 27954* & *H. Ramsay* (F 1078726); Wooroonooran National Park, Mount Bartle Frere, vicinity of unofficial North West campsite, 200 m SE of centre peak, 17°23'14"S 145°48'58"E, 1500 m, 15 Jul 2005, *M.A.M. Renner 2265* & *E.A. Brown* (NSW 980505); Cook, Wooroonooran National Park, Bartle Frere, between North West Summit and Bartle Frere summit, broad shallow gully heading NE away from track, 17°23'36"S 145°48'54"E, 1510 m, 2 Sep 2014, *M.A.M. Renner 7298* & *L.J. Gray* (NSW 880471); Bellenden Ker Range, Wooroonooran National Park, Russell River catchment, track to Choorichillum from end of Gourka Road, between NW summit and Choorichillum, 17°23'45"S 145°48'56"E, 1460 m, 30 Mar 2012, *M.A.M. Renner 6425*, *V.C. Linis* & *E.A. Brown* (NSW 896964); Cook, Wooroonooran National Park, Brtle Frere, stream flowing south past Western Summit camp from summit ridge north of Bartle Frere summit, 17°23'46"S 145°48'56"E, 1459 m, 2 Sep 2014, *M.A.M. Renner 7310* & *L.J. Gray* (NSW 880457); Mt Bartle Frere summit, 17°23'57"S 145°49'07"E, 1640 m, 2 Sep 2014, *M.A.M. Renner 7326* & *L.J. Gray* (NSW 880767); Mt Bellenden ker, south peak, 23 km SSE of Gordonvale, 1550 m, 17°18'S 145°52'E, 3 Mar 1983, *H. Streimann 27376* (CANB 8305341); Summit ridge of Mount Bellenden Ker, between the radio mast and W end of centre peak, 17°15'48"S 145°51'12"E, 1370–1420 m, 13 Jun 2001, *D.C. Cargill 111* (CANB 644594.1); Bellenden Ker, 17°16'S 145°51'E, *W.A. Sayer* & *A. Davidson* (MEL 1039441).

***Plagiochila baylisii*** Inoue & R.M.Schust., Journal of the Hattori Botanical Laboratory 34: 150 (1971)

*Type citation:* New Zealand: South Island: Fiordland Natl. Park, SE corner of Secretary I., Doubtful Sd., in dense, undisturbed forest on steep, peaty slopes, 10–250 ft, *RMS 57492a*, in MASS; dupl. in TNS.

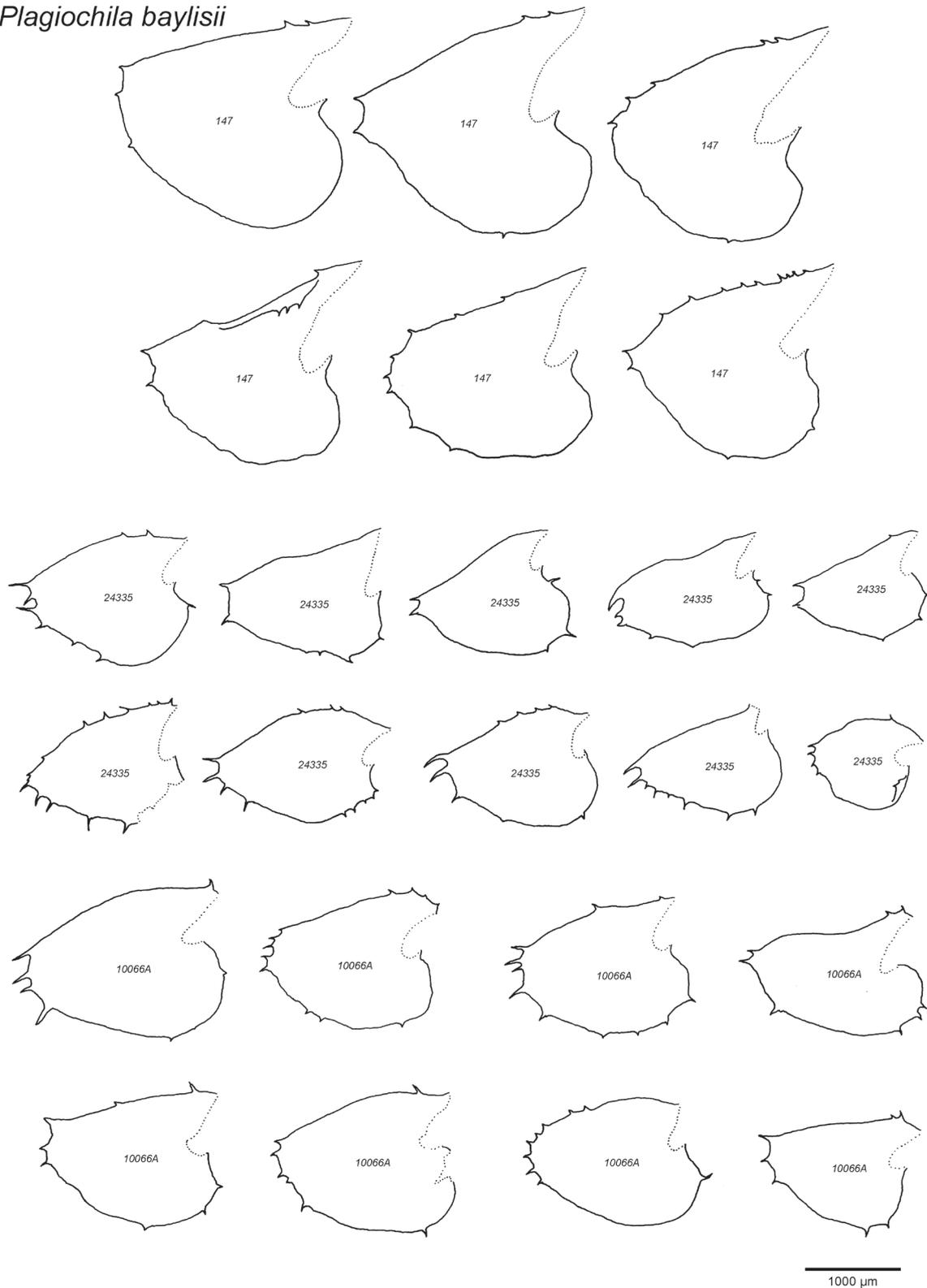
*Type:* n.v.

**Etymology:** named as a token of esteem and gratitude for Geoff T.S. Baylis, New Zealand botanist and head of the Otago University Department of Botany.

**Description:** Plants with irregularly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; forming loose turfs; green to bronze-green, shoot systems to 100 mm long, monomorphic; shoots 2.5–4 mm wide, branches arising by *Frullania*-type or lateral-intercalary branches. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 300 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, reddish-brown fading to yellow on the innermost cortical cell walls, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls beneath with walls thickened but tapering, other walls without trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, often appressed to stem when dry, ovate to triangular ovate, 2100–2650 µm long × 1500–2650 µm wide, dorsal margin straight to shallowly curved, ventral margin curved in outer half and ampliate at base, margins bearing 5–13 triangular to spinose teeth, teeth one to three cells broad at base, uniseriate above, two or three teeth at the apex larger, and two to five closely spaced teeth at the base of the dorsal margin, ventral margin typically with 0 to 6 teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with bulging trigones but not continuously thickened; medial leaf cells

isodiametric to ovoid, 20–32  $\mu\text{m}$  long  $\times$  17–26  $\mu\text{m}$  wide, walls unpigmented, with bulging trigones, medial thickenings absent; cells in leaf base oblong to polyhedral, 38–50  $\mu\text{m}$  long  $\times$  22–28  $\mu\text{m}$  wide walls with bulging to nodulose trigones, medial thickening present, trigones not confluent. Cell surfaces smooth. Oil-bodies 3 or 4 per cell, pale, smooth, long-oval, *fide* note on HO 576894. Underleaves absent. Asexual reproduction absent.

*Plagiochila baylisii*



**Fig 22.** *Plagiochila baylisii* leaves, from M.A.M. Renner 147 (AK 255189), J.J. Engel 24335 et al. (F), and A. Moscal 10066A (HO 577128).

Dioicous. Androecia intercalary on shoots that continue vegetative growth produced singly or in pairs, branching within male branches by *Frullania*-type branching, lateral- and ventral-intercalary branches not associated with male branches; bracts in 5–15 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin entire, epistatic; stem among bracts smooth. Gynoecia at apices of shoots; bracts oblong-ovate, 1000–2000  $\mu\text{m}$  long  $\times$  850–2000  $\mu\text{m}$  wide, larger than subtending leaves; dorsal margin plane or inrolled, ventral margin ampliate; dorsal, ventral, and apical margins all with scattered spinose teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts with or without fertilisation. Perianth oblong, 1200–2700  $\mu\text{m}$  long  $\times$  700–1600  $\mu\text{m}$  wide at mouth, dorsal keels with a low keel in the basal half or unwinged, long paraphyllia present along dorsal keel, attached near base; laterally compressed but with an inflated base, lateral walls plane; labia rounded, with around 8–14 dentate-lacerate teeth. Fig. 22.

**Variation:** As circumscribed here, *Plagiochila baylisii* encompasses a range of forms whose relationships have not been satisfactorily resolved. At one extreme are small plants corresponding with the type of *Plagiochila baylisii* in having elliptic leaves bearing two prominent apical teeth and smaller teeth scattered along the ventral leaf margin, the outline of which is moderately ampliate, in addition there are a couple of teeth at the base of the dorsal leaf margin whose insertion line is moderately decurrent. At the other extreme are much larger plants such as those collected on Rakiura (Stewart Island) and in Tasmania having two or three small teeth at the leaf apex, the ventral leaf margin entire or with at most one to three teeth and broadly ampliate in outline, and two to five or occasionally more teeth at the base of the dorsal leaf margin, whose insertion is long decurrent. In particular, the plant I collected on Rakiura in 2001 (AK 255189) has fewer teeth than the type plant, but the diagnostic bifid apex is discernible, if not pronounced, and the straight dorsal margin has the 6 or 7 teeth described by Inoue and Schuster (1971). These two extremes are linked by individuals such as *Engel* 24335 that has more numerous but smaller teeth at the leaf apex, variable tooth production on the ventral margin and on the base of the dorsal leaf margin, and a moderately ampliate leaf base. The relationships between the variants here attributed to *Plagiochila baylisii* warrant further scrutiny, possibly one of more of the forms described above will prove distinct.

**Recognition:** *Plagiochila baylisii* can be recognized by the combination of the bilobed leaf apex, scattered teeth on the dorsal leaf margin especially near the stem insertion, deltoid leaf shape with an ampliate leaf base in larger specimens, decurrent dorsal stem insertion line, vegetative branching by *Frullania*-type and lateral-intercalary modes and, in female plants, the one or two large paraphyllia on the perianth.

*Plagiochila baylisii* could be confused with *P. circinalis*, but *P. circinalis* does not have *Frullania*-type vegetative branches, the two teeth prominent at the leaf apex, or the few small spinose teeth on the dorsal leaf margin near the end of the stem insertion that are characteristic of *P. baylisii*.

*Plagiochila baylisii* could be confused with *P. circumdentata*, but *P. circumdentata* has teeth distributed around all leaf margins, not just at the apex and at the base of the dorsal leaf insertion; vegetative branching is lateral-intercalary only, and the perianths of *P. circumdentata* are ligulate and do not bear paraphyllia.

*Plagiochila baylisii* could be confused with *P. deltoidea*, but *P. deltoidea* does not have *Frullania*-type vegetative branches, the two teeth prominent at the leaf apex, or the few small spinose teeth on the dorsal leaf margin near the end of the stem insertion that are characteristic of *P. baylisii*, and stolons of *P. deltoidea* originate by ventral-intercalary branching, not lateral-intercalary branching as in *P. baylisii*.

**Distribution and Ecology:** *Plagiochila baylisii* occurs in Tasmania and New Zealand. In Tasmania *P. baylisii* is a widely distributed in the west and south west where it occurs in cool hyperhumid forests dominated by *Nothofagus* and broadleaf species or scrubs dominated by *Leptospermum*. *Plagiochila baylisii* is a versatile species, and may grow as an epiphyte on tree trunks, on tree roots, or on exposed and poorly drained soil under a low scrub canopy. *Plagiochila baylisii* may be locally abundant at some sites.

In New Zealand *Plagiochila baylisii* has a scattered distribution from the Waima Range in Northland to Rakiura (Stewart) Island in the south.

**Representative specimens examined:** **Australia: Tasmania:** Mt. Wellington, *L. Rodway* 56a (HO 87713); North West, Montagu River, 41°02'S 144°58'E, 30 m, 28 Dec 1990, *A. Moscal* 20409 (HO 577506); West Coast, Hillend near Zeehan (Burnie-Zeehan Railway line, Apr 1900, *W.A. Weymouth* 939 (HO 87831, ex herb. *Levier* 3384 G 026857); Harman River, 41°38'54"S 145°20'26"E, 380 m, 2 Feb 2015, *L.H. Cave* 2577 (HO 576894); Murchison Highway near Mountain Creek, 41°47'S 145°34'E, 400 m, 18 Mar 2008, *J. Jarman* (HO 572107); West Coast, Zeehan, Grubb's Tramway, 41°53'S 145°22'E, 18 Oct 1893, *W.A. Weymouth* 485 (HO 87674); South West, Wanderer River, c. 0.5 km from mouth, 42°43'S 145°27'E, 20 m, 8 Mar 1985, *A. Moscal* 10066A (HO 577128); On wood, Grubb's Tramway, Zeehan, West Coast, 41°53'S 145°22'E, 18 Oct 1893, *W.A. Weymouth* 171 (HO 85956); East Coast, Orielson Rivulet, 12 km NNW of Sorell, 42°40'S 147°31'E, 11 Sep 1988, *A. Moscal* 16521

(HO 577034); Harman River, Meredith Range Regional Reserve, 41°38'54"S 145°20'26"E, 380 m, 2 Feb 2015, *L.H. Cave* 2577 (HO 576894); South West, Port Davy, 1 mile east of Melaleuca Lagoon, head of Melaleuca Inlet, 43°24'S 146°09'E, 6 m, 12 Mar 1954, *M. Davis* 1217i (MEL 1035158); Port Davey, Southwest National Park, 43°25'S 146°10'E, 1960, *D. Martin* (HO 305615); Deadmans Bay, 43°32'S 146°30'E, 15 m, 21 Jan 1987, *A. Moscal* 14263 (HO 113075, CANB 781853); *ibid.*, *A. Moscal* 14267 (HO 123073 CANB 781959); **New Zealand: Rakiura (Stewart Island)**: Rakiura National Park, Mt Rocky summit area, 530 m, 46°51.7'S 167°56.8'E, 26 Feb 2003, *J.J. Engel* 24335, *M.J. von Konrat* & *J.E. Braggins* (F); Rakiura Ecological Region, Anglem Ecological District, Rocky Mountain, 9 Apr 2001, 46°52'S 167°57'E, 545 m, 9 Apr 2001, *M.A.M. Renner* 147 (AK 255189); Stewart Island, *L. Cockayne* 8286 as *P. deltoidea* (AK 18663, G 001174).

***Plagiochila fasciculata*** Lindenb., *Species Hepaticarum* 1: 7 (1839)

Basionym: *Jungermannia fasciculata* (Lindenb.) Hook.f. & Taylor, *London Journal of Botany* 3: 371 (1844)

*Type citation*: In nova Hollandia a *Frazero* inventa asservatur in herbario cl. *Hookeri*, qui specimina communicavit.

*Type*: Australia, ex herb. auctoris, ex herb. Stephani (isotype *fide* So (2001): G 00064442!)

Epitype (designated here): Australia, New South Wales, Central Tablelands, Blue Mountains National Park, Dante's Glen walking track, Fairy Falls, 32°42'46"S 150°25'27"E, 650 m, 17 Dec 2013, *M.A.M. Renner* 6801 (NSW 900149).

=*Plagiochila aculeata* (Hook.f. & Taylor) Taylor & Hook.f. ex Gottsche, Lindenb. & Nees *Synopsis Hepaticarum* 5: 627 (1847)

Basionym: *Jungermannia aculeata* Hook.f. et Taylor, *London Journal of Botany* 3: 578 (1844)

*Type citation*: Van Diemen's Land.

*Type*: Van Diemens Land, 1840, *J.D. Hooker*, (lectotype designated here: FH 00284122!).

=*Plagiochila fasciculata* var. *fraseri* Gottsche, *Fragmenta Phytographiae Australiae* 11, suppl. 4: 54 (1880)

*Type citation*: Australia, N.S.Wales, leg. Fraser & leg. Cunningham; Grampians, Wilhelmi, Apollo Bay, Sources of River Yarra, leg. Ferd. v. Müller.

*Type*: Sources of the Yarra, *F. von Müller* (syntype: MEL1039429!)

=*Plagiochila fasciculata* var. *muelleriana* Gottsche, *Linnaea* 28: 547 (1856) [1857]

*Type citation*: Habitat var.  $\beta$  in truncis putrescentibus valium umbrosarum traciuss Dandenon-Range, (ubi male et female mense Januario 1853 lecta est, no. 7.) apud Melbourne, et in Sealers Cove (n. 162).

*Type*: Australia, Victoria, Eastern Highlands, Dandenong Ranges, Jan 1853, [*F. Mueller*] no. 7 (lectotype designated here: MEL 1039433!); Wilsons Promontory, Sealers Cove, 1854, *F. von Müller* 162 (residual syntype: MEL 1039432!)

=*Plagiochila fasciculata* var. *labillardieriana* Gottsche, *Linnaea* 28: 547 (1856) [1857]

*Type citation*: Labillardière, in Herbario Webbiano e Terra van Diemen

*Type*: n.v.

=*Plagiochila rossii* Steph., *Journal and Proceedings of the Royal Society of New South Wales* 48: 1300 (1914)

*Type citation*: Australia, N. S. Wales (The Jungle, Blackheath): Watts, 1035.

*Type*: Australia, New South Wales, The Jungle, Blackheath, on face of boulder, 7 Jan 1911, *W.W. Watts* 810 ex herb. Watts 1035, (holotype: G 00121213!)

=*Plagiochila victoriae* Steph., *Journal and Proceedings of the Royal Society of New South Wales* 48: 131 (1914)

*Type citation*: Australia, Victoria (Lorne: leg Miss E. L. Watts) Hb. Watts, 910.

*Type*: Australia, Victoria, Lorne, Dec 1908, *Ethel Watts*, herb. Watts 910 (lectotype designated here: G 00121214! isolectotype: MEL 1039489!)

**Notes**: Engel and Merrill (2010a) did not include the statement 'designated here' in their lectotypification of *P. aculeata* on FH 00284122, as required by the code for lectotypifications after 1 January 2001 (Article 7.10 of Melbourne code, Article 7.11 of Shenzhen code). Syntypes of *Jungermannia aculeata* bear the inscription 'Taylor mss' and the name *Jungermannia aculeata*. The lectotype of *P. aculeata* is male, and has 2 to 4 teeth

on the male bract lobes. The leaf apex is truncate and toothed, and the teeth on the postical leaf margin are relatively large though variable in size, the interior margin is often without teeth, and the specimen has *Frullania*-type vegetative branches.

**Etymology:** fascicled, reference unclear.

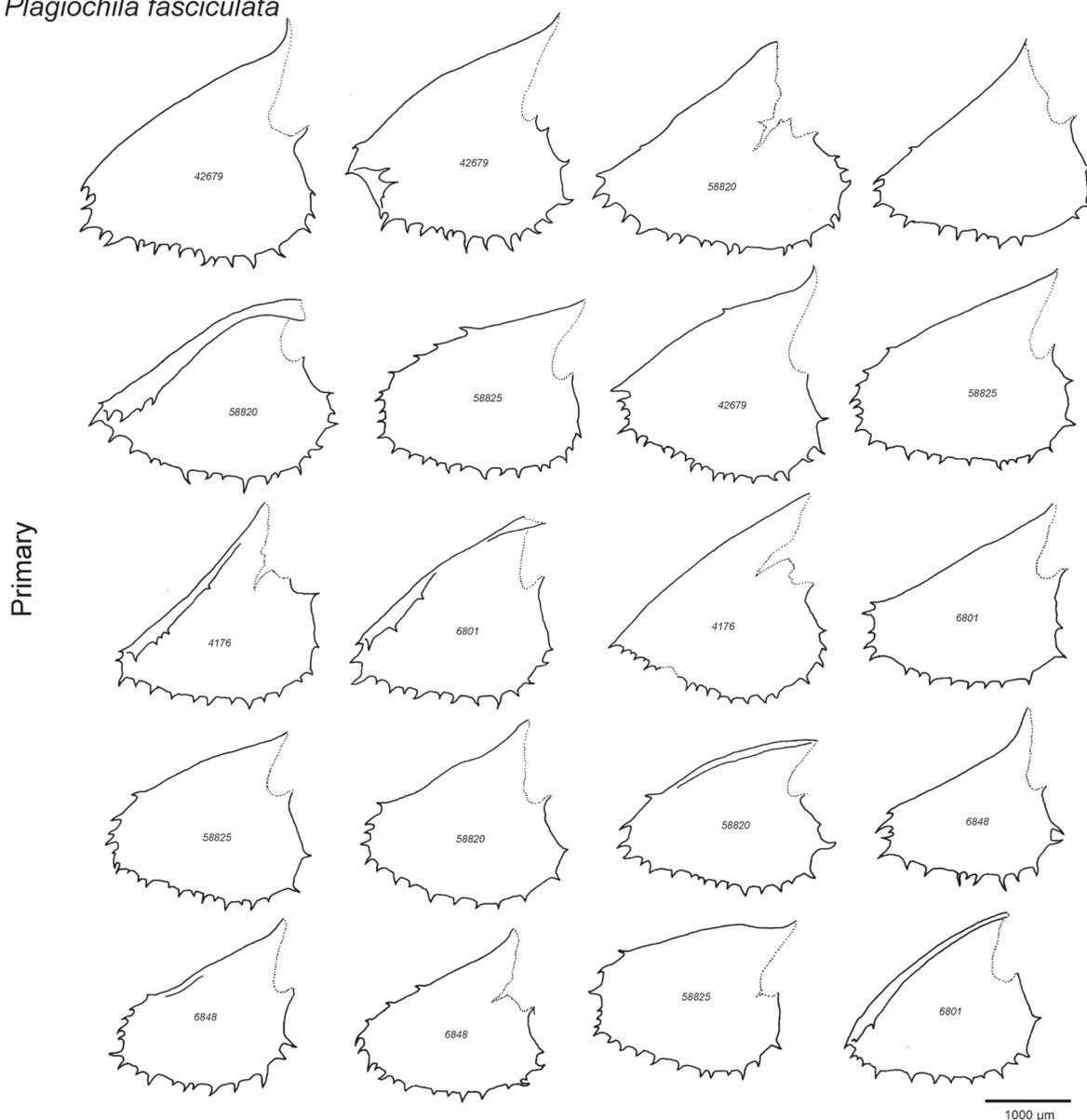
**Description:** Plants with pinnately branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; forming turfs; mid-green to brown-green, shoot systems to 100 mm long and 30 mm wide, dimorphic; primary shoots 2.5–4 mm wide, branches arising by *Frullania*-type and lateral-intercalary branches. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 450 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 3 to 5 layers, cortical cell walls strongly and continuously thickened, reddish-brown fading to yellow on the innermost cortical cell walls, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls beneath with walls thickened but tapering, other walls without trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots contiguous to imbricate, succubously inserted and orientated, triangular ovate, 1600–2870 µm long × 1220–2330 µm wide, dorsal margin straight to shallowly arched, ventral margin curved in outer half and ampliate at base, apex and ventral margins bearing 13–23 triangular teeth, teeth one to four cells broad at base, sometimes two or three teeth at the apex slightly larger, dorsal margin entire; leaves on secondary shoots 1120–2475 µm long × 790–1615 µm wide; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, 7–13 µm long × 5–14 µm wide, long axis parallel or perpendicular to leaf margin, walls with bulging trigones often confluent, walls often more or less continuously thickened; medial leaf cells isodiametric to ovoid, 14–26 µm long × 10–19 µm wide, walls unpigmented, with large bulging trigones, medial thickenings absent; cells in leaf base oblong, 30–58 µm long × 14–21 µm wide walls with bulging to nodulose trigones, medial thickening present, smaller than trigones, trigones not confluent. Cell surfaces smooth. Oil-bodies 3 or 4 per cell, hyaline, homogeneous or with two or three transverse bars, smooth. Underleaves present, vestigial, triangular or filiform. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth produced singly, pairs or fascicles of three, branching within male branches by *Frullania*-type branching, lateral- and ventral-intercalary branches not associated with male branches; bracts in 5–20 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin with acute apex and obscure teeth, lobule epistatic lobes on basal bracts with a single oblique lamella that is fused with the lobule of the preceding bract on the same side of the shoot, antheridia not seen; stem among bracts smooth. Gynoecia at apices of shoots; bracts oblong-ovate, larger than subtending leaves; dorsal margin plane or inrolled, ventral margin ampliate; dorsal, ventral, and apical margins all with scattered long triangular teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts with or without fertilisation. Perianth obovate, to 3000 µm long and 2000 µm wide at mouth, keels unwinged; laterally compressed but with an inflated base, lateral walls plane; labia rounded, with around 10–15 dentate-lacerate teeth. Figs 23, 24.

**Recognition:** *Plagiochila fasciculata* can be recognized by the combination of pinnate shoot systems with *Frullania*-type vegetative branching, stolons originating by lateral-intercalary branching, the deltoid leaves with an obscurely truncate apex, and up to 24 triangular teeth distributed around the apex and along the ventral margin; male plants have dentate bract lobes, bracts bearing a dorsal lamella particularly the first bracts produced within a male branch, and male branches often produced in threes at the apex of a shoot comprising an intercalary androecium and two androecia on *Frullania*-type branches; female plants have perianths whose labia are armed by sharp triangular-lacerate teeth.

*Plagiochila fasciculata* could be confused with *P. strombifolia*, but *P. strombifolia* does not have pinnate shoot systems, and vegetative branches arise by lateral-intercalary mode only. *Plagiochila strombifolia* leaves have margins armed with several spinose-ciliate teeth, rather than sharp triangular teeth; and male plants of *P. strombifolia* have entire androecial bract lobes.

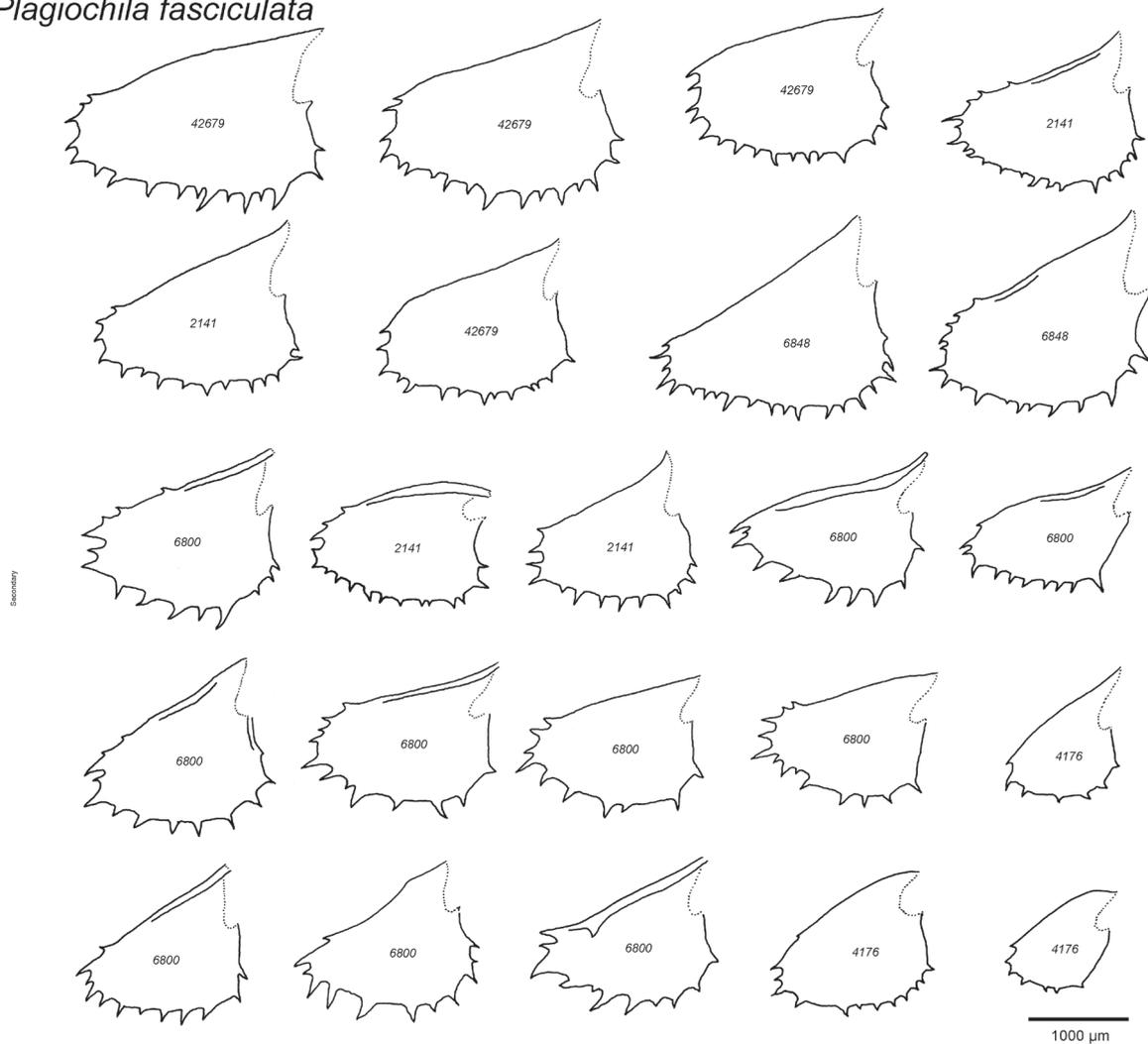
*Plagiochila fasciculata* could be confused with *P. deltoidea*, but *P. deltoidea* has stolons arising by ventral-intercalary branching, and vegetative branching of lateral-intercalary mode only. Male plants of *P. deltoidea* have entire androecial bract lobes.

*Plagiochila fasciculata*

**Fig 23.** *Plagiochila fasciculata* primary shoot leaves, from J.A. Curnow 2141 (CANB 8807469), CANB 8915211, H. Streimann 58820 (CANB 9802491), J.A. Curnow 4176 & H. Streimann (CANB 9501564), H. Streimann 58825 (CANB 9802496), and M.A.M. Renner 6848 (NSW 900152).

*Plagiochila fasciculata* could be confused with *P. subfasciculata*, but *P. subfasciculata* has narrower, triangular-ovate leaves, that are not as closely spaced on primary shoots, and which inroll along both dorsal and ventral margins when dry. The best way to appreciate the differences in leaf shape and dentition between *P. fasciculata* and *P. subfasciculata* is to compare the leaf outlines in Figs 23 and 24 with Fig. 25.

**Distribution and Ecology:** *Plagiochila fasciculata* is widespread and common in south east Australia from the Macpherson Ranges on the New South Wales-Queensland border south to the Otway Ranges in Victoria's south west, and in Tasmania. Throughout this range *Plagiochila fasciculata* inhabits rainforests and occasionally wet sclerophyll forests, usually in association with permanent watercourses where it is typically a lithophyte on bedrock and large boulders, or terrestrial on streambanks, but may occasionally be corticolous on tree trunks within riparian forest or on decaying tree trunks fallen into the streambed. In the Blue Mountains west of Sydney, *Plagiochila fasciculata* is a common riparian lithophyte on sandstone, whereas in north eastern New South Wales it occupies the same microsites but on rhyolite and other igneous rocks.

*Plagiochila fasciculata*

**Fig 24.** *Plagiochila fasciculata* secondary shoot leaves, from J.A. Curnow 2141 (CANB 8807469), J.A. Curnow 4176 & H. Streimann (CANB 9501564), M.A.M. Renner 6800 (NSW), M.A.M. Renner 6848 (NSW 900152), and H. Streimann 42679 (CANB 8915211).

In New Zealand *Plagiochila fasciculata* is apparently not common, I have seen no specimens from the North Island, and only a handful of specimens from the South Island, where it has been collected in similar microsites to those inhabited in Australia. Collections from Otago grew on rock under overhang of vegetation and on streambanks. All North Island specimens identified as *P. fasciculata* I examined proved to be *P. subfasciculata*. However, I have not examined specimens from two collections with regionally significant collections, F and CHR, and it may be that *P. fasciculata* is more widespread in the lower North Island and the South Island than the small list of specimens examined indicates.

**Representative specimens examined:** **Australia:** **Queensland:** Moreton, Lamington National Park, Macpherson Range, Canungra Creek west branch, upstream from Picnic Rock, 28°14'42" 159°09'13"E, 840 m, 7 Mar 2014, M.A.M. Renner 6842 & A.E. Orme (NSW 859320); Moreton, Lamington National Park, Macpherson Range, west of Toolona Lookout, 28°15'37"S 153°10'19"E, 1176 m, 6 Mar 2014, M.A.M. Renner 6824 & A.E. Orme (NSW 870747); Moreton, Coomera River catchment, MacPherson Range, O'Reillys track to Bithongabel, 28°15'28"S 153°09'46"E, 1111 m, 5 Mar 2014, M.A.M. Renner 6810 & A.E. Orme (NSW 850852); Moreton, Coomera River catchment, MacPherson Range, Lamington National Park, O'Reillys, track to Bithongabel, 28°15'43"S 153°10'11"E, 1186 m, 5 Mar 2014, M.A.M. Renner 6811 & A.E. Orme (NSW 850853); **New South Wales:** North Coast, Tweed Range, Border Ranges National Park, Brindle Creek, crossing of Helmholtzia Loop track, 28°22'45"S 153°04'18"E, 750 m, 3 Sep 2013, M.A.M. Renner 6771 (NSW 978730); Pinnacle Hill, Border Ranges National Park, 22 km NE of Kyogle, 28°25'S 153°07'E, 910 m, 24 Apr 1998, H. Streimann 61245 (CANB 9910863.1); Tweed Range, Border Ranges National Park, Bar Mountain Loop track, 28°27'37"S 153°07'12"E, 2 Sep 2012, M.A.M. Renner 6758 (NSW 978717); Weeping Rocks, New England National Park,

72 km E of Armidale, 30°30'S 152°24'E, 1400 m, 5 Apr 1991, *H. Streimann* 47674 (CANB 9107719); Track to Wrights Lookout, New England National Park, 72 km E of Armidale, 30°31'S 152°24'E, 1000 m, 5 Apr 1991, *H. Streimann* 47856 (CANB 9107902); Moppy Lookout, Northern Tablelands, Barrington Tops State Forest, 40 km WNW of Gloucester, 31°53'S 151°32'E, 1200 m, 26 Apr 1990, *H. Streimann* 44457 (CANB9008881); Jerusalem Creek Falls, Chichester State Forest, 19 km NNE of Dungog, 32°15'S 151°44'E, 350 m, 27 Aug 1987, *H. Streimann* 38243 (CANB 9006252); Central Tablelands: Blue Mountains National Park, Blackheath, Grand Canyon, between ascent to Evans Lookout and Beauchamp Falls, 33°39'S 150°19'E, 700 m, 12 Apr 2014, *M.A.M. Renner* 6848 (NSW 900152); South Coast, SE side of Mt Dromedary summit, along Rainforest Track, 13 km SW of Narcooma, 36°18'S 150°02'E, 21 Aug 1984, *K.R. Thiele* 783 (MEL 2341298); Beehive Falls, Beehive Creek, Coopracambra National Park, 26 km NNE of Cann River Township, 37°20'S 149°13'E, 320 m, 3 May 1992, *H. Streimann* 49561 (CANB 9216583); **Victoria:** Victoria, Gippsland, prope Rosedale, corticola, *Topic* 1889 comm. Schiffner (F! as *P. deltoidea* var. *pachydictyon* Herzog); Raymond Falls, Snowy River National Park, 28 km NW of Orbost, 37°29'S 148°18'E, 200 m, 18 Apr 1991, *J.A. Curnow* 4176 & *H. Streimann* (CANB 9501564); Otway State Forest, 13 km NNW of Apollo Bay, Beauchamp Reserve, 38°39'S 143°36'E, 460 m, 4 Dec 1996, *H. Streimann* 58820 (CANB 9802491); *ibid.*, *H. Streimann* 58825 (CANB 9802496); Otway State Forest, 12 km NW of Apollo Bay, 38°40'S 143°34'E, 260 m, 4 Dec 1996, *H. Streimann* 58768 (CANB 9802439); 30 km NE of Orbost, Arte River, 37°35'S 148°46'E, 280 m, 14 Feb 1990, *H. Streimann* 43785 (CANB 9007700); Binns Road, 8 km WNW of Apollo Bay, 38°45'S 143°35'E, 320 m, 29 Jun 1989, *H. Streimann* 42679 (CANB 8915211); Dandenong Ranges, Sherbrook Creek in Monbulk State Forest, 1.5 km W of Kallista, 37°53'S 145°21'E, 8 Aug 1984, *K.R. Thiele* 757 (MEL 2352960); Grampians, Castle Rock, 37°13'S 142°28'E, 11 Dec 1966, *J.H. Willis s.n.* (MEL 1004677); Eastern Highlands, Yarra Ranges National Park, Marysville Woods Point Road, Cumberland Scenic Reserve, walking track from Cambarville picnic area to crossing of Cumberland creek (along The Big Tree), 900 m, 37°33'S 145°53'E, 24 Jun 2001, *N. Klazenga* 5849 & *V. Stajsic* (MEL 2114288). **Tasmania:** Flinders Island, c. 320 metres at 39 degrees N of E of the summit of Big Badger Hill, 3.5 metres N of the bed of the major mapped gully, 40°02'15"S 148°01'21"E, 240 m, 5 Aug 2004, *J.S. Whinray* B1877 (MEL 2209256); Flinders Island, 630 m at 4.5 degrees W of S of the summit of Walkers Hill, 40°03'47"S 148°04'47"E, 300 m, 5 May 2001, *J.S. Whinray* 1291 (MEL 2238068); Van Diemens Land, in woods, Jun 1844, *J.D. Hooker* (FH 00284123); Van Diemen's Land, *Gunn*, apparently communicated via Dr R.K. Greville, 1 Mar 1843 (FH 00284118); Van Diemens Land, 1832, *Gunn*, (FH 00284124); Turua Beach, Deadmans Bay, 43°32'S 146°31'E, 2 m, 21 Jan 1987, *A. Moscal* 14255 (CANB 781957); Great Western Tiers, track to Westmoreland Falls, 24.5 km SW of Deloraine, 41°37'S 146°23'E, 500 m, 27 Nov 1988, *J.A. Curnow* 2141 (CANB 8807469); near Liffey Bluff, 22.5 km, SSE of Deloraine, 41°43'S 146°43'E, 1150 m, 30 Apr 1992, *J.A. Curnow* 4551 (CANB 9504733); Mt Wellington, South Trig Direttissimo, 42°55'S 147°14'E, 12 Apr 1982, *A.V. Ratkowsky* H1766 (HO 304335); Mt Wellington, Organ Pipes Track, 42°54'S 147°14'E, 21 Apr 1982, *A.V. Ratkowsky* H1765 (HO 304340); Sumac Road, South Arthur Road area, 41°10'S 145°03'E, 7 Feb 1979, *C. Turnbull* herb. Ratkowsky H1591 (HO 304313); Mt Eliza, below summit rocks, 42°58'S 146°25'E, 17 Apr 1982, *A.V. Ratkowsky* H1768 (HO 66965). **New Zealand: South Island:** Nelson Province, Papanoa Range, upper slopes of north side of Tiropahi River, 41°57'S 171°24'E, 130–170 m, 7 Feb 1983, *J.J. Engel* 19235 (F 1141623); Westland Province, Gillespies Beach Road, 12 km west of Fox Glacier, 43°25'S 169°55'E, 175 m, 24 Dec 1983, *J. Child* H4846 (F 1088121); Otago Province, Morrisons Creek, north of Dunedin, 45°51'S 170°30'E, 330 m, 12 Dec 1982, *J.J. Engel* 17693 (F 1141628); South Otago, Purakaunui Falls, 46°31'14"S 169°33'51"E, 18 Sep 1971, *G.M. Taylor* (AK 316656); Southland Province, Waikaia, Heriot Road, 45°44'S 168°51'E, 200 m, 6 Dec 1981, *J. Child* H3954 (F 1087590).

Representative misidentified specimens

*Plagiochila conturbata*

Mt Bellenden Ker, south peak, 23 km SSE of Gordonvale, 1550 m, 17°18'S 145°52'E, 3 Mar 1983, *H. Streimann* 27379 (CANB 8305344).

***Plagiochila subfasciculata*** Colenso, Transactions and Proceedings of the New Zealand Institute 20: 247 (1888)

*Type citation:* On logs and trunks of trees, wet woods near Dannevirke, County of Waipawa; 1887: *W.C.*

*Type:* New Zealand, North Is., Waipawa Co., near Dannevirke, Wood Creek, 10 Feb 1887, *Colenso a.1343* (lectotype designated by Bonner (1962): G 00128909!; isolectotypes: BM! NY WELT!d).

*Epitype* (designated here): New Zealand, North Island, Waitakere Ecological District, Spragg Bush, Turanga Road end, near small stream, 36°54'S 174°33'E, 320 m, 29 Sep 2005, *J.E. Braggins* 05/059 (AK 293730).

=*Plagiochila berggreniana* Colenso, Transactions and Proceedings of the New Zealand Institute 21: 52 (1889)

*Type citation:* On trees, woods south of Dannevirke, County of Waipawa; 1888: *W.C.*

*Type:* New Zealand, *Colenso a.1332* (lectotype designated by Bonner (1962) G 00115841!; isolectotypes: BM WELT!d)

= *Plagiochila reischeckiana* Steph., Bulletin de l'Herbier Boissier, sér. 2, 3: 331 (1903) = Species Hepaticarum 2: 315 (1903)

*Type citation:* New Zealand (Reischeck)

*Type:* New Zealand, *Reischeck 2* ex herb. Jack (lectotype designated by Bonner (1962): G 0069852!)

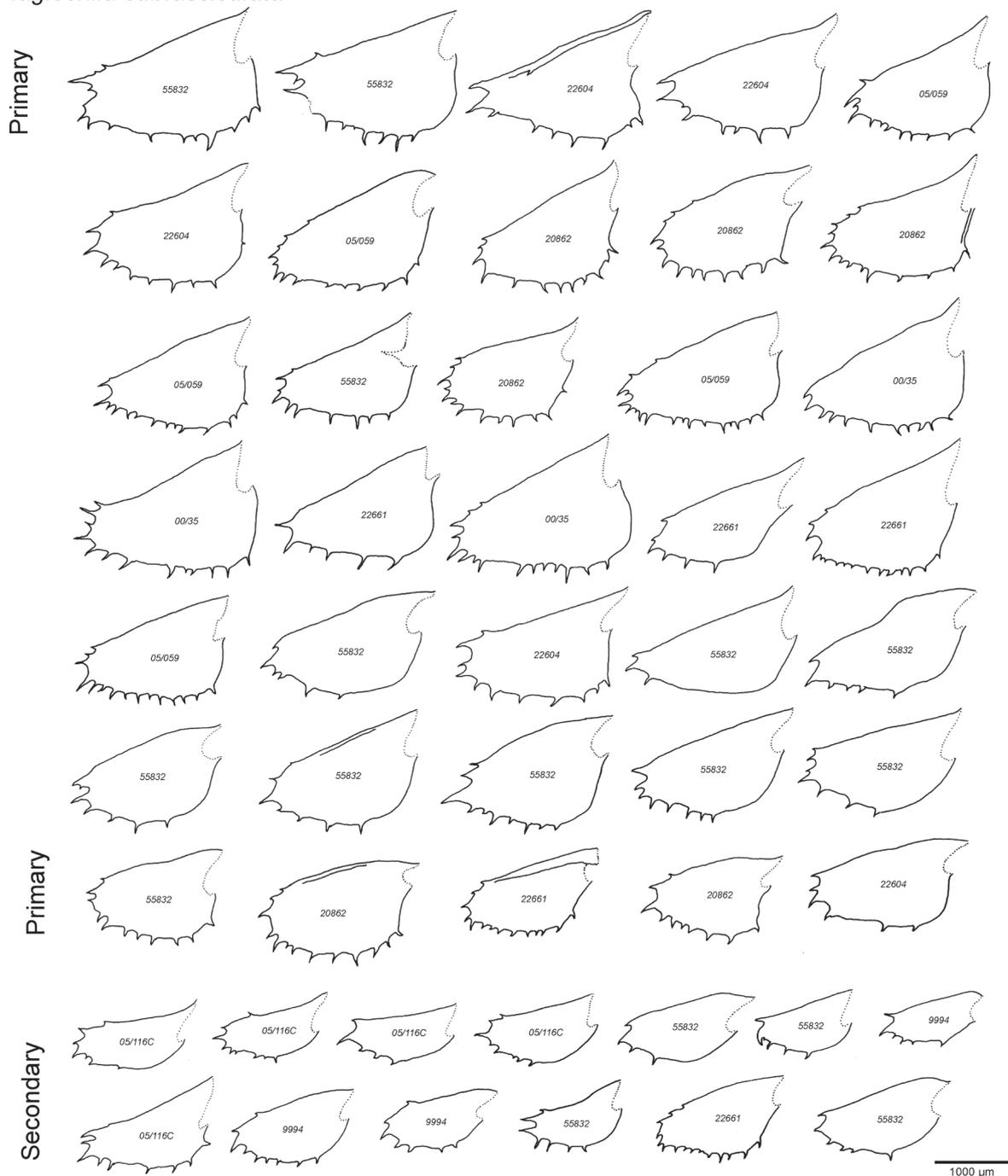
**Notes:** *Plagiochila berggreniana* Colenso is a large plant with remote-contiguous leaves on primary shoots with teeth continuous round the postical margin, and two larger teeth at the lobe apex. On secondary and tertiary shoots the leaves are smaller, more obovate, and have a narrow insertion bounded by inrolled antical and postical leaf margins. *Frullania*-type vegetative branching is common in the type, and stolons arise by lateral-intercalary branching, though these may originate very very close to the ventral merophyte.

The type of *P. reischeckiana* agrees with *P. berggreniana*. *Plagiochila reischeckiana* was listed as a synonym of *P. intertexta* in So (2001), and a synonym of *Plagiochila sinclairii* by Inoue & Schuster (1971). Engel and Merrill (2010a) placed *P. reischeckiana* in synonymy of *P. subflabellata* Colenso, which is itself a synonym of *P. trispicata* as discussed below.

**Etymology:** below *P. fasciculata*, probably referencing the many similarities these two species share.

**Description:** Plants with pinnately branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; forming turfs; mid-green, shoot systems to 100 mm long and 30 mm wide, dimorphic; primary shoots 2.5–4 mm wide, branches arising by *Frullania*-type and lateral-intercalary branches. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 450 µm diameter, transversely elliptic, surfaces apparently smooth, irregular; cortical cells in 3 to 5 layers, cortical cell walls strongly and continuously thickened, reddish-brown fading to yellow on the innermost cortical cell walls, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls beneath with walls thickened but tapering, other walls without trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots contiguous, succubously inserted and orientated, triangular-oblong to more or less elliptic, 1550–2450 µm long × 950–1575 µm wide, dorsal margin straight to shallowly arched, apex truncate, ventral margin straight in outer half and ampliate at base or continuously curved in more elliptic leaves, apex and ventral margins bearing 3–16 triangular teeth, teeth one to four cells broad at base, dorsal margin entire usually two teeth at the apex prominent, inner quarter of ventral margin at base of ampliate portion usually entire; leaves on secondary shoots elliptic to asymmetrically elliptic-ovate 1200–1750 µm long × 550–900 µm wide, margins bearing 4–9 teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, 9–15 µm long × 7–12 µm wide, long axis parallel to leaf margin, walls with bulging and confluent trigones, external and internal walls more or less continuously thickened; medial leaf cells isodiametric to ovoid, 11–28 µm long × 11–21 µm wide, walls unpigmented, with angular bulging trigones, medial thickenings rare; cells in leaf base oblong, 20–39 µm long × 14–21 µm wide walls with bulging trigones, medial thickening present, trigones not confluent. Cell surfaces smooth. Oil-bodies 4–6 per cell, homogeneous, ovoid, hyaline, 10–12 by 6–7 µm (*vide* notes on specimen AK 293730). Underleaves present, vestigial, triangular or filiform. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth produced singly, pairs or more commonly fascicles of three, branching within male branches by *Frullania*-type branching, lateral- and ventral-intercalary branches not associated with male branches; bracts in 5–13 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin with acute apex and 2–5 teeth, lobule epistatic lobes on basal bracts with a single oblique lamella that is fused with the lobule of the preceding bract on the same side of the shoot, antheridia not seen; stem among bracts smooth. Gynoecia at apices of shoots; bracts oblong-ovate, to 2600 µm long, larger than subtending leaves; dorsal margin recurved, ventral margin ampliate; dorsal margin entire, apex and ventral margins with triangular acuminate teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts with or without fertilisation. Perianth obovate, to 2000 µm long and 1600 µm wide at mouth, keels unwinged; laterally compressed but with an inflated base, lateral walls plane; labia rounded, with lacinate-dentate teeth. Fig. 25.

*Plagiochila subfasciculata*

**Fig 25.** *Plagiochila subfasciculata* leaves, from H. Streimann 55832 (CANB 9514159), J.J. Engel 22604 (F 1141589), J.J. Engel 20862 (F 1141137), J.J. Engel 22661 (F 1141192), J.E. Braggins 05/059 (AK 293730), J.E. Braggins 05/116C (AK 297119), P.J. de Lange 9994 & M.A.M. Renner (AK 327798), and E.A. Brown 00/35 & A.J. Leishman (NSW 444725).

**Notes:** Application of the name *Plagiochila baileyana* has been associated with confusion that warrants examination and explanation. Stephani (1903) described *Plagiochila baileyana* from collections made by F.M. Bailey at Palm Camp (see Dowe and Broughton 2007) during the Bellenden Ker expedition in 1889. Bailey collected at least two species of *Plagiochila* at this location, *P. baileyana* and *P. conturbata* Steph., the latter is common in tropical montane forests throughout the Wet Tropics Bioregion. Both species were evidently included in the original material of *Plagiochila baileyana*, and unfortunately this admixture is not now evenly distributed among contemporary specimens derived from that original gathering. While the type specimen in Stephani's herbarium in Genève comprises two shoot systems that agree with Stephani's protologue, a presumed duplicate of the type in NY contains *P. conturbata* alone. The lack of admixture in this specimen does not

immediately hint at the mismatch between the plant contained in the specimen, and the plant described by Stephani, however heterogeneity in the composition of the original material and uneven distribution of these components among specimens derived from the original gathering are the genesis of confusion associated with the application of the name *Plagiochila baileyana*, initiated by Inoue and Schuster (1971) and perpetuated until application of the name *P. baileyana* was clarified by Engel and Merrill (2010).

*Plagiochila baileyana* is now understood to be a species endemic to the Wet Tropics of north-east Queensland, and though similar to *P. gigantea*, is distinct from it. How then, did Inoue and Schuster (1971) come to use the name *P. baileyana* for plants of wide distribution in southern temperate Australia and New Zealand? One explanation is that Inoue and Schuster (1971) made three errors of interpretation when they applied the name *P. baileyana* to Tasmanian and New Zealand plants. Firstly, Inoue and Schuster (1971) did not examine the full suite of original material of *P. baileyana*, and so overlooked the fact that the original material was mixed. They did not examine the specimen in G inadvertently designated as the lectotype of *P. baileyana* by Bonner (1962). Secondly, they failed to effectively assess the specimen held by NY against the protologue. Thirdly, they failed to appreciate the significance of subtle morphological differences between the NY specimen and plants from Tasmania and New Zealand.

The first error is surprising, but in their revision of *Plagiochila* was not unique to *P. baileyana*, see for example their typification of *P. deltoidea* as discussed above where Inoue and Schuster (1971) apparently did not seek original material from the describing author's own herbarium. The second error is equally surprising, because although Stephani's descriptions have a reputation for being 'usually little informative, without mention of important diagnostic characters, and often contain errors' (Gradstein 2006 p. 560) Stephani's *P. baileyana* protologue contains detail of several distinctive characters all of which conflict with plants attributed to that species by Inoue and Schuster (1971) in particular:

- 1) Stems: 'ad 7 cm... geniculatim et alterne flexuosis (zigzag)' [stems to 7 cm... geniculate and alternately flexuose (zigzag)]
- 2) leaves: 'omnia ex angusta basi elliptica' [all elliptic from a narrow base]
- 3) leaf margins: 'dentibus majusculis ubique subaequalibus numerosis' [teeth almost equal everywhere numerous]
- 4) marginal cells: 'maxime incrassates, lumine cellularum saepe oblitterato' [maximally incrassate, cell lumen often obliterated]

These four characters are at such variance with the NY specimen that a mismatch between the description and the NY specimen considered as the type should really have been perceived by Inoue and Schuster (1971). All the characters above are, by contrast, compatible with the lectotype in Geneva, and are characteristic of *P. baileyana* as we know it from more recent collections. That the specimen of *P. baileyana* examined by Inoue and Schuster (1971) held in NY, although bearing the same collection details as the holotype of *P. baileyana* in G, does not contain the same plant was missed. The illustration of the type of *P. baileyana* in Inoue and Schuster (1971 Fig. 61: 2, 3, 5) shows the characteristic leaf shape and dentition of *P. conturbata* Steph., specifically the triangular ovate leaf shape, with a long shallowly curved dorsal margin extending to near a vertex with the ventral margin, the lack of teeth on the dorsal margin, the shallow ampliation at the leaf base, and the few (8 and 9 illustrated) sharp, relatively evenly sized teeth.

The third error committed by Inoue and Schuster (1971) was one of application. Having fixed the identity of *P. baileyana* on a Queensland endemic now known as *P. conturbata* Steph., they proceeded to apply this name to plants from Southern Temperate Australasia. This led to inevitable difficulties, as southern temperate plants do not match those from Queensland exactly, but differ in details of leaf size, shape and dentition, and may explain why Inoue and Schuster (1971) applied of the name *P. baileyana* to plants now attributed to three different species, namely *P. fasciculata*, *P. incurvicolla*, and *P. subfasciculata*. The characters used to circumscribe *P. baileyana* employed by Inoue and Schuster (1971) encompass all three species:

- 1) broadly ovate to somewhat asymmetrically quadrate-ovate leaves with moderately to strongly ampliate postical bases.
- 2) leaves varying from as long as to slightly longer than broad or very occasionally slightly wider than long
- 3) 8-9 strong, occasionally 20-29, irregular, rather coarse, broad-based teeth, with two of the apical ones sometimes stronger and occasionally feebly lobe-like.
- 4) basal leaf cells moderately elongated, usually twice as long as broad or little more, with very strong trigones

- 5) very frequent terminal *Frullania*-type branching
- 6) gynoecia and androecia both usually clustered near shoot apices.

Inoue and Schuster (1971) identified subtle differences among specimens attributed to their *P. baileyana*, including plant size, frequency and distribution of *Frullania*-type branching, and leaf marginal teeth ('stronger' in New Zealand plants). However: 'these minor differences seem of slight taxonomic value in this variable complex' (Inoue and Schuster 1971 p. 177).

Comments on recognition and variation of *P. baileyana* by Inoue and Schuster (1971) are consistent with this broad circumscription. They note that *P. baileyana* 'is more likely to be confused with *P. deltoidea* complex than with the *P. fasciculata*-*incurvicolla* complex' (p. 177) and their illustrations in Figs 62 and 63, derive from the inclusion of *P. fasciculata* within their concept of *P. baileyana*. Their illustration of leaves in Fig. 62 (4, 6) and comment that *P. baileyana* is a variable plant with respect to vigour, within which 'small phases occur that are found procumbent on moist cliff faces... that are only 2-3.5(4) cm long × 2.9-3.8 mm wide, and are quite sparingly branched, chiefly with intercalary branches from older shoot sectors, but occasionally with a few terminal branches from the apices of mature shoot sectors' derive from the inclusion of *P. incurvicolla*. Inoue and Schuster (1971)'s Figure 64, and 65:1 are from a plant of *P. subfasciculata*, illustrating well its remote narrow-deltoid leaves and are evidence that *P. subfasciculata* was also included within their concept of *P. baileyana*. They also attributed a couple of Australian plants of *P. fasciculata* to *P. baileyana*. As another twist to this misinterpretation, while most of the plants associated with *P. baileyana* by Inoue and Schuster (1971) were *P. fasciculata*, their concept of *P. fasciculata* was also based on a mixture of *P. subfasciculata* and *P. fasciculata*. All three of their illustrations of *P. fasciculata* (Figs 64–66) are of *P. subfasciculata*, and this in combination with an emphasis on characters distinctive of *P. subfasciculata* in their recognition section, may have contributed to propagating the confusion between *P. fasciculata* and *P. subfasciculata*.

Engel and Merrill (2010a) concluded that *Plagiochila aculeata* (Hook.f. & Taylor) Gottsche, Lindenb. & Nees whose type specimen was collected in Tasmania by J.D. Hooker, was the same as 'the rather common and widely-distributed New Zealand species treated as *P. baileyana* Steph. by Inoue and Schuster (1971) and Inoue (1986)' (Engel and Merrill 2010a p. 502). However, the type of *P. aculeata* is a better match with *Plagiochila fasciculata* in its leaf dentition, the spacing of the leaves, and the presence of a broad ampliate leaf base on primary shoot leaves, besides which *P. subfasciculata* is not known from Tasmania. The statement that *P. aculeata* is widespread in Australia and New Zealand, and the attribution of *P. subfasciculata* to synonymy of *P. aculeata* both suggest that *P. fasciculata* and *P. subfasciculata* were subsumed within the circumscription of this species by Engel and Merrill (2010a).

Engel and Merrill (2010a) introduced an additional complication when they reinstated *P. subflabellata* from synonymy of *P. fasciculata*, where it had been placed by Stephani (1892), Inoue and Schuster (1971), and So (2001), describing *Plagiochila subflabellata* as 'a distinctive species differing from *P. fasciculata* in several important respects.... primarily in the form of the leaves on the main shoot, which are "sub-trapeziform" (Colenso 1888) in outline, with straight, "cilio-serrate" ventral margins aligned at 90° to the stem. The overall aspect is that of a gracile *P. obscura*' (p. 503). As described, the perianths were strongly keeled both dorsally and ventrally, and distinctly peduncled, and the male bracts were not lamellate or fused with the preceding bract, as is the case in *P. fasciculata*.

I too have contributed to this confusion. In Renner *et al.* (2017a, c) I incorrectly applied the name *Plagiochila subflabellata* to plants that are actually *P. subfasciculata*. At that time I had not seen the type of *P. subflabellata*, and was applying the name based on my interpretation of Engel and Merrill's (2010) treatment of *Plagiochila subflabellata*, in particular the implied affinities with *P. fasciculata* and description of tightly revolute leaves in dried plants. However, time spent learning the plants pays dividends and has convinced me of my error, which I first realized when it became apparent that my application of the name *P. subflabellata* was inconsistent with Engel and Merrill (2010a) in that males of my plants were lamellate, as in *P. fasciculata*, rather than elamellate as reported for *P. subflabellata*. Secondly, inspection of digital images on Te Papa's website suggested, in lieu of my study of the *Plagiochila arbuscula* complex (Renner *et al.* 2018), that leaf spacing, shape and dentition in the types of both *Plagiochila heterophylla* and *Plagiochila subflabellata* were consistent with the type of *Plagiochila trispicata*, hence Engel and Merrill's allusion to the similarity between *P. trispicata* (as *P. arbuscula*) and *P. subflabellata*, and Colenso's description of 'peduncled' perianths for the latter. So, while Engel and Merrill (2010a) correctly excised *P. subflabellata* from synonymy of *P. fasciculata* they did not fully appreciate the affinities between it and *P. trispicata*. In this I have perhaps been fortunate, as I was for a time convinced that a gracile plant from coastal forest at Maunganui Bluff in western Northland belonged to a species distinct from *P. trispicata*, yet it nested among other individuals of that species in my molecular phylogeny (Renner *et al.* 2017a), suggesting morphological differences represented infra-specific variation only. In my treatment both *P. heterophylla* Colenso and *P. subflabellata* are treated as synonyms of *P. trispicata*, below.

**Recognition:** *Plagiochila subfasciculata* can be recognised as a member of the *P. fasciculata* complex by the combination of *Frullania*-type vegetative branching, lateral-intercalary stolon origin, lamellate male bract lobules whose lamellae are fused with the preceding bract, and homogeneous oil-bodies. Within the *P. fasciculata* complex *P. subfasciculata* can be recognized by its leaf shape and spacing. On primary shoots of *P. subfasciculata* the leaves are remote to contiguous and have at best a weakly ampliate base such that the leaf length is longer than its breadth, where length is measured parallel to the leaf antical margin, and breadth is measured perpendicular to the length, the interior leaf margin is often entire. On primary shoots of *Plagiochila fasciculata* the leaves are contiguous to imbricate and have an ampliate base such that the leaf length and breadth measured as above are roughly equal. The leaves of *P. incurvicolla* are contiguous on primary shoots, though may spread to remote in conditions of abundant moisture and shade, they are broadly ovate with the apex and postical margin armed by a few conspicuous spinose teeth. On secondary shoots of *P. subfasciculata* the leaves are slightly obovate, and have around 10 teeth around the apex and on the ventral margin, the leaf base is not ampliate. In *P. fasciculata* secondary shoot leaves are ovate, similar to the primary shoot leaves, and bear anywhere up to 18 teeth.

**Distribution and Ecology:** *Plagiochila subfasciculata* occurs on Lord Howe Island, and New Zealand where it is widely distributed in forested habitats of the North Island and the north west of the South Island. *Plagiochila subfasciculata* is an epiphyte or lithophyte, or occasionally an inhabitant of exposed soil. In the North Island some of the forests it inhabits are susceptible to intermittent summer drought, so *P. subfasciculata* may be found close to or within waterways on boulders, bedrock, and stream banks. In cool hyperhumid forests *P. subfasciculata* may grow as an epiphyte on tree trunks, and does not appear to exhibit forest-type or host species preference, having been collected in forests as diverse as mixed podocarp-broadleaf forest with *Agathis* and *Laurelia*, and wind-pruned scrubs of *Melicytus ramiflorus*, *Coprosma grandiflora*, and *Olearia rani*.

**Representative specimens examined:** **Australia: Lord Howe Island:** 1882, A.C. de la Camara (MEL 1039449); Goathouse Cave, 31°33'50"S 159°05'15"E, 420 m, 7 Feb 1995, H. Streimann 55832 (CANB 9514159); *ibid.*, H. Streimann 55882 (CANB 9514209); Mount Gower, northern reaches of summit, 31°35'00"S 159°04'55"E, 820 m, 10 Jun 2000, E.A. Brown 00/35 & A.J. Leishman (NSW 444725); Top of Mount Gower, 31°35'S 159°04'E, 8 Sep 1963, A.C. Beauglehole 73063 (MEL 1041574); Lord Howe Island, without further data (MEL 1039451). **New Zealand: North Island:** North Auckland Province, Radar Bush, WSW of Cape Reinga, S of Mt Te Paki, 34°28'S 172°46'E, 100 m, 6 Feb 1995, J.J. Engel 20862 (F 1141137); Te Paki, Radar Bush, Upper Waitiki Stream, 34°28'07"S 173°51'23"E, 100 m, 19 Sep 2011, P.J. de Lange 9994 & M.A.M. Renner (AK 327798); North Auckland Province, Waima Forest, Hauturu Highpoint track, in vicinity of Hauturu Trig off Waitemarama track, 35°31'S 173°28'E, 650-680 m, 23 Feb 1997, J.J. Engel 22604 (F 1141589); North Auckland Province, Waipoua Forest, Waikohatu Stream at Waikohatu Kauri Bridge, 35°38'S 173°33'E, 290 m, 24 Feb 1997, J.J. Engel 22661 (F 1141192); Waipoua Forest, track to Te Matua Ngahere, 35°36'S 173°31'E, 340 m, 22 Feb 1997, J.J. Engel 22557 (F 1141144); NE Waitakere Ranges, Spraggs Bush, 360 m, 36°54'S 174°33'E, 7 Feb 1997, J.J. Engel 22174 (F 1141650); *ibid.*, J.J. Engel 22185 (F); Waitakere Ranges, Spraggs Bush, 320 m, 29 Sep 2005, J.E. Braggins 05/059 (AK 293730); South Auckland Province: Coromandel State Forest Park, summit of Table Mountain, 37°03'S 175°40'E, 835 m, 14 Feb 1997, J.J. Engel 22355 (F 1141685); Kaimai-Mamaku Forest Park, Kaimai Range, Aongatete River, upstream from intersection of North-South track and river, 37°41'S 175°54'E, 425 m, 7 Feb 2003, J.J. Engel 23639, M.J. von Konrat & J.E. Braggins (F C0311971F); Kaimai Range, Kaimai-Mamaku Forest Park, near crest and headwaters of Wairere Falls, 37°44'02"S 175°52'48"E, 405 m, 8 Feb 2006, J.J. Engel 26697 (F C0311975F); Tararua Range, South Manawatu Gorge, Sledge Track, Kahuterawa, 40°28'36"S 175°37'04"E, 170 m, 12 Dec 2005, J.E. Braggins 05/116C (AK 297119); **South Island:** North-West Nelson Ecological Region, Wakamarama Ecological District, Mt Burnett, west of and below 4WD track to south summit (The Three Sisters), between junction with road up and last bend, 40°38'36"S 172°38'10"E, 590 m, 30 Nov 1995, J.E. Braggins 95/695D (AK 286012); Nelson Province, Paparoa National Park, Bullock Creek Road, along Bullock Creek, 42°06'S 171°23'E, 25 m, 23 Feb 1995, J.J. Engel 21601 (F 1141142).

***Plagiochila annotina*** Lindenb., Species Hepaticarum 1: 34 (1839)

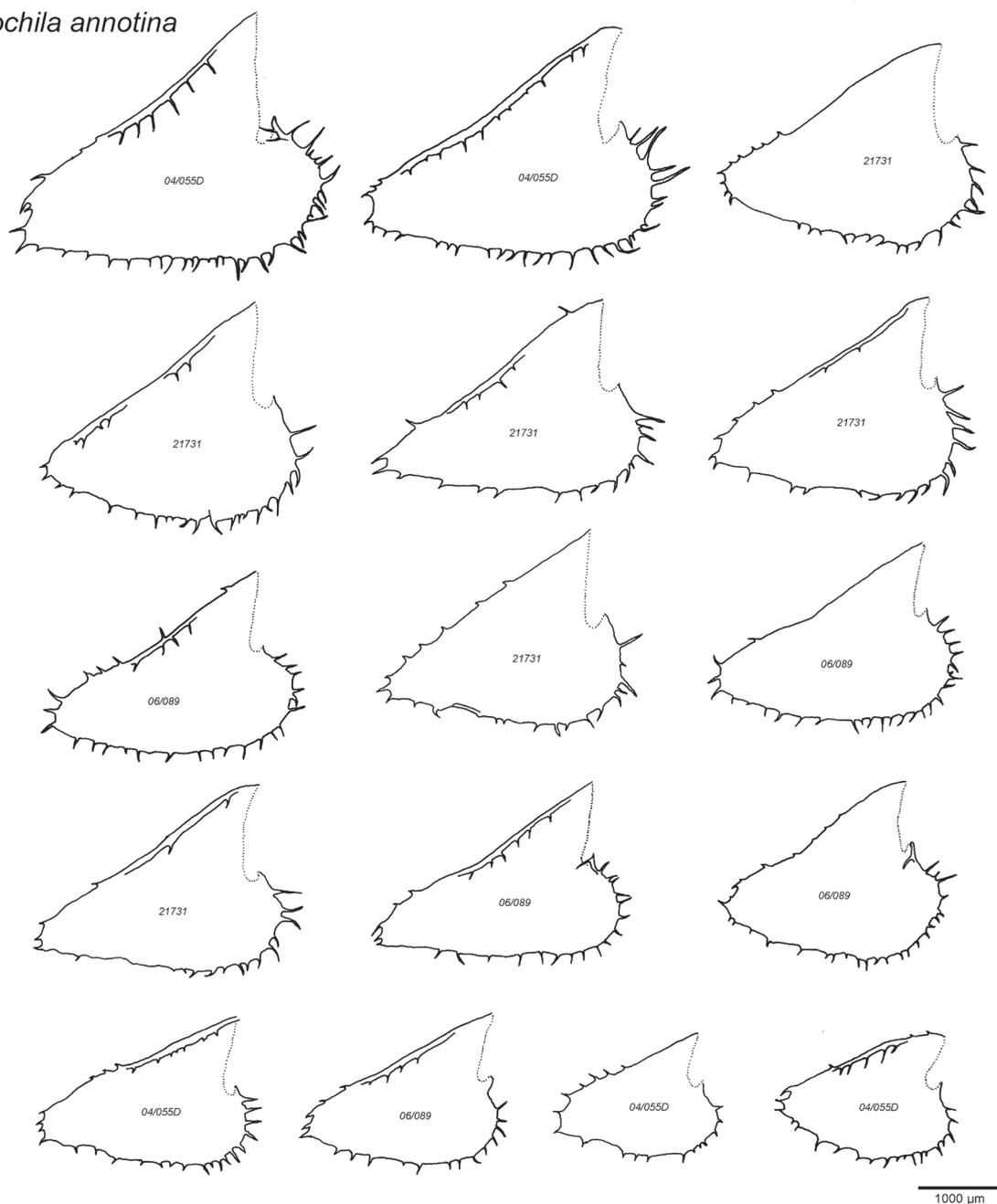
*Type citation:* in sinu Dusky Bay dicto Novae Zeelandiae unde retulit Menziesius anno 1791. Specimen benevole communicavit cl. Hookerus.

*Type:* n.v.

*Jungermannia annotina* Menzies ex Hook., Musci Exotici 1: 90 (1818) *nom. inval.*

*Type citation:* Dusky Bay, 1791, leg. D. Menzies.

**Etymology:** of the preceding or previous year, reference obscure.

*Plagiochila annotina*

**Fig 26.** *Plagiochila annotina* leaves, from J.E. Braggins 04/055D (AK 290979), J.E. Braggins 06/089 (AK 303109), and J.J. Engel 21731 (F 1141204).

**Description:** Plants with irregularly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons and from leafy shoots by lateral-intercalary branching; forming turfs; shoot systems to 80 mm long, monomorphic; primary shoots 3–6.5 mm wide, branches arising by lateral-intercalary branches, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 600 μm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell yellow-pigmented, walls without trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, triangular ovate to narrow triangular ovate, 1900–3660 μm long × 1310–2550 μm wide, dorsal margin straight to shallowly arched, inrolled, ventral margin straight in outer half and amplexate at base, apex narrowly rounded, all margins bearing 18–46 spinose teeth, teeth two cells broad at base, uniseriate above, teeth on ventral margin

longer than those on dorsal margin, longest on ampliate base; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with bulging trigones but not continuously thickened; medial leaf cells isodiametric to ovoid, 24–46 µm long × 20–33 µm wide, walls unpigmented, with bulging trigones, medial thickenings absent; cells in leaf base polyhedral, 40–60 µm long × 33–42 µm wide walls with bulging to nodulose trigones, medial thickening absent, trigones not confluent. Cell surfaces smooth. Oil-bodies 4–8 per cell, hyaline, granular botryoidal. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth produced singly, branching within male branches uncommon, by lateral-intercalary branching, *Frullania*-type and ventral-intercalary branches not associated with male branches; bracts in 5–40 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin toothed, epistatic, antheridia 2–3 per bract, stalk biseriate; stem among bracts smooth. Gynoecia at apices of shoots; bracts oblong-ovate, 3000–4000 µm long and 1800–3000 µm wide, larger than subtending leaves; dorsal margin plane or inrolled, ventral margin ampliate; dorsal, ventral, and apical margins all with spinose teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations produced by lateral-intercalary branching from between the female bracts, a single innovation without fertilisation or two with fertilisation. Perianth oblong, 3700–4500 µm long and 700–1600 µm wide at mouth, dorsal keels with a low spinose dentate wing; laterally compressed but with an inflated base, lateral walls plane; labia rounded, each with around 20–25 spinose teeth. Fig. 26.

**Recognition:** *Plagiochila annotina* can be recognized by the robust, sparingly branched shoots with densely imbricate, succubously orientated, triangular leaves bearing sharp triangular to spinose teeth on all margins, including the dorsal margin (Fig. 26). The perianths have paraphyllia and winged keels. The male branches are intercalary, serial, and have leaf-like toothed male bracts.

*Plagiochila annotina* could be confused with *P. kirkii* but has spreading (not ventrally secund) triangular-ovate (not narrow triangular and weakly falcate) leaves with straight (not curved) teeth on the ampliate postical margin and is golden-brown (not fuscous).

*Plagiochila annotina* could be confused with *P. baylisii* but has triangular-ovate (not rotund-ovate) leaves with numerous teeth on all margins (not a few teeth at the base of the dorsal margin, two apical teeth, and no of a few scattered teeth on the ventral margin) and vegetative branching exclusively by lateral-intercalary mode (not mixed lateral-intercalary and *Frullania*-type).

**Distribution and Ecology:** *Plagiochila annotina* is endemic to New Zealand, where it occurs from Northland to Rakiura in cool hyperhumid forests. *Plagiochila annotina* is an epiphyte on tree trunks and branches, and forms dense tall turfs, often on the trunks of large canopy trees including for example on *Beilschmiedia* and *Weinmannia* in mixed broadleaf forest; on *Nothofagus menziesii* in mixed *Nothofagus*-podocarp forest; and on the base of *Dacrycarpus dacrydioides* trunk in Kahikatea forest. *Plagiochila annotina* may also grow on fallen corticated logs, and on roots on the forest floor. *Plagiochila annotina* has been recorded from Australia, but all reports are based on misidentifications of other species.

**Representative specimens examined:** **New Zealand: North Island:** North Auckland Province, Mangamuka Walkway, Maungataniwha Range ESE of Kaitaia, saddle on SH1, 35°12'S 173°27'E, 390 m, 8 Feb 1995, *J.J. Engel* 20962 (F 1141203); Western Northland Ecological Region, Maungataniwha Ecological District, Puketi Forest, Waihoanga Gorge, Kauri Walkway, on banks of Waihoanga Stream, 35°15'13"S 173°44'51"E, 250 m, 20 Mar 2006, *J.E. Braggins* 06/089 (AK 303109); Omahuta State Forest, 35°12'02"S 173°37'53"E, 160 m, 22 Oct 1980, *J.E. Braggins* (AK 326436); Waipoua Forest, track to Yakkas Kauri, 35°37'S 173°32'E, 300 m, 25 Nov 1994, *J.E. Braggins* 94/204 (AK 257208); Little Barrier Island (Hauturu), just past summit of Kiriraukawa, 36°12'00"S 175°05'00"E, 690 m, 26 Jan 1980, *J.E. Braggins* 80/805d & *J.E. Beever* (AK 312442); Coromandel Peninsula, Tairua Ecological District, Kaitarakihi Track, 37°09'S 175°40'E, 31 Jan 1987, *J.E. Braggins* 87/011 (AK 259062); Waikato, Kawhia, Lake Koraha, 38°09'34"S 174°55'21"E, 210 m, 28 Oct 1989, *J.E. Braggins* 89/94 (AK 316641); Pureora State Forest, Waipapa Ecological Area, 38°27'27"S 175°33'40"E, 565 m, 26 Jan 1982, *J.E. Braggins* 35h (AK 321111); Wellington District, Tararua Range, Puffer track, to Smiths Creek track, 41°04'S 175°14'E, Nov 1981, *T. Moss* (AK 316649); Wellington District, Akatarawa, ridge above Waterfall Creek, 40°57'36"S 175°06'42"E, 9 Dec 1984, *J.E. Braggins* 84/443 (AK 316850); **South Island:** Richmond Ecological Region, Pelorus Ecological District, Brown River Reserve on SH6 north of Rai Valley township, 41°12'37"S 173°34'46"E, 60 m, 28 Oct 2004, *J.E. Braggins* 04/055D (AK 290979); Westland Province, Ship Creek, 14.5 km N of Haast River, 43°46'S 169°10'E, 1 m, 26 Feb 1995, *J.J. Engel* 21731 (F 1141204); South Westland, Lake Ellery, 44°05'S 168°43'E, 60 m, 12 Dec 1981, *J. Child* H4591 (F 1088378); **Rakiura (Stewart Island):** 1909, *L. Cockayne* 8226 (AK 18667); Anglem Ecological District, Freshwater Valley, 500 m along track to Rocky Mountain from junction with track to North Arm, 46°52'S 167°56'E, 80 m, 9 Apr 2001, *M.A.M. Renner* 137 (AK 255216)

*Representative misidentified specimens**Plagiochila baylisii*

Tasmania: Mt. Wellington, *L. Rodway 56a* (HO 87713); Deadmans Bay, 43°32'S 146°30'E, 15 m, 21 Jan 1987, *A. Moscal 14287* (HO 123072); East Coast, Orielson Rivulet, 12 km NNW of Sorell, 42°40'S 147°31'E, 11 Sep 1988, *A. Moscal 16521* (HO 577034).

*Plagiochila kirkii*

New Zealand, North Island, Western Northland Ecological Region, eastern edge of Waipoua Forest, Mataraua Plateau west of Waoku Road, 35°38'S 173°39'E, 480 m, 24 Apr 2003, *J.E. Braggins 03/127* (AK 360297); *ibid*, Mataraua Plateau, Toronui Stream headwaters, 35°38'S 173°38'E, 450 m, 10 Nov 2001, *M.A.M. Renner 253c*, *C.D. Kilgour & J. Lux* (AK 282337); Rangitoto Island, near base of cone, 36°48'S 174°51'E, Jul 1971, *J.E. Braggins* (AK 316784); Coromandel Peninsula, Whitianga-Coromandel Road, Waiau River, 36°50'S 175°33'E, 28 Jan 1973, *J.E. Braggins s.n.* (AK 316594).

*Plagiochila retrospectans*

Tasmania, East Coast, Plummers Creek State Forest, 43°07'S 147°47'E, 250-300 m, 30 Dec 1998, *A. Moscal 30231* (HO 577035).

***Plagiochila strombifolia*** Taylor ex Lehm., *Novarum et Minus Cognitarum Stirpium Pugillus* 8: 5 (1844)

*Type citation:* Habitat in Terro van Diemen, ubi legit cel. Gunn. (Hb. Greville et Tayl.)

*Type:* Leg. Gunn hb Greville & Taylor (lectotype designated by Bonner (1962): G; (?)isolectotype: herb. Lehmannianum, no. 83<sup>s</sup>, S)

=*Jungermannia strombifolia* Hook.f. & Taylor, *London Journal of Botany* 3: 578 (1844)

*Type citation:* Van Diemen's Land.

*Type:* Tasmania, ex Macquaries River, 1836, *R. Ball* (syntype: FH 00458022!); Leg. Gunn hb Greville & Taylor (syntypes: G, S)

=*Plagiochila kingiana* Gottsche, *Annales des Sciences Naturelles; Botanique, sér. 4, 8:* 323 (1857)

*Type citation:* Habitat in Novae Hollandiae insula King, ubi sterilis et cum peridoniis, a cel. Guichenot lecta est. (*Herb. Mus. Paris*, no. 22).

*Type:* Australia: King Island, *Guichenot* (holotype: P; isotypes: G! BM!)

=*Plagiochila neohoweana* Pearson, *University of California Publications in Botany* 10: 315 (1923)

*Type citation:* None provided.

*Type:* Tasmania, Mt Wellington, December 1886, *Bastow 530* (lectotype designated here: MANCH!)

=*Plagiochila stuartiana* Gottsche, *Linnaea* 28: 548 (1856) [1857]

*Type citation:* in insula van Diemen a cel. C. Stuart lecta.

*Type:* Tasmania, *C. Stuart*, olim *P. stuartiana* G ms, ex herb. Stephani (lectotype designated by Bonner (1962): ex herb. Melbourne G 026166! isolectotypes: ex herb. Gottsche, Mitten dedit G 00164987! MEL 1039248!)

**Notes:** *Plagiochila strombifolia* Taylor ex Lehm. and *Jungermannia strombifolia* Hook.f. & Taylor have been thought based on the same specimen, but while the protologue of *Plagiochila strombifolia* Taylor ex Lehm. identified a single gathering as the type, the protologue of *Jungermannia strombifolia* Hook.f. & Taylor is less restrictive, stating 'Hab. Van Diemen's Land'. In Taylor's herbarium at FH there is a specimen collected by R. Ball in 1836 from Macquaries River labelled '*Jungermannia strombifolia* Taylor mss', that also bears a near verbatim copy of the Latin protologue of *Jungermannia strombifolia*, in Taylor's handwriting. It seems likely that this specimen is a syntype of *Jungermannia strombifolia* Hook.f. & Taylor. Details of the perianth are missing from this handwritten description, and no perianths are present in the associated specimen, so either a duplicate piece bore perianths or the perianth description was taken from another of the specimens comprising the original material, possibly the specimen collected by Gunn. Interestingly, the specimen collected by R. Ball is *Plagiochila fragmentissima*, and the description of the obovate perianths with rounded labia bearing teeth in Hooker and Taylor's protologue is compatible with *P. fragmentissima*, and arguably a better match with this species than with *P. strombifolia*. However, I have not seen the Gunn collection identified as the type of *Plagiochila strombifolia* Taylor ex Lehm.

**Etymology:** maybe meaning twisted leaf, but reference unclear.

**Description:** Plants with irregularly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; forming turfs; shoot systems to 70 mm long, monomorphic; primary shoots 3–6 mm wide, branches arising by lateral-intercalary branches, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 500 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, outer layer and free external wall thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell yellow-pigmented, walls with triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, triangular ovate, 1940–3250 µm long × 1350–2690 µm wide, dorsal margin straight to shallowly arched, inrolled, ventral margin shallowly curved in outer half and ampliate at base, apex rounded, all margins except basal half of the dorsal margin bearing 9–29 spinose-ciliate teeth, teeth two or three cells broad at base, uniseriate above, teeth on ventral margin longer than those on dorsal margin, longest on ampliate base; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with bulging to nodulose trigones but not continuously thickened; medial leaf cells isodiametric to ovoid, 25–46 µm long × 24–35 µm wide, walls unpigmented, with nodulose trigones, medial thickenings absent; cells in leaf base polyhedral, 45–64 µm long × 24–32 µm wide walls with bulging to nodulose trigones, medial thickening uncommon, trigones not confluent. Cell surfaces smooth. Oil-bodies 4–8 per cell, hyaline, homogenous or few segmented, smooth. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, series of three or four at the apex of vegetative shoots, or in loose fascicles produced by lateral-intercalary or *Frullania*-type branching at the base of the leading male branch; ventral-intercalary branches not associated with male branches; bracts in 5–9 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin entire, or rarely with a few triangular teeth, epistatic, antheridia 1 or 2 per bract, stalk biseriolate; stem among bracts smooth. Gynoecia at apices of shoots; bracts oblong-ovate, 3500 µm long and 2500 µm wide, larger than subtending leaves; dorsal margin plane or inrolled, ventral margin ampliate; outer half of dorsal, ventral, and apical margins all with spinose teeth, teeth more numerous and longer on the ventral margin; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations, if present, produced by lateral-intercalary branching from between the female bracts. Perianth campanulate, 3500–4100 µm long and 2500–3300 µm wide at mouth, dorsal keel with a narrow wing; laterally compressed but with an inflated base, lateral walls plane; labia straight, each with around 20–25 spinose teeth. Fig. 27.

**Recognition:** *Plagiochila strombifolia* can be recognized by the sparingly branched more or less monomorphic leaf shoots with imbricate leaves whose ampliate bases are also imbricate across the ventral stem midline, so obscuring the stem in ventral view, the apical and ventral leaf margins have evenly sized and spaced sharp spinose-triangular teeth while the dorsal margin is entire (Fig. 27); the teeth are ‘relatively broad based, although they may end in 5–9 superimposed, elongate uniseriate cells’ (Inoue and Schuster 1971 p. 135); the male bracts are entire or nearly so.

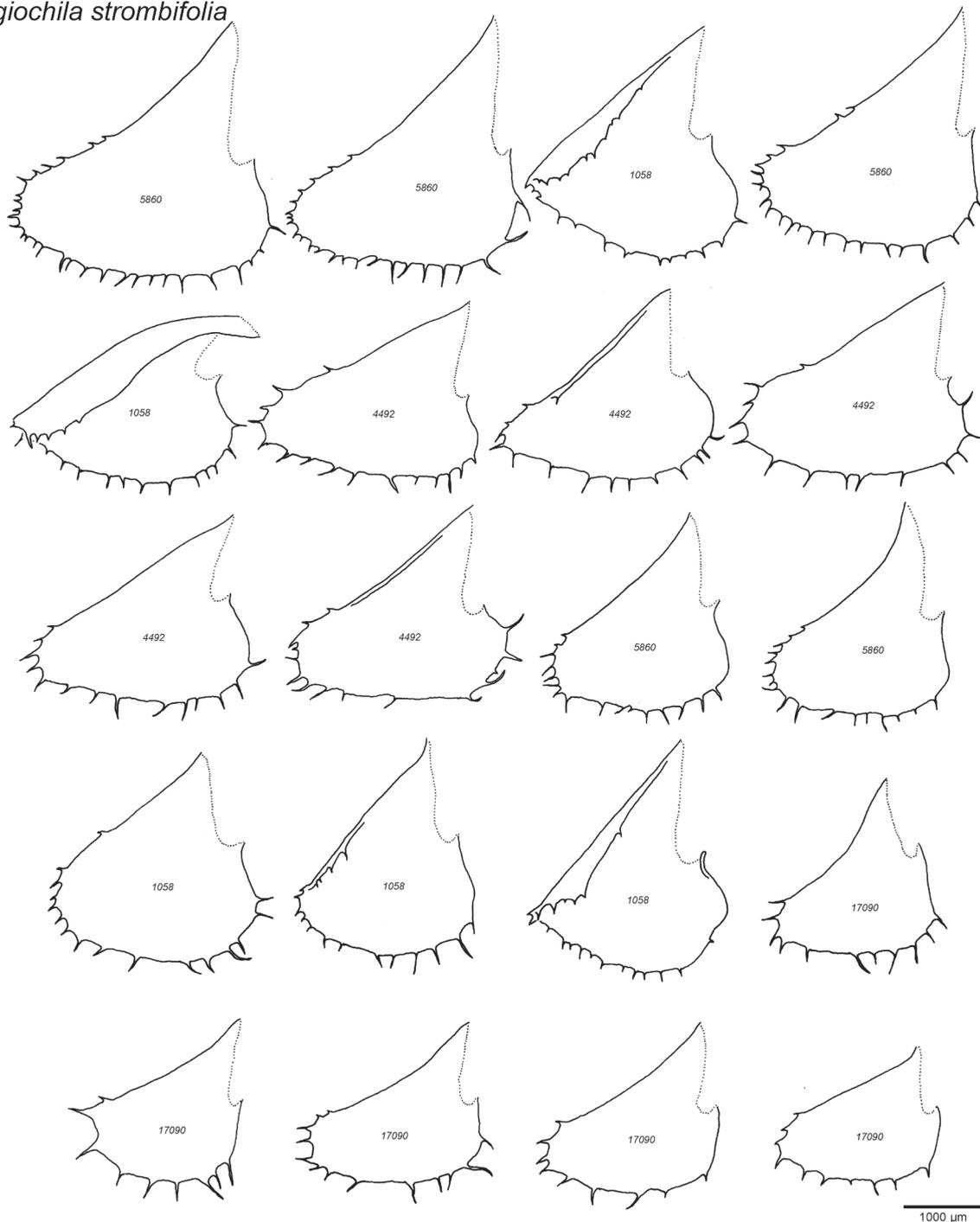
*Plagiochila strombifolia* could be confused with *P. deltoidea* but has narrower teeth, triangular ovate leaves, and stolons originating by lateral-intercalary branching.

*Plagiochila strombifolia* could be confused with *P. fasciculata* but has vegetative branching almost exclusively by lateral-intercalary mode, triangular ovate leaves with a broad ampliate base that covers the stem in ventral view, and longer, narrower teeth on the leaf margins.

**Distribution and Ecology:** *Plagiochila strombifolia* occurs in Australia from New England National Park in the Northern Tablelands of New South Wales south to the Otway Ranges in western Victoria, and in Tasmania. *Plagiochila strombifolia* also occurs in New Zealand, but is not as common there as in Tasmania. *Plagiochila strombifolia* may be a common component of epiphytic bryophyte communities, particularly in Tasmania and Victoria, and increases in abundance and frequency from north to south. At New England National Park and Werrikimbe National Park, near the northern limit of the species, *P. strombifolia* is rare, at the latter encountered once in eight hours of collecting, in a wet south-facing gully dominated by *Nothofagus moorei* over a dense stand of *Dicksonia antarctica*. Throughout its range *P. strombifolia* can be found growing in forests containing *Nothofagus* species, including forests with *Nothofagus* dominated canopy, *Nothofagus-Eucalyptus* mixed forests, and forests with *Nothofagus* growing with other canopy dominant angiosperms including *Elaeocarpus*, *Arthrotaxis*, and *Atherosperma*. It may also inhabit exotic plantation forests as an epiphyte on other indigenous

opportunists such as *Acacia*. In hyperhumid environments in Tasmania, *Plagiochila strombifolia* may grow as a lithophyte, and it may also grow on corticated logs on the forest floor.

*Plagiochila strombifolia*



**Fig 27.** *Plagiochila strombifolia* leaves, from M.A.M. Renner 5860 (NSW 898641), K.R. Thiele 1058 (MEL 2339210), A. Moscal 17090 (HO 577111), and J.A. Curnow 4492 (CANB 9504674).

**Representative specimens examined:** **Australia: New South Wales:** Northern Tablelands: Track to Wrights Lookout, New England National Park, 72 km E of Armidale, 30°31'S 152°24'E, 1000 m, 5 Apr 1991, *H. Streimann* 47876 (CANB 9107922); Barrington Tops National Park, Dilgry River, Devils Hole, 31°54'58"S 151°28'54"E, 1408 m, 15 Dec 2011, M.A.M. Renner 5860 (NSW 898641); **Victoria:** Roger River, Waratah Road, Snow River National Park, 31 km SE of Bendoc, 37°17'S 148°34'E, 700 m, 18 Apr 1991, J.A. Curnow 4153 & *H. Streimann* (CANB 9501541); Coast Range Road, Errinundra National Park, 18 km SSE of Bendoc,

37°17'S 148°58'E, 920 m, 12 Feb 1990, *H. Streimann* 43616 (CANB 9007597); Eastern Highlands, Yarra Ranges National Park, Marysville Woods Point Road, Cumberland Scenic Reserve, walking track from Cambarville picnic area to crossing of Cumberland Creek, 37°33'S 145°53'E, 900 m, 24 Jun 2001, *N. Klazenga & V. Stajsic* 5846 (MEL 2114285); Tarra National Park, 27 km S of Traralgon, 38°27'S 146°32'E, 450 m, 14 Dec 1992, *H. Streimann* 50471 (CANB 9219468); Beauchamp Reserve, Otway State Forest, 13 km NNW of Apollo Bay, 38°39'S 143°36'E, 460 m, 4 Dec 1996, *H. Streimann* 58818 (CANB 9802489); Hopetoun Falls, Otway State Forest, 12 km NW of Apollo Bay, 38°40'S 143°34'E, 260 m, 4 Dec 1996, *H. Streimann* 58774 (CANB 9802445); East Gippsland, Errinundra Valley Road, 500 m, 37°21'40"S 148°51'52"E, 3 Dec 1999, *N. Klazenga* 5250 (MEL 2075708); East Gippsland, Errinundra Plateau, Errinundra Road 1km from Gunmark Road, 1160 m, 37°17'S 148°52'E, 21 Sep 1985, *K.R. Thiele* 1058 (MEL 2339210); **Tasmania:** Flinders Island, Darling Range, 40°04'S 148°06'E, 335 m, 9 Oct 1995, *A. Moscal* 27588 (HO 577446); Van Diemens Land, *La Billardier*, ex Hooker's Herb., ex herb. Taylor as *Plagiochila aculeata* (FH 00284120); North West, 6 km east of Scheffield, corner of Bridle and Beulah Roads, 41°24'S 146°24'E, 180 m, 12 Jan 1987, *A. Moscal* 28800 (HO 577420); West Coast, Pieman River, Pieman River State Reserve, 41°39'S 145°04'E, 40 m, 10 Feb 1995, *A. Moscal* 26710 (HO 576899); Corrina Road, 2k SW of Waratah, 41°28'S 145°31'E, 600 m, 12 May 1997, *H. Streimann* 59690 (CANB 9803373); New road from Daisy Dell to Murchison Highway, 17 km W of Daisy Dell, 41°32'S 145°51'E, 950 m, 22 Apr 1992, *J.A. Curnow* 4310 (CANB 9503011); Cradle Mountain, 41°41'S 145°57'E, Jan 1914, *L. Rodway* (HO 87655); Central Highlands, Liffey Bluff, 41°43'S 146°46'E, 1120 m, 20 Apr 1989, *A. Moscal* 17618 (HO 577476); Little Fisher River, 41°45'S 146°20'E, 880 m, 5 Nov 1991, *J. Jarman* (HO 46846); Williamsford-Montezuma Falls track, 7 km SW of Roseberry, 41°48'S 145°30'E, 500 m, 9 May 1997, *H. Streimann* 59563 (CANB 9803242); Great Northern Creek, North East Dundas Tramway, 41°50'S 145°28'E, 350 m, 4 Dec 1981, *A.E. Orchard* 5673 (HO 306503); Central Highlands, 1 km north of Gunns Lake, 41°53'S 146°58'E, 1920 m, 2 Mar 1989, *A. Moscal* 17090 (HO 577111); Gordon River, opposite Little Eagle Creek, 25 km from mouth of river in Macquarie Harbour, 42°28'20"S 145°40'30"E, 2 m, 25 Feb 1989, *J.R. Croft* 10377 & *M.M. Richardson* (CANB 8904602); South West Region: Spero River, 0.5 km from mouth, 42°36'S 145°20'E, 3 m, 20 Jan 1984, *A.M. Buchanan* 2710 (HO 99552, MEL 2277130); East Coast, Sandspit River, 8.5 km WNW of Cape Bernier, 42°42'S 147°50'E, 180 m, 30 Oct 1988, *A. Moscal* 16654 (HO 577487); East Coast, Sandspit River Forest Reserve 42°42'S 147°50'E, 200 m, 7 Jun 2000, *A. Moscal* 31048 (HO 577143); 400 m from the Gap, Florentine Valley, 42°42'37"S 146°28'38"E, 550 m, 29 Apr 1999, *L. Cave & S.J. Jarman* 162 (HO); South West, Marriotts Falls State Reserve, 42°43'S 146°40'E, 280 m, 23 May 1992, *A. Moscal* 23864 (HO 301791); Junction of the Florentine Road and Whytes Road, 8 km W of Maydena, 42°44'S 146°33'E, 240 m, 26 Apr 1992, *J.A. Curnow* 4476 (CANB 9503774); Timbs Track, 27 km WSW of Maydena, 42°49'S 146°19'E, 350 m, 27 Apr 1992, *J.A. Curnow* 4492 (CANB 9504674); *ibid.*, *J.A. Curnow* 4512 & *H. Lepp* (CANB 9504694); Tasmania, *Oldfield* (G 026169); Mt Wellington, Deep Creek Track, on rock, 23 Jan 1899, *W.A. Weymouth* 543 ex herb. Levier as *Plagiochila deltoidea* (G 026165); 5-Road, near the Gordon Road, 42°44'S 146°25'E, 440 m, 11 May 1992, *J. Jarman* (HO 46850); Mt Wellington, Snake Plains track, 42°57'S 147°13'E, 300 m, 2 Jan 1894, *W.A. Weymouth* 127 (HO 85845); Central Highlands, Liffey River, 41°43'S 146°44'E, 800 m, 19 Apr 1989, *A. Moscal* 17553 (HO 133332); Mt Victoria, Una forest, 41°21'S 147°48'E, c.700 m, 8 Nov 1913, *W.A. Weymouth* 1562 (HO 87670); Forestier Peninsula, Wellard Rivulet, 42°56'S 147°52'E, 6 Feb 1899, *W.A. Weymouth* 832 (HO 87680); West Coast, West Strahan, Macquarie Harbour, 42°09'S 145°19'E, 21 Oct 1893, *W.A. Weymouth* 176 (HO 87678); Deep Creek Track [=Long Creek], 42°36'S 147°14'E, 23 Jan 1899, *W.A. Weymouth* 543 (HO 87673); St Crispin's 42°56'S 147°13'E, 24 Jan 1899, *W.A. Weymouth* 547 (HO 87675); East Coast, The Glen, St Marys Pass, on *Dicksonia*, 900 ft, 23 Nov 1911, *W.A. Weymouth* (HO); South West, Deadmans Bay, 43°32'S 146°30'E, 5 m, 17 Jan 1987, *A. Moscal* 15538 (HO 577115); South West, Huon River, 1 km SW of Scotts Peak Dam, 43°02'S 146°17'E, 320 m, 18 Feb 1996, *A. Moscal* 28197F (HO 577431); Celery Tops Islands, Bathurst Harbour, Island 4, on north coast of Island, 43°22'S 146°09'E, 13 Apr 1978, *Charles Turnbull* (HO 304556); **New Zealand: North Island:** Northland, Maungataniwha Range, Mangamuka Walkway from saddle on State Highway 1, 35°12'S 173°27'E, 390 m, 8 Feb 1995, *J.J. Engel* 20953 (F 1141333); **South Island:** Nina Valley Track, 23 km SE of Springs Junction, 42°48'S 172°23'E, 710 m, 3 Feb 1993, *H. Streimann* 51223 (CANB 9306673); Bush on slopes of Mt Winterslow (Canterbury) 27 May 1906, *T.W.N. Beckett* 426 ex herb. Levier 5205 (G 001179); Lake Wakatipu, 25 mile creek, 1907, *J. Nicklejohn* (? spelling), ex herb. Rev. D. Gillies (G 001183); South Westland, Haast Pass summit, start of track to Davis Flat, east side of road, 44°05'S 169°22'E, 560 m, 7 Jan 1997, *J.E. Braggins* 03/255 (AK 360460).

*Plagiochila stephensoniana* Mitt. in Hooker, *Flora Novae Zelandiae* 2: 133 (1854)

*Type citation:* Northern and Middle Islands: ravines near Wellington, *Stephenson*. Thomson's Sound, Port Cooper, and Port Nicholson, *Lyall*. Ruahine mountains and East Coast, *Colenso*.

*Type*: New Zealand, 1843-1844, *W. Stephenson No.2* (lectotype designated by Bonner (1962): G 00128833!); New Zealand, 1843-1844, *W. Stephenson 12* (residual syntype: NY 01273591!); New Zealand, 1843-1844, *W. Stephenson s.n.* (residual syntype: NY 1273590!).

=*Plagiochila polycarpa* Colenso, Transactions and Proceedings of the New Zealand Institute 19: 280 (1887)

*Type citation*: In wet dark woods in deep gulleys between hills, growing luxuriantly and thickly in very large continuous patches of several feet, on rotten logs, roots and bases of trunks of large trees, completely covering them; near Norsewood, County of Waipawa; 1885–86: *W.C.*

*Type*: New Zealand: near Norsewood, County of Waipawa, 1885-6: *W.Colenso a.1502* (WELT, BM! ex herb. Kew G 00283134!)

=*Plagiochila subsimilis* Colenso, Transactions and Proceedings of the New Zealand Institute 14: 340 (1882)

*Type citation*: On standing (living) and fallen rotten trees, and on earth damp sides of watercourses, “Seventy-Mile Bush” forest, head of the Manawatu River, Hawke’s Bay; 1875–1881.

*Type*: New Zealand: Seventy-Mile Bush’ forest, head of the Manawatu River, Hawke’s Bay, *Colenso a.1241* (BM! ex herb. Kew, G 00264822!)

= *Plagiochila obscura* Colenso, Transactions and Proceedings of the New Zealand Institute 19: 281 (1887)

*Type citation*: On decaying logs and branches, wet dark woods near Norsewood, County of Waipawa; 1886: *W.C.*

*Type*: New Zealand. ‘... near Dannevirke, County of Waipawa, 1886’, *W. Colenso a.1358* (lectotype designated here: WELT; isolectotypes: BM! ex herb. Kew G 00282165!)

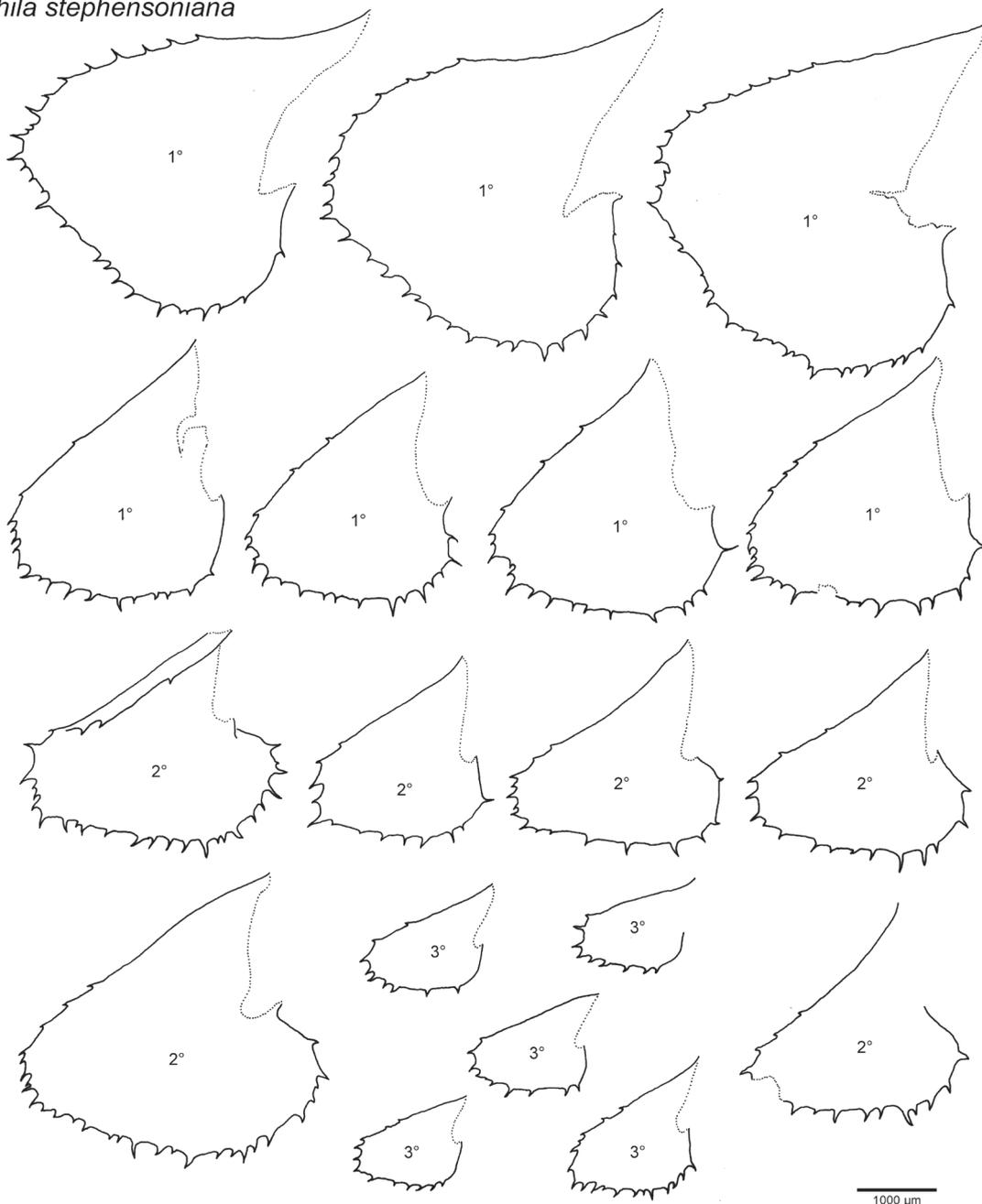
**Notes**: The type of *P. subsimilis* is typical *P. stephensoniana*, having large tripinnately branched shoots with *Frullania*-type vegetative branching, leaves with spinose dentate teeth on the margins and prominent at apex and base.

**Etymology**: named for W. Stephenson (c. 1810–c. 1863) who collected bryophytes in the Wellington Region of New Zealand.

**Description**: Plants with bipinnately branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 300 mm long and 60 mm wide, trimorphic; primary shoots 7–9 mm wide, branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; reddish-brown, in primary shoots to 1100 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 3 to 5 layers, cortical cell walls strongly and continuously thickened, outer layer of cells slightly larger, but walls, including free external wall, thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, walls with triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoots triangular-ovate, 2490–3820 µm long × 2250–3910 µm wide, dorsal margin shallowly arched on basal half then shallowly curved on outer half, ventral margin straight in outer half and ampliate at base, apex broadly rounded, all margins except basal half of the dorsal margin bearing 17–31 triangular teeth, teeth two or three cells broad at base; leaves on secondary shoots triangular-ovate 2190–3380 µm long × 1770–2930 µm wide, dorsal margin shallowly arched or straight, ventral margin straight in outer half and ampliate at base, apex broadly rounded or truncate, apex and ventral margin bearing 13–30 triangular teeth; leaves on tertiary shoots oblong-ovate 1300–1600 µm long × 920–1120 µm wide, dorsal margin straight, ventral margin straight in outer half and curved at base, apex broadly rounded or truncate, apex and ventral margin bearing 9–18 triangular teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with bulging to nodulose trigones but not continuously thickened; medial leaf cells isodiametric to ovoid, 23–36 µm long × 20–30 µm wide, walls unpigmented, with nodulose trigones, medial thickenings absent, cells in leaf base polyhedral, slightly elongated, 33–52 µm long × 15–28 µm wide walls with bulging to nodulose trigones, medial thickening absent or present on basal-most longitudinal walls, trigones not confluent. Cell surfaces smooth. Oil-bodies in median leaf cells 4–10 per cell, hyaline, homogenous or divided into a few coarse septa, smooth. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on tertiary shoots that continue vegetative growth, in opposing pairs or in loose fascicles produced by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 4–10 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, decreasing in stature along the male branch, margin with a few triangular teeth, epistatic, antheridia 1 or 2 per bract, stalk biseriate; stem among bracts smooth. Gynoecia at apices of short secondary or tertiary shoots; bracts widely ovate, 1800  $\mu\text{m}$  long and wide; dorsal margin plane or inrolled, ventral margin ampliate; outer half of dorsal, ventral, and apical margins all with coarse triangular teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations absent, or one produced by lateral-intercalary branching from between the female bracts in the absence of fertilization. Perianth oblong obovate, 2800–3000  $\mu\text{m}$  long and 2000–2200  $\mu\text{m}$  wide at mouth, dorsal and ventral keels unwinged; laterally compressed but with an inflated base, lateral walls plane; labia straight, dorsal and ventral ends laterally flexed in opposing directions, each with numerous ciliate teeth. Fig. 28.

*Plagiochila stephensoniana*



**Fig 28.** *Plagiochila stephensoniana* leaves, all from J.E. Braggins 05/084 (AK 294765).

**Recognition:** *Plagiochila stephensoniana* is a distinctive plant that can be recognized by its combination of large size, pinnately branched shoot systems with secondary shoots arising by *Frullania*-type branching, leaves with numerous triangular teeth that are often curved close at leaf base, and perianths that are slightly contracted at mouth. Confusion is possible with three other large *Plagiochila* species, *P. rutlandii*, *P. gigantea*, and *P. trispicata*. *Plagiochila rutlandii* differs from *P. stephensoniana* by the secondary shoots arising by lateral-intercalary branching and primary shoot leaves having entire margins except for a few small triangular teeth at the apex, while the secondary and tertiary shoot leaves bear spinose teeth. *Plagiochila gigantea* differs by the flabellate, rather than pinnate shoot form and leaves with numerous spinose teeth and presence of a border of thickened, golden pigmented, cell walls around the leaf margin. *Plagiochila trispicata* differs by the oblong-triangular primary-shoot leaves that have an obtuse apex and teeth usually distributed around the apex and on the ampliate basal margin, leaving the ventral margin entire.

**Distribution and Ecology:** *Plagiochila stephensoniana* occurs in Tasmania and New Zealand. In Tasmania *P. stephensoniana* is known from a few collections made in mixed cool hyper-humid forests dominated by *Eucalyptus*, *Nothofagus*, and *Atherosperma* at low elevation in the south-west. In New Zealand *Plagiochila stephensoniana* occurs from at least the Hauraki Gulf south to Otago, and east to the Chatham Islands, again in cool hyperhumid forests. At the northern end of this range *P. stephensoniana* occurs in forests on higher peaks and ranges, as on Hauturu. Further south, the altitudinal range of *P. stephensoniana* increases, possibly as the desiccation stress on forests is relaxed as summer temperatures decrease with increasing latitude, such that on the West Coast of the South Island *P. stephensoniana* grows in forests close to sea level. *Plagiochila stephensoniana* occupies a range of microsites, and while it is often observed growing as an epiphyte on the trunks, usually the trunk base, of large canopy trees, including *Beilschmiedia tawa*, *Podocarpus totara*, *Weinmannia racemosa* and on larger shrubs including *Coprosma grandiflora*, it also grows as a lithophyte on large boulders within streams and on rocks on wet grounds.

**Representative specimens examined:** **Australia: Tasmania:** South West, Wallaby Bay, Port Davey, 43°17'S 145°57'E, 50 m, 10 Jan 1987, A. Moscal 13866E (HO 577419); South West, Deadmans Bay, 43°32'S 146°29'E, 10 m, 20 Jan 1987, A. Moscal 15776 (HO 301785); **New Zealand: North Island:** Hauraki Gulf, Hauturu (Little Barrier) north of Whেকauwhেকau, 36°12'S 175°06'E, 26 Jan 1980, J.E. Braggins 80/640 & J.E. Beever (AK 320986); Pureora State Forest, Waipapa Ecological Area, 38°27'27"S 175°33'40"E, 565 m, 26 Jan 1982, J.E. Braggins et al. 34j (AK 321109); Central Plateau, Tongariro National Park, 26 November 2013, J.E. Braggins 13/279 (NSW); Manawatu Gorge Ecological Region, North Manawatu Gorge Ecological District, Totara Reserve Pohangina, Fern Walk, No 1 Line Road off Pohangina Valley East Road, 40°08'56"S 175°50'32"E, 480 m, 9 Dec 2005, J.E. Braggins 05/084 (AK 294765); **South Island:** Westland, Teremakau Valley, 7 Feb 1903, T.W.N. Beckett 353 (BM); near Clifden, Dean Forest, at junction of loop track to Halls Totara, 45°51'59"S 167°38'08"E, 140 m, 6 Dec 2010, L.H. Cave 1324 (HO 571522); South Otago, Purakaunui Falls, 46°31'14"S 169°33'51"E, 18 Sep 1971, G.M. Taylor (AK 316659); **Chatham Islands:** Rekohu (Chatham Island) Southern Tablelands, Lake Rakeinui, 44°05'S 176°35'W, 240 m, 17 Sep 2007, P.J. de Lange CH1231 & P.B. Heenan (AK 302649).

### ***Plagiochila aemula* M.A.M. Renner sp. nov.**

**Diagnosis:** *Plagiochila aemula* is similar to *Plagiochila arbuscula*, in its large size, pinnate shoots, and bronze-green colour, but differs by its exclusively lateral-intercalary vegetative branching, leaves with teeth confined to the outer margins, and oblate male bract lobes whose margins bear 7-10 small triangular teeth distributed evenly around the margin.

**Type:** Upper West Mulgrave River, below Bobbin Bobbin Falls, 17°22'S 145°46'E, 600 m, 3 Sep 2014, M.A.M. Renner 7334 & L.J. Gray (holotype: NSW 880509; isotypes: BRI, CANB).

**Etymology:** *aemula* imitator, referencing the outward similarity to *Plagiochila arbuscula*.

**Description:** Plants with irregularly pinnately branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; forming turfs; shoot systems to 70 mm long and 35 mm wide, dimorphic; primary shoots 3.5–5.5 mm wide, branches arising by lateral-intercalary branches, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 400 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, outer layer thickened to lesser degree than inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cells not sharply distinct from cortical cells, outer medulla cells with continuously thickened walls, degree of thickening decreasing toward stem centre, yellow-pigmented, walls with faint trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves contiguous to imbricate, succubously inserted and orientated, triangular ovate to triangular oblong, 2050–3150 µm long

× 1100–2070 µm wide, dorsal margin straight to shallowly arched, particularly toward base, apex broadly rounded, ventral margin straight in outer two thirds, weakly ampliate at base, apex and outer two thirds of ventral margin bearing 6–20 spinose-ciliate teeth, teeth two to four cells broad at base, uniseriate toward apex, apical cell slightly elongated; leaves on secondary shoots triangular-ovate to oblong ovate, 1640–2480 µm long × 870–1550 µm wide, dorsal margin shallowly arched or straight, apex rounded, ventral margin straight in outer two thirds and curved at base but not ampliate, apex and ventral margin bearing 8–18 triangular teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, not attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells oblong, 26–33 µm long × 10–21 µm long axis parallel to leaf margin, walls with bulging to nodulose trigones, free external wall continuously thickened; medial leaf cells isodiametric to ovoid, 18–36 µm long × 18–27 µm wide, walls unpigmented, with nodulose trigones, medial thickenings absent; cells in leaf base polyhedral, 27–41 µm long × 15–21 µm wide walls with bulging to nodulose trigones, medial thickening uncommon, trigones not confluent. Cell surfaces smooth. Oil-bodies unknown. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on primary or secondary shoots that continue vegetative growth, singly or in pairs produced by *Frullania*-type branching at the base of the leading male branch; lateral- and ventral-intercalary branches not associated with male branches; bracts in 3–7 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, margin with 3–5 triangular teeth around the apex; bract-lobule entire or with one or two projections or small teeth, epistatic; antheridia 1 or 2 per bract, stalk biseriate; stem among bracts smooth. Gynoecia at apices of shoots; bracts triangular-ovate, 2600–3500 µm long and 1400–2400 µm wide, larger than subtending leaves; dorsal margin inrolled, ventral margin ampliate; apex and ventral margins with spinose dentate teeth, teeth unevenly sized, bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Two subfloral innovations, produced by lateral-intercalary branching from between the female bracts. Perianth campanulate, 2100–2300 µm long and 1500–2300 µm wide at mouth, dorsal and ventral keels unwinged; laterally compressed but with an inflated base, lateral walls plane; labia curved, with numerous long spinose teeth. Figs 29–32.

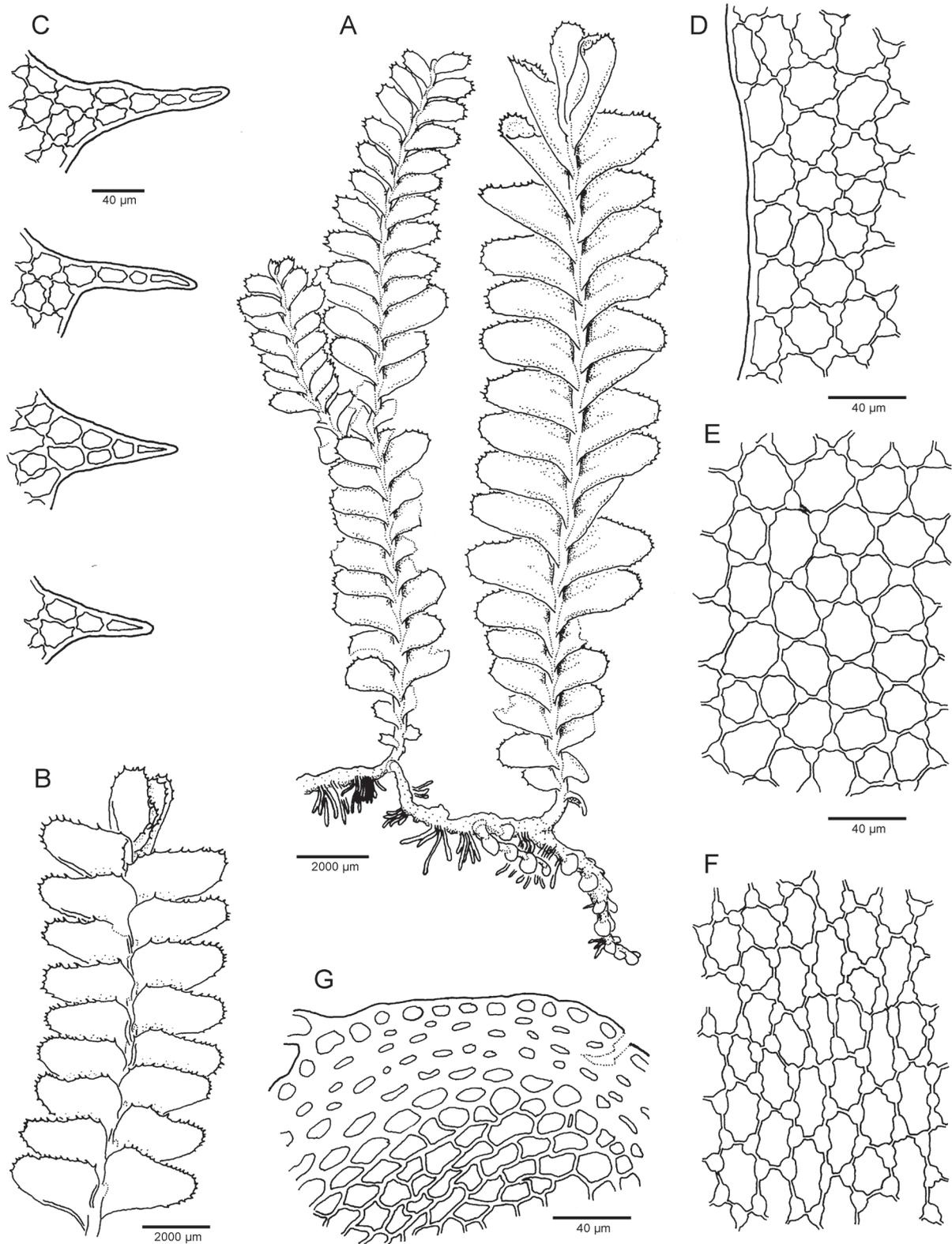
**Notes:** I have been unable to match this species with any type material observed during the course of this revision. Given the distribution, and relative paucity of knowledge about this species in Australia, the usual caveats apply to the proposal of a new species, namely that it may yet be found outside of Australia, and may be represented in extra-territorial type material not examined during this study. A new species is proposed for this entity so that within an Australian context a single formal name is available for these plants whose meaning and application are fixed. Validly published names are readily reconciled and dealt with via proposal of formal synonymy, if this is found warranted sometime in the future.

**Recognition:** *Plagiochila aemula* can be recognized by the combination of ovate leaves with triangular teeth distributed around the apex and the outer two thirds of the ventral margin, leaving the interior of the ampliate base entire, vegetative branching by lateral-intercalary mode only, the sparingly branched leafy shoots, and the fuscous coloration. *Plagiochila aemula* is similar to species of the *Plagiochila arbuscula* complex, but differs from all by its exclusively lateral-intercalary vegetative branching, primary shoot leaves with interior ampliate margin entire, and oblate male bract lobes whose margins bear 5–10 small triangular teeth distributed evenly around the margin.

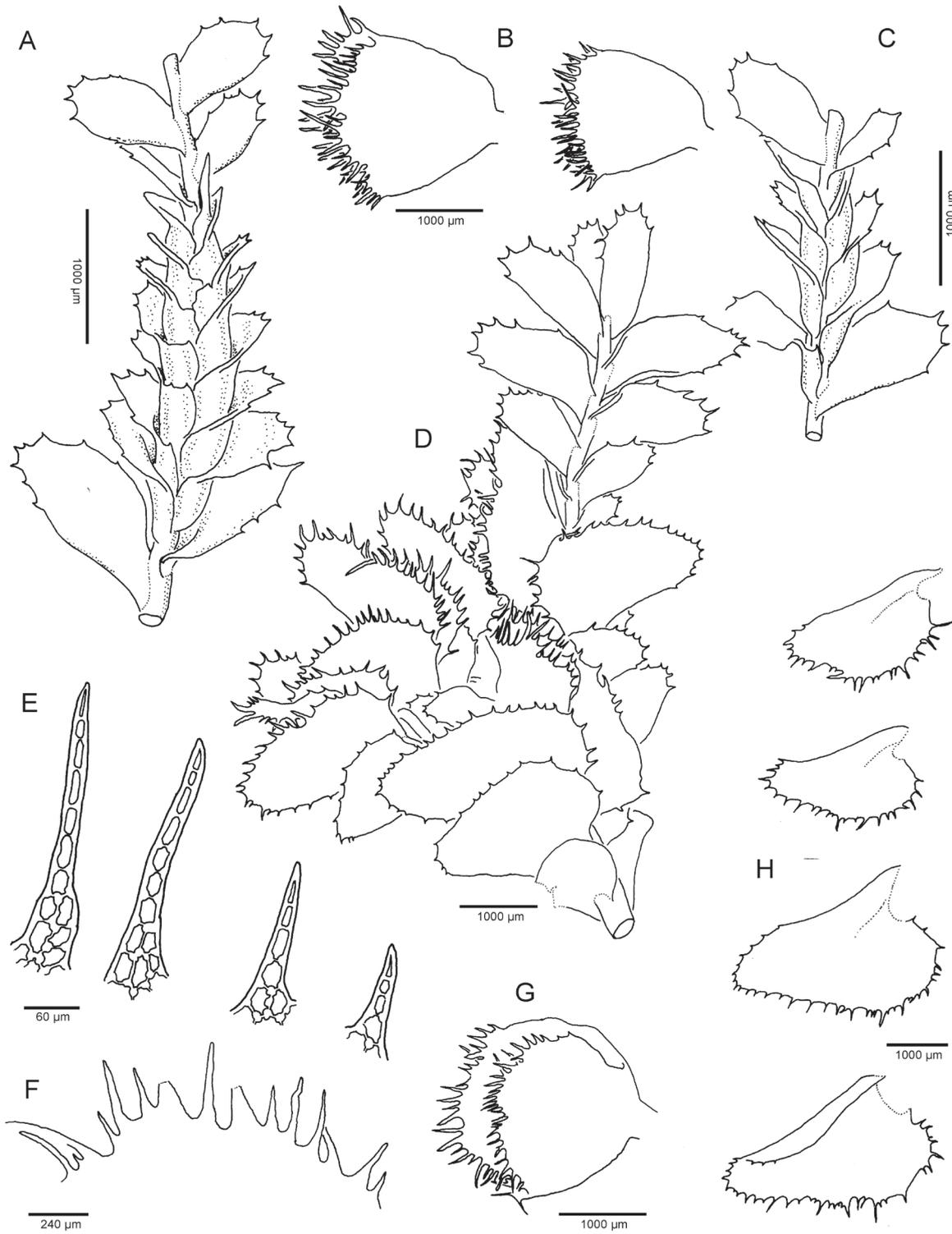
*Plagiochila aemula* differs from *P. fusca* by the distribution of leaf marginal teeth, in *P. fusca* the large triangular teeth are evenly spread around the apex and along the postical margin, whereas in *P. aemula* there are no teeth on the ampliate margin.

**Distribution and Ecology:** *Plagiochila aemula* is known only from the Wet Tropics of north east Queensland, where it has been collected at two sites on the western flank of Mount Bartle Frere, the highest peak in Queensland. At one site *Plagiochila aemula* was collected in upland microphyll-vine rainforest on face with NW aspect where it was a lithophyte on the sloping side of a granite boulder in dappled light. At the other site this species grew in complex notophyll-vine forest over basalt in a steep-sided gully with a NW aspect. Here *Plagiochila aemula* formed isolated patches on the trunks of large trees, and on coarse woody debris suspended over a stream.

**Specimens examined: Australia: Queensland:** Cook, Wooroonooran National Park, Bartle Frere, track to summit from Gourka Road end, Mulgrave River catchment, 17°22'48"S 145°47'14"E, 1020 m, 30 Mar 2012, M.A.M. Renner 6406, E.A. Brown, & V.C. Linis (NSW 900037); Upper West Mulgrave River, below Bobbin Bobbin Falls, 17°22'S 145°46'E, 600 m, 3 Sep 2014, M.A.M. Renner 7331 & L.J. Gray (NSW 880506).

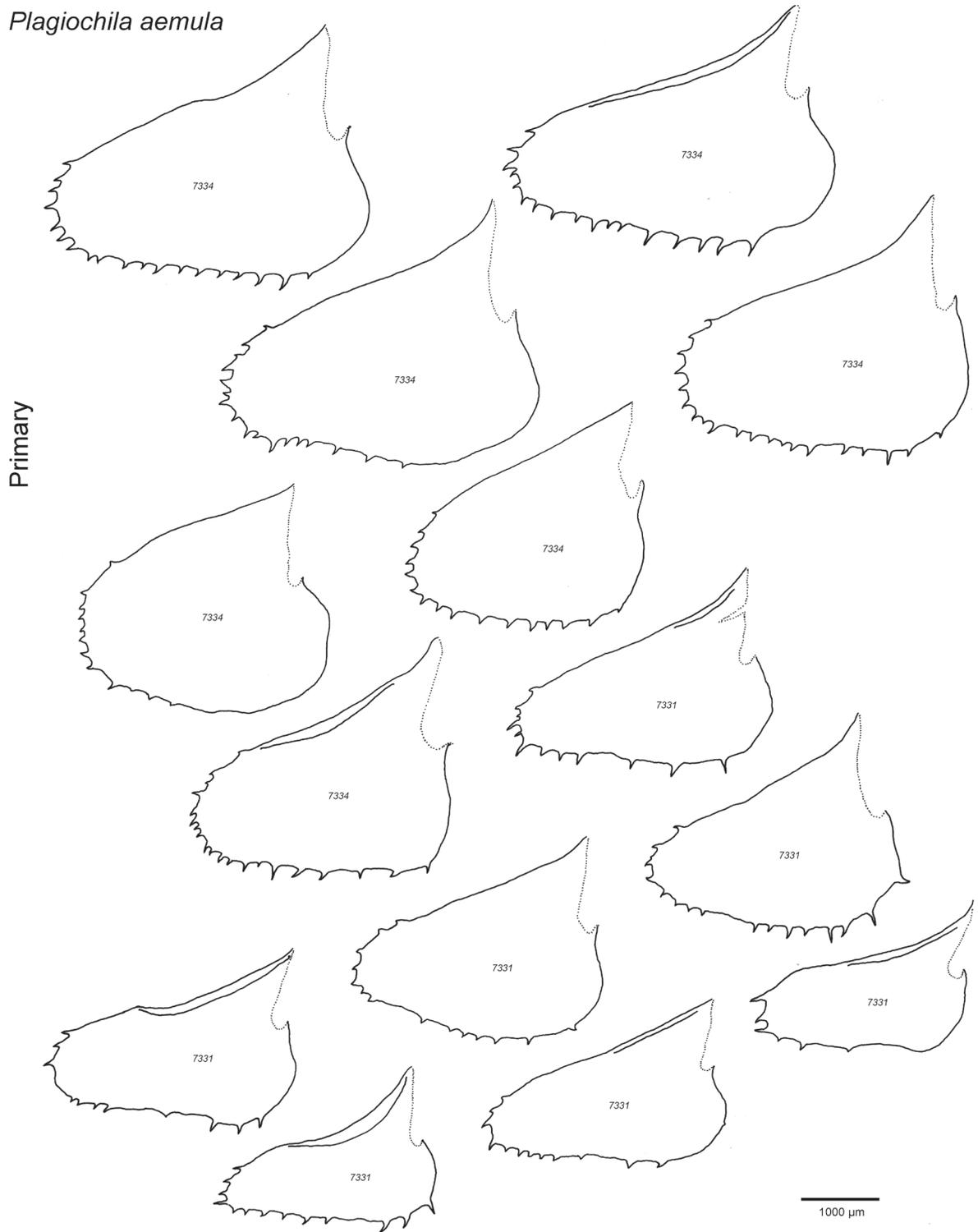


**Fig 29.** *Plagiochila aemula*. A: leafy shoots and basal stolons in dorsal view. B: primary shoot in ventral view. C: four teeth from the leaf margin. D: leaf marginal cells. E: leaf medial cells. F: leaf basal cells. G: dorsal sector of transverse stem section. All from *M.A.M.Renner 7334 & L.J. Gray (NSW 880509)*.

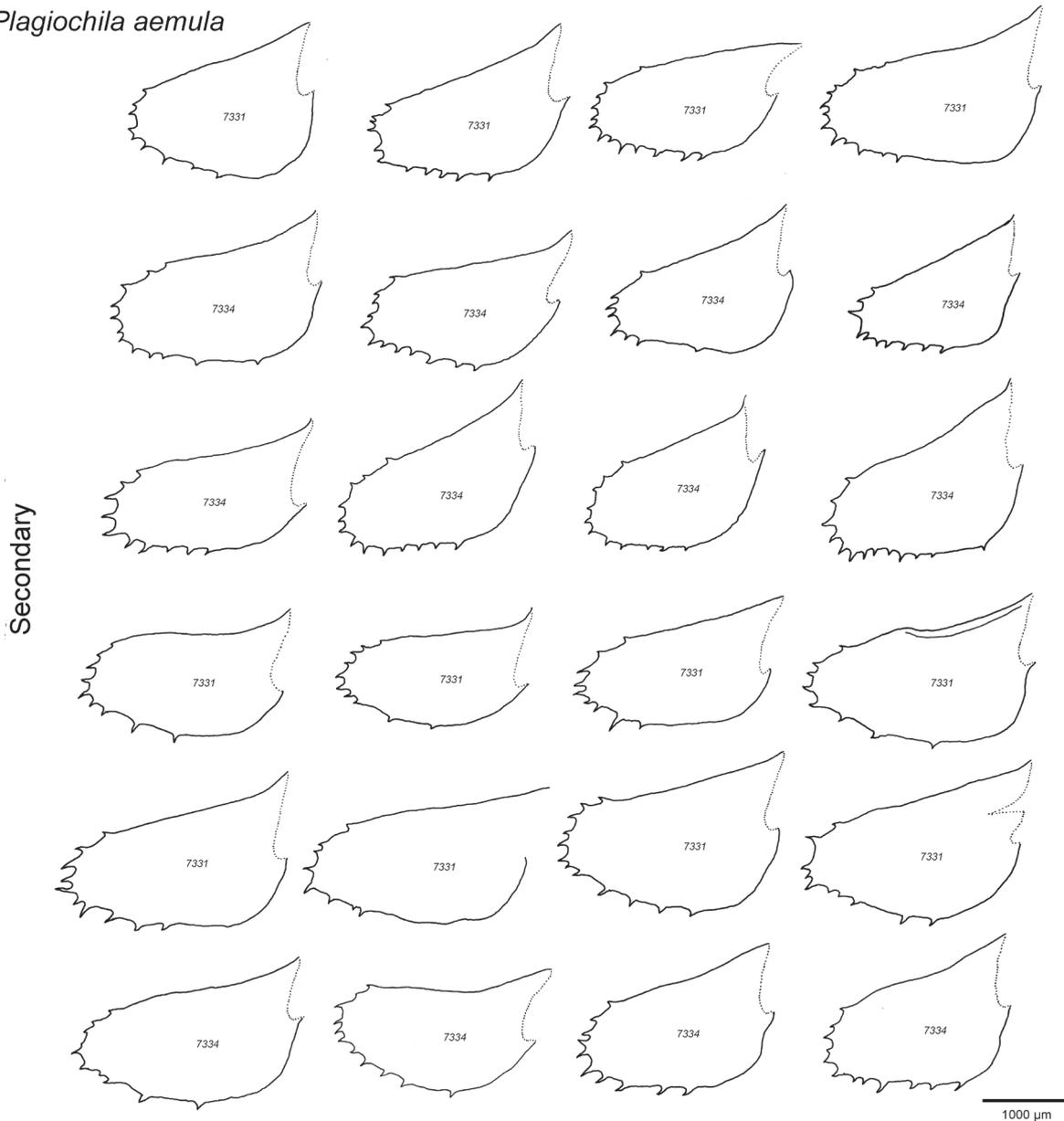


**Fig 30.** *Plagiochila aemula*. A: dorsal view of male branch. B: Two perianths in lateral view. C: dorsal view of male branch. E: four teeth from perianth mouth. F: perianth mouth. G: immature perianth in lateral view. H: four female bracts. All from M.A.M.Renner 7334 & L.J. Gray (NSW 880509).

*Plagiochila aemula*



**Fig 31.** *Plagiochila aemula* leaves, from M.A.M. Renner 7331 & L.J. Gray (NSW 880506) and M.A.M. Renner 7334 & L.J. Gray (NSW 880509).

*Plagiochila aemula*

**Fig 32.** *Plagiochila aemula* leaves, from M.A.M. Renner 7331 & L.J. Gray (NSW 880506) and M.A.M. Renner 7334 & L.J. Gray (NSW 880509).

***Plagiochila arbuscula*** (Brid. ex Lehm. & Lindenb.) Lehm. & Lindenb., Species Hepaticarum 1: 23 (1839)

Basionym: *Jungermannia arbuscula* Brid. ex Lehm. et Lindenb., Novarum et Minus Cognitarum Stirpium Pugillus 4: 63 (1832)

*Type citation:* Habitat in Java insula. Commerson. Specimina adsunt in Herbario Brideliano

*Type:* Java, ex Herb. Bridel, Herbarium Lehmannianum, Commerson (S-B6394!d, S-B6395!d, S-B6396!d); (superceded neotype designated by Grolle & So 1998): Java. Prov. Preanger. in decliv. austral. montis Pangerango, in silvis primaevae supra Tjibodas ad arborum truncos, 21. 4. 1894, alt. 1540 m, *Schiffner 667* (FH)

=*Plagiochila belangeriana* Lindenb., Species Hepaticarum 2–4: 109 (1840)

*Type citation:* Java, leg. Belangeriana n.v.

*Type:* Java, *Belanger* ex herb. Bischerelle (G 00121311! ex herb. Sande Lacoste G 00121239! ex herb. Meissner G 00115478!)

=*Plagiochila ferdinandi-muelleri* Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 777 (1904) = Species Hepaticarum 2: 455 (1904)

*Type citation:* Australia, Queensland, (Ferd. von Müller).

*Type:* Australia, Rockingham Bay, *F. v. Müller* (lectotype designated by Bonner (1962): G 00067844!)

=*Plagiochila australis* Steph., Species Hepaticarum 6: 126 (1917) *syn. nov.*

*Type citation:* Australia. Sydney. (Remy legit)

*Type:* Australia, Vallerach, prope Sydney, 1905, *G. Remy 192* ex herb. Laconture (lectotype designated by Bonner (1962): G 00069842!)

=*Plagiochila fuscorufa* Steph., Species Hepaticarum 6: 158 (1918)

*Type citation:* Java. Tjibodas. (Fleischer legit).

*Type:* Java. Tjibodas, Dec 1910, *Fleischer* legit. 'fusco-rufa' (G 0064084!)

=*Plagiochila plicatula* Steph., Species Hepaticarum 6: 201 (1921)

*Type citation:* Insulae Philippinae (Robinson legit).

*Type:* Philippines, Luzon, Province of Laguna, Mt Banajao, 5-7 Mar 1910, *C.B. Robinson* ex Philippine Bureau of Science No. 9786 (G 00064085!)

=*Plagiochila belangeriana* f. *angustifolia* Herzog, Annales Bryologici 5: 130 (1932) *nom. inval.*

*Type citation:* Java, Hep. Select. & Crit. n.119 *n.v.*

=*Plagiochila bilabiata* Herzog, Hedwigia 78: 227 (1938)

*Type citation:* 'Sumatra orientalis: Gouv. S.O.K., in monte Sibajak, ... 1300m-1600m, leg. F. Verdoorn, IX 1930 (n.74a & b)'

*Type:* *n.v.*

**Notes:** I have some reservations about my interpretation of the type of *Plagiochila australis* and my attribution of it to synonymy of *P. arbuscula*. It is possible that the plant in the type is actually *Plagiochila alta*, and this specimen from 'near Sydney' represents an Australian occurrence for this Oceanian species, in an island of rainforest at a latitude consistent with its range across the Pacific, or the specimen does originate from an island in the western Pacific. At the time of my investigation of the type (2014) I did not appreciate the significance of subtle morphological differences between species of the *P. arbuscula* complex (Renner *et al.* 2018), and reassessment of this type based on detailed examination is warranted. Whether *P. alta* occurs on mainland Australia within the south-eastern mesothermic archipelago should be ascertained.

**Etymology:** diminutive tree in reference to the shoot system form.

**Description:** Plants with bipinnately branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 120 mm long and 50 mm wide, trimorphic; primary shoots 5–7 mm wide, branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 900 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 to 6 layers, cortical cell walls strongly and continuously thickened, outer layer of cells slightly larger, but walls, including free external wall, thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, walls with trigones absent small and triangular. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves triangular-ovate to broadly ovate, 2490–3980 µm long × 1550–3250 µm wide, base shallowly ampliate, apex rounded, dorsal margin straight to evenly and shallowly convexly curved, margins with 12–27 narrow triangular teeth distributed continuously around the ventral margin and apex, in some leaves extending along the dorsal margin, teeth of similar stature around apex and base. Secondary shoot leaves triangular ovate to trapeziform 1760–3000 µm long × 1030–1740 µm wide, base not or shallowly ampliate, apex truncate, dorsal margin straight to shallowly concavely curved, margins with 9–21 teeth distributed evenly along the postical margin and apex, or with a short gap at the middle of the ventral margin. Tertiary shoot leaves rectangular to narrow-elliptic, 1005–2080 µm long × 455–1330 µm wide, apex truncate to rounded, dorsal and ventral margins more or less parallel, straight to shallowly convexly curved, margins with 4–16 teeth distributed around the apex and

extending onto both dorsal and ventral margins; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, 13–25  $\mu\text{m}$  long  $\times$  8–16  $\mu\text{m}$  wide, long axis parallel or perpendicular to leaf margin, walls with bulging to nodulose trigones but not continuously thickened; medial leaf cells isodiametric to ovoid, 14–25  $\mu\text{m}$  long  $\times$  11–18  $\mu\text{m}$  wide, walls unpigmented, with bulging trigones, medial thickenings absent, cells in leaf base polyhedral, slightly elongated, 23–40  $\mu\text{m}$  long  $\times$  13–22  $\mu\text{m}$  wide walls with bulging to nodulose trigones, medial thickening present or absent present on basal-most longitudinal walls, trigones not confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves present amid leaves at shoot apex, ciliate, disaggregating and dislocating, apparently absent from mature shoot sectors. Asexual reproduction by leaf-borne propagules or leaf fragments absent.

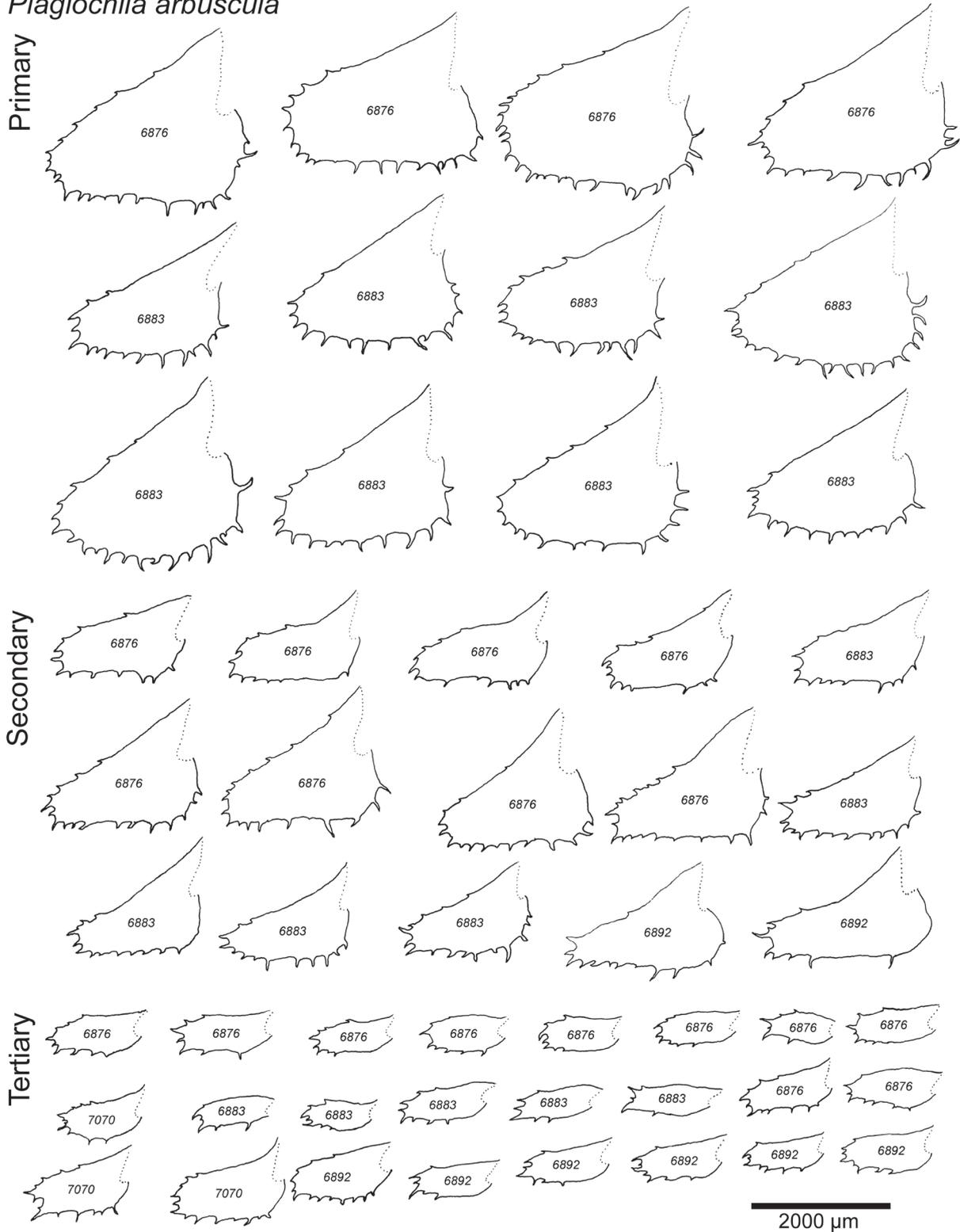
Dioicous. Androecia intercalary on shoots that continue vegetative growth, singly, in pairs or in fascicles of three produced by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 4–15 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, decreasing in stature along the male branch, margin with a few triangular teeth, epistatic, antheridia 1 per bract; stem among bracts smooth. Gynoecia at apices of secondary or tertiary shoots; bracts widely ovate, to 2500  $\mu\text{m}$  long and 1400  $\mu\text{m}$  wide; dorsal margin revolute, apex rounded, ventral margin ampliate at base; all margins with coarse triangular teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations present, one or two produced by lateral-intercalary branching from between the female bracts in the absence of fertilization. Perianth oblong cylindrical, to 2000  $\mu\text{m}$  long and 1500  $\mu\text{m}$  wide at mouth, dorsal and ventral keels unwinged; laterally compressed but with an inflated base, lateral walls plane; labia straight, each with numerous spinose-ciliolate teeth. Fig. 33.

**Recognition:** *Plagiochila arbuscula* can be recognized by its combination of large, bipinnate shoot systems in which shoot stature decreases with shoot order, and vegetative branching *Frullania*-type. This combination of characters is shared with the other Australasian species *P. alta* and *P. trispicata*, and these three species are best differentiated on the basis of leaf shape and dentition. The primary shoot leaves of *Plagiochila arbuscula* are nearly the same dimension at their widest and longest, and are more ovate than oblong (Fig. 33). The ventral leaf margin is straight to convex then curved around the ampliate leaf base. The leaf margin bears 12–27 evenly spaced teeth around the leaf apex and along the ventral margin, including the margin around the ampliate base. The teeth are more or less the same size at the apex and the base, though those at the base may be slightly longer.

**Distribution and Ecology:** *Plagiochila arbuscula* is widespread throughout Malesia, from Java and Sumatra in the west, the Philippines in the north, to Papua New Guinea and the Solomon Islands in the east, with an outlying population in the Wet Tropics Bioregion of north-east Queensland to the south. In Australia *Plagiochila arbuscula* is confined to north east Queensland, where it ranges from Mt Finnegan in the north to the Paluma Range in the south, always inhabiting tropical rainforests and between sea level and 1200 m as an epiphyte or a lithophyte. *Plagiochila arbuscula* grows as an epiphyte on tree and treefern trunks, and as a lithophyte on exposed bedrock or large boulders in wet tropical rainforest from sea level to more than 1100 m elevation. *Plagiochila arbuscula* may be a conspicuous and dominant component of the bryoflora in some situations, due to its capacity to form large, thick, pure wefts to the exclusion of other species on tree trunks, often between 0.5 and 3 m or more above ground, and on the sides of granite boulders and exposed granite bedrock, often alongside waterways. In rainforests that experience a seasonal reduction in rainfall such as those in the Paluma Range behind Townsville, *Plagiochila arbuscula* may be restricted to microsites in close proximity to watercourses, growing on bedrock, boulders, and roots alongside permanent streams, often with patches in capillary contact with stream water in situations where high water flows are not destructive, or in situations protected from wet-season flows. In forests that receive year-round precipitation, *Plagiochila arbuscula* may be found throughout the forest interior.

The type of *Plagiochila australis* was reportedly gathered near Sydney, but just how near is hard to tell, as *Plagiochila arbuscula* is otherwise unknown in Australia south of Townsville. If this specimen is *P. arbuscula* (and it may not be, see note above) then it is unlikely that the specimen was collected near Sydney, or even in New South Wales. *Plagiochila arbuscula* has been recorded for New Zealand (Engel and Merrill 2010a), but these reports are referable to *P. trispicata* (Renner *et al.* 2018).

*Plagiochila arbuscula*



**Fig 33.** *Plagiochila arbuscula* leaves, from M.A.M. Renner 6876 & T.C. Wilson (NSW 870537), M.A.M. Renner 6883 & T.C. Wilson (NSW 870547), M.A.M. Renner 6892 & T.C. Wilson (NSW 870653), and M.A.M. Renner 7070 & T.C. Wilson (NSW 870688), modified from Renner *et al.* (2018).

**Representative specimens examined: Indonesia: Sumatra:** North Sumatra Province, Gunung Sinagung (SW de Brastagi), vesant E, a partir du lac Kawar, 1500 m, 17 Nov 1989, *L. Hoffman* 89-209bis (CANB 9310875); **Australia: Queensland:** Cook: Mt Finnegan, Cedar Bay National Park, 39 km S of Cooktown, 760 m, 15°49'S 145°16'E, 20 Oct 1995, *H. Streimann* 57051 (CANB 9519194); Mt Finnegan, Cedar Bay National Park, 39 km S of Cooktown, 880 m, 15°49'S 145°16'E, 20 Oct 1995, *H. Streimann* 57098 (CANB 9519241); Mt Finnegan,

Cedar Bay National Park, 39 km S of Cooktown, 1110 m, 15°49'S 145°16'E, 20 Oct 1995, *H. Streimann* 57221 (CANB 9606106); Daintree National Park, Between Thornton Beach and Noah Creek, 16°09'04"S 145°26'28"E, 5 m, 25 Mar 2012, *M.A.M. Renner* 6328a, *V.C. Linis*, & *E.A. Brown* (NSW 896723); Daintree National Park, track to Manjil Jimalji, between coral fern patch and split rock, 16°23'32"S 145°17'31"E, 1136 m, 30 Aug 2014, *M.A.M. Renner* 7277 & *L.J. Gray* (NSW 849263); Kauri Creek, Mt Haig Road, Lamb Range, 22 km NE of Atherton, 17°08'S 145°36'E, 800 m, 27 Jun 1984, *H. Streimann* 29884 (CANB 8408239); Wooroonooran National Park, South Johnston River, McMillan Creek catchment, Gorrell Track c 2 km S of South Johnston River picnic area (old forestry camp), 17°40'26"S 145°43'58"E, 600 m, *M.A.M. Renner* 6575, *V.C. Linis*, & *E.A. Brown* (NSW 970430); Wooroonooran National Park, upper West Mulgrave River, below Bobbin Bobbin Falls, 17°22'S 145°46'E, 600 m, 3 Sep 2014, *M.A.M. Renner* 7335 & *L.J. Gray* (NSW 880510); North Kennedy: Mount Hypipamee National Park, Dinner Creek Falls, 17°24'53"S 145°30'19"S, 1130 m, 31 May 2014, *M.A.M. Renner* 7070 & *T.C. Wilson* (NSW 870688); Paluma Range National Park, road to Paluma Dam and Mount Spec, 18°59'29"S 146°10'03"E, 853 m, 7 May 2014, *M.A.M. Renner* 6876 & *T.C. Wilson* (NSW 870537); Paluma Range National Park, road to Paluma Dam and Mount Spec, 18°59'48"S 146°10'18"E, 871 m, 7 May 2014, *M.A.M. Renner* 6873 & *T.C. Wilson* (NSW 859315); Paluma Range National Park, road to Paluma Dam and Mount Spec, 18°57'55"S 146°09'39"E, 845 m, 7 May 2014, *M.A.M. Renner* 6883 & *T.C. Wilson* (NSW 870547); Paluma Range National Park, Paluma, track to Cloudy Creek, 19°00'02"S 146°12'03"E, 843 m, 8 May 2014, *M.A.M. Renner* 6887 & *T.C. Wilson* (NSW 870551); Paluma Range National Park, Paluma, track to Cloudy Creek, 19°00'02"S 146°12'03"E, 843 m, 8 May 2014, *M.A.M. Renner* 6892 & *T.C. Wilson* (NSW 870653); Paluma Range National Park, Paluma, track to Cloudy Creek, 19°00'02"S 146°12'03"E, 843 m, 8 May 2014, *M.A.M. Renner* 6895 & *T.C. Wilson* (NSW 859116); Paluma Range National Park, Road to Paluma Dam and Mount Spec, tributary of Birthday Creek, 18°58'21"S 146°09'55"E, 850 m, 7 May 2014, *M.A.M. Renner* 6879 & *T.C. Wilson* (NSW 870542).

Representative misidentified specimens:

*Plagiochila fasciculata*

Tasmania, Sandfly Rivulet, 43°03'S 147°10'S 3 Jan 1910, *W.A. Weymouth* 1159 (HO 87601, as *P. ferdinandimulleri* Steph.)

***Plagiochila trispicata*** Colenso, Transactions and Proceedings of the New Zealand Institute 20: 246 (1888)

*Type citation:* On trees and logs, damp woods near Dannevirke. County of Waipawa ; 1887: *W.C.*

*Type:* 31 Jan. 1887, *W. Colenso a.1340* (lectotype designated here: WELT-H7795!d; isolectotype: BM)

*Epitype* (here designated): Auckland Ecological Region, Tamaki Ecological District, St Heliers, Dingle Dell Reserve, start of track from open area to South Fern Glen Road, 36°51'35"S 174°51'25"E, 25 m, 16 Mar 2004, *J.E. Braggins* 04/015A (AK 286177).

=*Plagiochila calcarata* Herzog, Transactions and Proceedings of the Royal Society of New Zealand 68: 41 (1938)

*Type citation:* 'Marlborough, leg. J.H. McMahon (E.A. Hodgson mis. sub n.17)'

*Type:* *n.v.*

=*Plagiochila heterophylla* Colenso, Transactions and Proceedings of the New Zealand Institute 20: 245 (1888) *nom. illeg. non* Lindenb. ex Lehm.

*Type citation:* On logs and trunks of trees, wet woods near Dannevirke, County of Waipawa; 1887: *W.C.*

*Type:* New Zealand, *Colenso* 1334, ex herb. Kew, ex herb. Steph. (lectotype designated by Bonner (1962): G 00283137! isolectotype: BM)

=*Plagiochila longissima* Colenso, Transactions and Proceedings of the New Zealand Institute 21: 49 (1888)

*Type citation:* On trees, thick woods, Dannevirke, County of Waipawa; 1888: *W. C.*

*Type:* New Zealand, North Island, Waipawa County, Dannevirke, Tramway Bush, 1888, *W. Colenso a.1341* (lectotype designated here: WELT-H7767!d; isolectotypes: WELT-H7766!d, WELT-7768!d, BM, G 00264746!)

=*Plagiochila polystachya* Colenso, Transactions and Proceedings of the New Zealand Institute 21: 51 (1889)

*Type citation:* In deep woods, Dannevirke, County of Waipawa ; 1888 : *W. C.*

*Type:* Humile Creek, Dannevirke, Hawkes Bay, 1888, *W. Colenso a.1333* (lectotype designated here: WELT-H7765!d; isolectotype: G 00264756!)

=*Plagiochila subflabellata* Colenso, Transactions and Proceedings of the New Zealand Institute 21: 51. 1889. *syn. nov.*

*Type citation:* Woods near Dannevirke, County of Waipawa; 1888: W.C.

*Type:* New Zealand, North Island, Waipawa County, near Dannevirke, 3 Feb 1888, W. Colenso a.1335 (lectotype designated here: WELT!d)

=*Plagiochila trispicata* var. *rekohuensis* (J.J.Engel & G.L.Merr.) M.A.M.Renner, Botanical Journal of the Linnean Society 186: 125 (2018) *syn. nov.*

Basionym: *Plagiochila arbuscula* var. *rekohuensis* J.J.Engel & G.L.Merr., Nova Hedwigia 91: 509 (2010)

*Type citation:* 'Holotype Chatham Is., Southern Tablelands, Lake Rakeinui, ca. 240 m, 17 Sept. 2007, de Lange CH1230 and Heenan (AK – c. sporophyte + male); isotype: (F).'

*Type:* Chatham Is., Southern Tablelands, Lake Rakeinui, ca. 240 m, 17 Sept. 2007, P.J. de Lange CH1230 and P. Heenan (holotype: AK n.v.)

**Notes:** Plants with toothed dorsal leaf margins can be found on Tuhua (Mayor Island), Coromandel Peninsula, and Te Pahi, in some instances this feature is variably expressed within individuals, and within single primary shoots.

**Etymology:** three spikes, possibly in reference to the triplets of male branches borne at shoot apices, one intercalary on the leading shoot and two lateral, one on each side of the shoot, by *Frullania*-type branching at the base of the first.

**Description:** Plants with bipinnately branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 120 mm long and 50 mm wide, trimorphic; primary shoots 5–7 mm wide, branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 900 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 to 6 layers, cortical cell walls strongly and continuously thickened, outer layer of cells slightly larger, but walls, including free external wall, thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, walls with trigones absent small and triangular. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves oblong-triangular, 2880–5020 µm long × 1660–3500 µm wide, with an ampliate base, apex rounded or truncate, dorsal margin straight to shallowly concave; with 6–23 triangular to long triangular teeth distributed discontinuously around the apex and along ventral margin, usually with a gap in the middle of the ventral margin, in some leaves extending along the dorsal margin to the base, teeth smaller in stature around apex than the base, where they may be long and curved. Secondary shoot leaves triangular to oblong, 2210–4170 µm long × 1055–2450 µm wide, with a shallowly ampliate base, apex truncate, dorsal margin straight; margins with 8–23 teeth distributed around the apex and base. Tertiary shoot leaves 1450–2930 µm long × 600–1555 µm wide with a shallowly ampliate base, apex truncate to rounded, dorsal margin straight, margins with 4–26 teeth distributed around the apex and base; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with bulging to nodulose trigones but not continuously thickened; medial leaf cells isodiametric to ovoid, 25–35 µm long × 20–30 µm wide, walls unpigmented, with bulging trigones, medial thickenings absent, cells in leaf base polyhedral, slightly elongated, 35–55 µm long × 24–36 µm wide walls with bulging to nodulose trigones, medial thickening present or absent present on basal-most longitudinal walls, trigones not confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves present amid leaves at shoot apex, a tuft of curved and branched cilia, disaggregating and dislocating, apparently absent from mature shoot sectors. Asexual reproduction by leaf-borne propagules or leaf fragments absent.

Dioicous. Androecia intercalary on secondary or shoots that continue vegetative growth, in opposing pairs or in fascicles of three produced by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 6–13 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, with two or three triangular teeth, epistatic, antheridia 1 or 2 per bract, stalk biseriate; stem among bracts smooth. Gynoecia at apices of short secondary or tertiary shoots; bracts triangular-oblong, 3300 µm long and 1800 µm wide; dorsal margin plane, ventral margin ampliate; outer half of dorsal, ventral, and apical margins all with coarse triangular teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole absent. Subfloral innovations absent, or one or

two produced by lateral-intercalary branching from between the female bracts in the absence of fertilization. Perianth ovate-oblong, to 5000  $\mu\text{m}$  long and 800  $\mu\text{m}$  wide at mouth, widest below mouth where up to 1200  $\mu\text{m}$  wide, dorsal and ventral keels unwinged; laterally compressed but with an inflated base, lateral walls plane; labia straight or shallowly curved, each with irregular spinose-dentate teeth. Fig. 34.

### *Plagiochila trispicata*



**Fig 34.** *Plagiochila trispicata* leaves, from J.E. Braggins 04/067 (AK 290513), P.J. de Lange 9705 (AK 322390), and P.J. de Lange 10631, T.J. de Lange, & F.J.T. de Lange (AK 330919).

**Recognition:** *Plagiochila trispicata* can be recognized by the combination of pinnate shoot systems with secondary shoots produced by *Frullania*-type branching, in some shoots the only branching is toward the shoot apex, but the shoots are still distinctly pinnate.

The triangular-oblong leaves with a broad ampliate base, and teeth discontinuously distributed around the margin, with a cluster of teeth at the leaf apex, and another on the margin of the ampliate base, usually no teeth are present on medial sectors of the ventral margin (Fig. 34). There are no underleaf remnants on mature shoot

sectors, though ciliiform underleaves are present among the youngest leaves at shoot apices. The leaf insertion approaches the ventral stem mid-line, leaving perhaps 2 ventral cortical cell rows leaf-free.

*Plagiochila trispicata* may be confused with *P. arbuscula* but differs in the discontinuous distribution of teeth on the leaf margin and the oblong-triangular shape of primary shoot leaves.

*Plagiochila trispicata* may be confused with *P. stephensoniana*, but *P. trispicata* has oblong-triangular leaves with an obtuse apex (Fig. 34) not ovate-rotund leaves with a rounded apex (Fig. 28); marginal teeth discontinuously distributed around the apex and leaf base, leaving the medial portion of the ventral leaf margin entire, not distributed evenly from the apex all the way to the leaf base; and larger lacinate-dentate teeth on the basal margin, not triangular.

*Plagiochila trispicata* may be confused with *P. fasciculata* or *P. subfasciculata* but again the leaf shape and distribution of teeth separate these species, the leaves of *P. trispicata* are oblong triangular and teeth are discontinuously distributed along the ventral margin whereas in *P. fasciculata* (Figs 23, 24) and *P. subflabellata* (Fig. 25) the leaves are ovate-triangular and the teeth are evenly spaced along the ventral leaf margin leaving no conspicuous gaps. *Plagiochila trispicata* has ciliiform underleaves among the leaves at the shoot apex, these are not found in *P. fasciculata* or *P. subfasciculata*. In male plants the male bracts of *P. trispicata* do not bear any lamellae whereas those of *P. fasciculata* and *P. subfasciculata* bear lamellae on at least the basal-most pair of bracts.

**Distribution and Ecology:** *Plagiochila trispicata* is endemic to New Zealand, where it occurs from Te Pahi at the northern end of the North Island to the Catlins and Rakiura in the south, and east to the Chatham Islands. *Plagiochila trispicata* inhabits a range of forest types including podocarp-broadleaf, and broadleaf forest including *Nothofagus* dominated forests, a range of topographic situations including alluvial terraces, gorges, faces, and ridges, and between sea level to around 400 m elevation. *Plagiochila trispicata* may grow as an epiphyte on the trunks of a range of tree species including *Dacrydium cupressinum*, *Knightia excelsa*, and *Meliccytus ramiflorus*, on all of which it may form a low ‘collar’ around the trunk base, or occur as scattered patches higher up, it may also grow on dead standing trunks, tree fern trunks, and dead tree ferns. *Plagiochila trispicata* may grow as a lithophyte on boulders and bedrock such as on damp gabbro, basalt, and greywacke.

*Plagiochila trispicata* (as *P. obscura* sensu Inoue and Schuster (1971)) has been recorded for Australia, but all reports are based on misidentifications of other species.

**Representative specimens examined: New Zealand:** *Knight*, BM! as *P. arbuscula*; *Colenso Hep a.1344* as *P. longissima* Col (BM); **North Island:** Te Pahi Ecological Region and District, Te Pahi, North Cape, Mokaikai Scenic Reserve, Upper Whiriwhiri Stream, 34°24'47"S 173°01'40"E, 110 m, 25 Feb 2011, *P.J. de Lange 9705* (AK 322390); North Auckland Province, Kiwanis Reserve, junction of Okahu stream and unnamed stream ca 5 miles S of Kaitaia, N edge of Herekino Forest area, So of Quarry, 35°10'S 173°16'E, 60-80 m, 7 Feb 1995, *J.J. Engel 20933* (F 1141705); North Auckland Province, Maunganui Bluff above Aranga Beach, S of Waipoua Forest and NW of Dargaville, 35°45'S 173°34'E, 115-195 m, 25 Feb 1997, *J.J. Engel 22686* (F 1141703); Coromandel Ecological Region, Tuhua (Mayor Island), western side of Tutaretare Trig, 37°17'40"S 176°15'13"E, 325 m, 29 Jan 2012, *P.J. de Lange 10649* (AK 330937); Tuhua (Mayor Island), Caldera, Te Paritu (Black Lake), 37°17'32"S 176°16'06"E, 10 m, 29 Jan 2012, *P.J. de Lange 10631*, *T.J. de Lange*, & *F.J.T. de Lange* (AK 330919); Wairoa, Mahia Peninsula, Kinikini Road, Mahia Scenic Reserve, upper tributary to the Whangawehi Stream, 39°07'52"S 177°53'03"E, 40 m, 21 Jan 2013, *P.J. de Lange 11530* (AK 337938); **South Island:** North-west Nelson Ecological Region, Golden Bay Ecological District, Wahbourne Reserve, Pohara, 40°44'40"S 172°41'22"E, 70 m, 29 Oct 2004, *J.E. Braggins 04/067* (AK 290513); Greymouth, 1885, *Helms*, ex herb. Stephani (BM); **Chatham Islands:** Rangiauria (Pitt Island), Waipapaku Creek (Second Water Creek), Waterfall, 44°17'S 176°12'W, 80 m, 30 May 2008, *P.J. de Lange CH1666* & *P.B. Heenan* (AK 303347).

Representative misidentified specimens

*Plagiochila fasciculata*

Australia: New South Wales, Pipers Creek, Guthega – Island Bend Road, Kosciusko National Park, 18 km NE of Mt Kosciusko, 36°21'S 148°25'E, 1400 m, 6 Apr 1981, *H. Streimann 15339*, (HO 8101997 as *P. obscura*); Southern Tablelands, just below summit, southeast slope of Mt Budawang, Braidwood area, 35°29'S 150°00'E, 1130 m, 30 Nov 1981, *D.H. Vitt 28941* & *H.P. Ramsay* (CANB 786133 as *P. obscura*).

***Plagiochila alta*** Steph., *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 23: 304 (1896)

*Type citation:* Samoa (R. n. 58)

*Type:* Samoa, Upolu, Lepua, May 1895, *Dr. Reinecke No. 58* (G, E 00002818!d FH).

Epitype (designated here): Fiji, Nabukelevu mountain above Nadakuni Village and between Waiaboa Stream and Sovi Basin, 17°56'59"S 178°16'16"E, 720–750 m, 1 Sep 2011, *M.A.M. Renner 5476, M. von Konrat, & F. Rakoro* (NSW 890152).

=*Plagiochila heterospina* Steph., Journal and Proceedings of the Royal Society of New South Wales 48: 128 (1914)

*Type citation*: Insulae Novae Hebridae (Aneityum): Gunn leg. (Watts, 43 b)

*Type*: New Hebrides, herb. Watts 43b (holotype: G 00113248!)

=*Plagiochila palmicola* Steph., Journal and Proceedings of the Royal Society of New South Wales 48: 129 (1914)

*Type citation*: Insulae Novae Hebridae (Aneityum): Gunn leg. (Watts, 28).

*Type*: Insulae Novae Hebridae, Aneityum, comm. *Dr Gunn* Mar 1911, ex herb. Watts 28, (lectotype designated here: G 00061529! isolectotype: NSW 445408!)

=*Plagiochila lanutosa* Steph., Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien. Mathematisch-Naturwissenschaftliche Klasse 91: 165 (1914) [1915].

*Type citation*: Samoa, in monte Lanutoo (Rechinger, Nr. 5401)

*Type*: W *fide* Inoue (1981) *n.v.*

=*Plagiochila colonialis* Steph., Species Hepaticarum 6: 139 (1918)

*Type citation*: Nova Caledonia. (Franc legit.)

*Type*: New Caledonia, Tao, forest, de 100 a 600 m, (?) January 1910, *Franc* (lectotype designated by Renner *et al.* (2018): G 00113524!); residual syntypes: New Caledonia, 'Caled'Armieu' (?), forest, 500 m, 29 Dec 1909, *Franc* (G 00113521!). New Caledonia, Tao, forest, 600 m, January 1910, *Franc*, (G 00113522!) New Caledonia, Mont Mou, 300 m, 1911, *Franc* (G 00113523!)

=*Plagiochila taona* Steph., Species Hepaticarum 6: 233 (1921)

*Type citation*: Nova Caledonia (Franc legit)

*Type*: Nova Caledonia, Tao, 600 m, Jan 1910, *Franc 241* (lectotype designated by Bonner (1962): G 00069884!)

=*Plagiochila comptonii* Pearson, Journal of the Linnean Society. Botany 46: 21 (1922)

*Type citation*: Ignambi. Rising from rocks. Moist forest, 2000 ft. 1546.

*Type*: New Caledonia, Ignambi, Moist forest, 2000 ft., 31 July 1914, *R.H. Compton 1546 N.C.* (BM 000576206!)

=*Plagiochila taitica* Gottsche ex Dugas, Contribution à l'Étude du Genre *Plagiochila* Dum.: 131 (1928) *nom. inval.*

*Type citation*: Tahiti 'in herb. Mus. Par.'

=*Plagiochila heterospina* Steph. ex Herzog, Hedwigia 78: 228 (1938) *nom. illeg. non Plagiochila heterospina* Steph. (1914)

=*Plagiochila belangeriana* var. *heterospina* E.O.Campb., Journal of the Royal Society of New Zealand 1: 20 (1971) *nom. nov. pro Plagiochila heterospina* Steph. ex Herzog

*Type citation*: Fiji leg. A.C. Smith, n.923.

*Type*: Taveuni on holotype *fide* Inoue (1984) *n.v.*

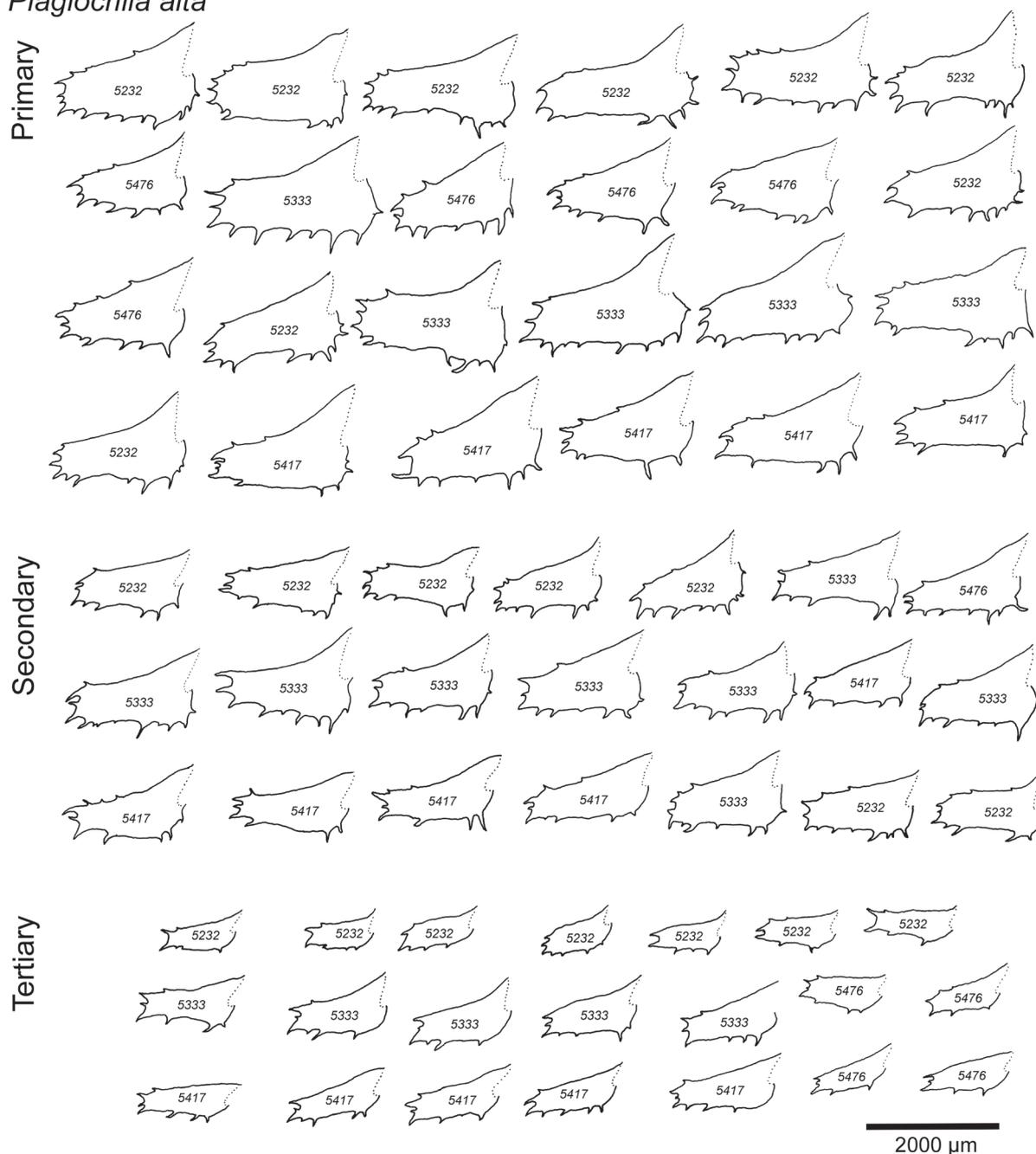
=*Plagiochila castanea* Inoue Journal of the Hattori Botanical Laboratory 33: 315 (1970) *nom. nov. pro Plagiochila badia* Steph.

Replaced synonym: *Plagiochila badia* Steph. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 23: 304 (1896) *nom. illeg.*

*Type citation*: Samoa (R. n. 34, 35, 72).

*Type*: Samoa, *Reinecke*, (lectotype designated by Bonner (1962): G 00112956!); residual syntypes: Samoa, Malaulavu 1200 m, October 1894, *Reinecke 34* (E 00049270!d) Samoa, September 1894, *Reinecke 35* (E 00049271!d) Samoa, Dec. 1894, *Reinecke 72* (E 00049272!d)

**Etymology**: high or elevated, reference unclear.

*Plagiochila alta*

**Fig 35.** *Plagiochila alta* leaves, from M.A.M. Renner 5232 et al. (NSW 889302), M.A.M. Renner 5476 et al. (NSW 890152), M.A.M. Renner 5333 et al. (NSW 889332), and M.A.M. Renner 5417 et al. (NSW 889522).

**Description:** Plants with bipinnately branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 100 mm long and 50 mm wide, trimorphic; primary shoots 4–6 mm wide, branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 900  $\mu\text{m}$  diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 to 6 layers, cortical cell walls strongly and continuously thickened, outer layer of cells slightly larger, but walls, including free external wall, thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, walls with trigones absent small and triangular. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, Primary shoot leaves oblong, 1570–2885  $\mu\text{m}$  long  $\times$  820–1505  $\mu\text{m}$  wide, with a shallowly ampliate base, apex truncate, dorsal margin shallowly convexly curved at its middle or, less commonly, straight; margins with 7–16 triangular teeth distributed discontinuously around

the ventral margin, usually with a gap along the ventral margin, in some leaves extending along the dorsal margin, teeth similar stature around apex and base. Secondary shoot leaves oblong, 1090–2265  $\mu\text{m}$  long  $\times$  505–1170  $\mu\text{m}$  wide, with a shallowly ampliate base, apex truncate, dorsal margin shallowly convexly curved at its middle or, less commonly, straight; margins with 4–16 teeth distributed continuously or more often discontinuously along the postical margin and apex with a gap at the middle of the ventral margin; tertiary shoot leaves oblong, 900–1670  $\mu\text{m}$  long  $\times$  330–730  $\mu\text{m}$  wide, base not ampliate, apex truncate with two or three teeth, dorsal margin shallowly convexly curved at its middle or straight; margins with 3–9 teeth irregularly spaced along the ventral margin and around the apex, and occasionally onto the dorsal margin where one or two teeth may be present near the apex; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, 14–21  $\mu\text{m}$  long  $\times$  8–12  $\mu\text{m}$  wide, long axis parallel or perpendicular to leaf margin, walls with bulging to nodulose trigones but not continuously thickened; medial leaf cells isodiametric to ovoid, 14–26  $\mu\text{m}$  long  $\times$  12–20  $\mu\text{m}$  wide, walls unpigmented, with bulging to bulging and angular (block-like) trigones, medial thickenings absent, cells in leaf base polyhedral, slightly elongated, 24–49  $\mu\text{m}$  long  $\times$  16–25  $\mu\text{m}$  wide, walls with bulging to nodulose to block-like trigones, medial thickening present or absent present on basal-most longitudinal walls, trigones and medial thickenings sometimes confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves present amid leaves at shoot apex, a tuft of curved and branched cilia, disaggregating and dislocating, apparently absent from mature shoot sectors. Asexual reproduction by leaf-borne propagules or leaf fragments absent.

Dioicous(?). Fertile material not seen. Fig. 35.

**Recognition:** The primary shoot leaves of *Plagiochila alta* are much longer than wide and distinctly oblong in shape, except for the ampliate base. The ventral leaf margin is straight. The leaf margin bears 7–12(–14) teeth that tend to cluster around the leaf apex and the ampliate basal portion of the ventral margin. However, some leaves will be found in every specimen where teeth are evenly distributed along the entire ventral margin between apex and base. As in *P. arbuscula* the teeth are more or less the same size at the apex and the base, though those at the base do tend to be slightly longer.

**Distribution and Ecology:** *Plagiochila alta* occurs on a number of islands within the western Pacific, including New Caledonia, Vanuatu, Samoa, Tahiti, Fiji and the Cook Islands. *Plagiochila alta* is also known, by a single collection, within the New Zealand Botanical Region on Raoul Island in the Kermadec Islands. Here *P. alta* grew with *Radula javanica* carpeting a damp boulder directly below the ephemeral waterfall, such that the plants would be flooded during rain. On Rarotonga in the Cook Islands *P. alta* grew in root holes and crevices under dense tangles of *Freycinetia arborea*. In Fiji *Plagiochila alta* has been collected growing as a trunk epiphyte on a wide range of tree species and sizes, including saplings and mature canopy trees within wet tropical rainforest between 400 and 1000 m elevation. For example along the southern sector of Namosi Road it grew on sapling trunks on a steep slope with SE aspect in a gully head within mesophyll rainforest; and on the summit of Nabukelevu mountain above Nadakuni Village it grew as an epiphyte on tree trunks mixed with other bryophytes.

**Representative specimens examined:** **Aneityum Island:** north side, May–Jun 1913, *R.C. Gunn* ex herb. Watts 124 (NSW 444158); **Fiji:** **Viti Levu:** Rairaimatuku Plateau, on a summit with telecommunication tower, 16 km S of Monasavu, 17°47'31"S 178°01'14"E, 1265 m, 3 Sep 2011, *M.A.M. Renner 5534 et al.* (NSW 890224); Naitasira District, Ulvi Nakoba, *M.A.M. Renner 5333 et al.* (NSW 889332); *ibid.*, *M.A.M. Renner 5232 et al.* (NSW 889302); Namosi Road, *M.A.M. Renner 5417 et al.* (NSW 889522); Nabukelevu mountain above Nadakuni Village and between Waiaboa Stream and Sovi Basin, 17°56'59"S 178°16'16"E, 720–750 m, 1 Sep 2011, *M.A.M. Renner 5471*, *M. von Konrat*, & *F. Rakoro* (NSW 890146); *ibid.*, *M.A.M. Renner 5476*, *M. von Konrat*, & *F. Rakoro* (NSW 890152). **Kadavu:** Nabukelevu-Ira Village, Nabukelevu mountain, north western edge of summit crater, 19°07'06"S 177°58'48"E, 800 m, 9 Sep 2011, *M.A.M. Renner 5769 et al.* (NSW 895646); **Cook Islands:** Rarotonga, Te Kou track, Te Kou Basin, upper headwaters of Te Kou Stream, 21°14'S 159°46'W, 530 m, 8 Jul 2010, *P.J. de Lange CK188* & *T.J. Martin* (AK 323596). **New Zealand: Kermadec Islands:** Raoul Island, Sunshine Valley, Sunshine Valley Waterfall, 29°17'10.8"S 177°55'45.7"W, 53 m, 16 May 2011, *P.J. de Lange K687* (AK 325477).

***Plagiochila pacifica*** Mitt., Seemann, Flora Vitiensis: 407 (1871) [1873]

*Type citation:* Sunday Island, ad arbores, (Milne! n. 87)

*Type:* Sunday Island, ad arbores, *Milne n. 87* (holotype: NY isotypes: BM 000671202! G 00282171!)

= *Plagiochila kermadecensis* J.J.Engel & G.L.Merr., Journal of the Hattori Botanical Laboratory 87: 295 (1999)

*Type citation:* Holotype: Kermadec Islands, Raoul Island, Pukekohu area, ca. 300–400 m, Sykes 401/K – c. young per. (F); isotype: (CHR).

*Type:* Kermadec Islands, Raoul Island, Pukekohu area, ca. 300–400 m, Sykes 401/K (holotype: F; isotype: CHR).

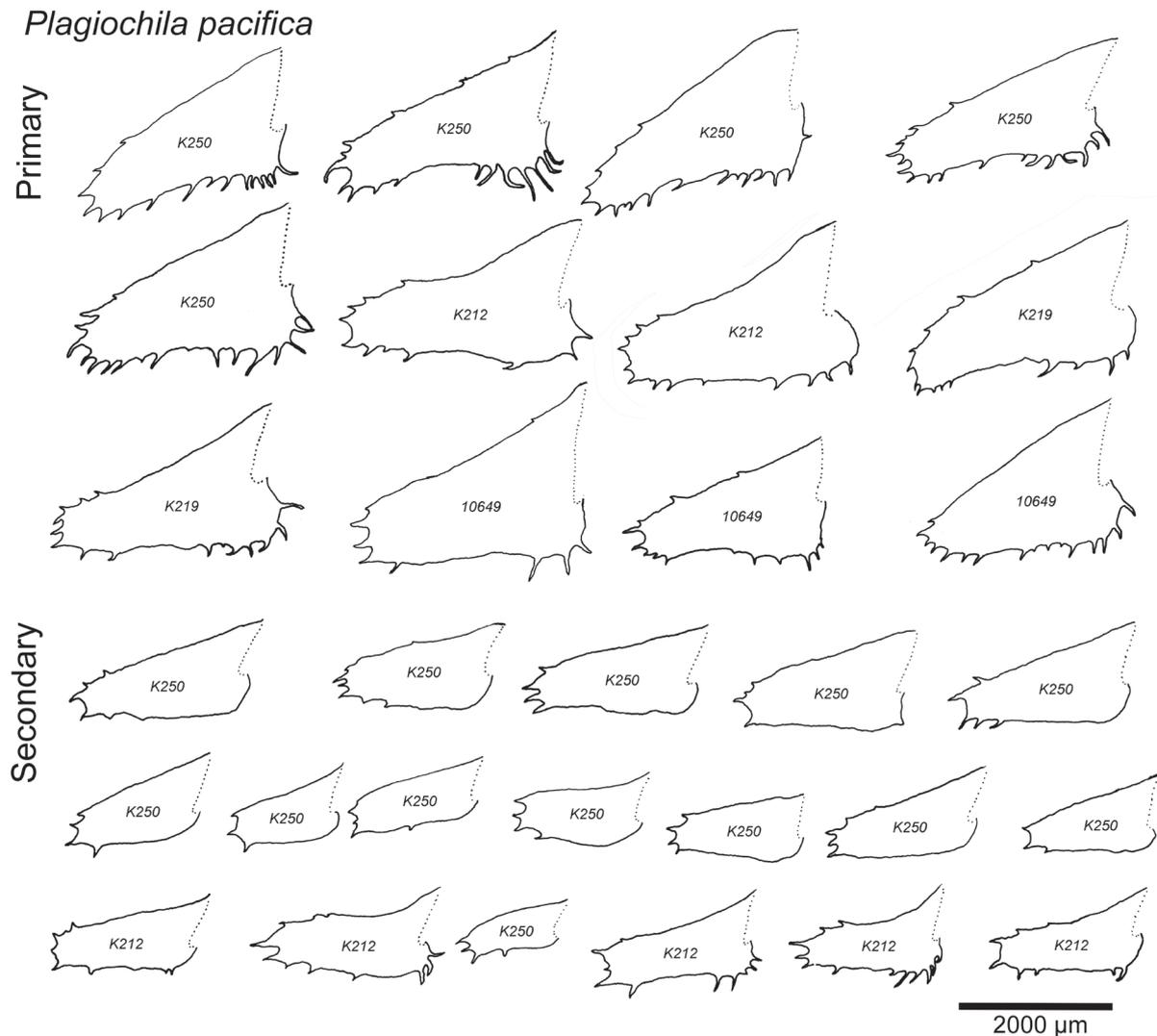
**Etymology:** *pacifica*, adjectival form from Pacific, referencing the Pacific Ocean.

**Description:** Plants with unbranched or pinnate shoot systems arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 100 mm long and 50 mm wide, trimorphic, bright emerald green in life; primary shoots 4–6 mm wide, branches arising by *Frullania*-type branching, lateral-intercalary branching present in response to apex damage, ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; reddish-brown, in primary shoots to 900 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 5 to 7 layers, cortical cell walls strongly and continuously thickened, outer layer of cells slightly larger, all cortical cells smaller than medulla cells; medulla cell walls pale yellow-brown pigmented, walls moderately and unevenly thickened. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, primary shoot leaves weakly falcate to oblong-triangular, 2040–3465 (average 2945) µm long × 1020–2005 (average 1580) µm wide, with a shallowly ampliate base, apex rounded or truncate, dorsal margin shallowly concavely or convexly curved or straight; margins with 6–19 (average 12.7) triangular to filiform teeth distributed discontinuously around the apex and along ventral margin, usually with a gap in the middle of the ventral margin, in some leaves extending along the dorsal margin to the base, teeth smaller in stature around apex than the base, where they may be long, ciliate and curved; secondary shoot leaves triangular to oblong, 1370–2605 (average 2080) µm long × 645–1390 (average 1000) µm wide, with a shallowly ampliate base, apex truncate, dorsal margin straight; margins with 3–14 (average 6.7) teeth distributed around the apex, occasionally at the ventral base as well, margins otherwise entire; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with bulging to nodulose trigones but not continuously thickened; medial leaf cells isodiametric to ovoid, 19–28 µm long × 19–23 µm wide, walls unpigmented, with bulging trigones, medial thickenings absent, cells in leaf base polyhedral, slightly elongated, walls with bulging trigones, medial thickening present or absent, trigones not confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves present amid leaves at shoot apex, a tuft of curved and branched cilia, disaggregating and dislocating, but leaving basal cells intact on mature shoot sectors. Asexual reproduction by leaf-borne propagules or leaf fragments absent.

Dioicous. Androecia not seen. Gynoecia at apices of secondary shoots; bracts triangular-oblong; dorsal margin revolute, ventral margin ampliate; outer half of dorsal, ventral, and apical margins all ciliate-laciniate; Subfloral innovations by lateral-intercalary branching from between the female bracts. Perianth subclavate, dorsal and ventral keels unwinged; laterally compressed but with an inflated base, lateral walls plane; labia straight or shallowly curved, each with ciliate-laciniate teeth. Fig. 36.

**Recognition:** The shoot systems of *Plagiochila pacifica* are pinnate and the primary shoot leaves are longer than wide and oblong-triangular in shape, except for the ampliate base. The ventral leaf margin is straight to slightly concave. The leaf margin bears 6–19 teeth that tend to cluster around the leaf apex and the ampliate basal portion of the ventral margin. However, some leaves will be found in every specimen where teeth also occur on the ventral margin between apex and base. Unlike *P. arbuscula* the teeth on the ampliate base are often much longer and narrower than those at the apex, and may be curved. *Plagiochila pacifica* has persistent, small, underleaf remnants on stems, and plants are bright emerald-green in life.

**Distribution and Ecology:** *Plagiochila pacifica* is currently known from two islands in the western Pacific, Raoul Island in the Kermadec Group within the New Zealand Botanical Region from where the species was described, and Rarotonga within the Cook Islands where the species was first collected in 2014. *Plagiochila pacifica* may eventually prove to be more widely distributed throughout the Pacific Islands as the bryophyte flora of this region becomes better documented. On Raoul Island *Plagiochila pacifica* grows as an epiphyte on the trunks of *Rhopalostylis baueri* and may extend onto the ground surrounding the trunk base, and on rocks within wet forest. On Rarotonga *Plagiochila pacifica* was collected growing threaded through *Neckeropsis lepinea* and roots of *Asplenium caudatum* on the side of a stream.



**Fig 36.** *Plagiochila pacifica* leaves, from P.J. de Lange K219 & D.C. Havell (AK 305119), P.J. de Lange 10649 (AK 330937), P.J. de Lange K212 & D.C. Havell (AK 313957), and P.J. de Lange K250 & D.C. Havell (AK 305205).

Specimens examined: **Cook Islands:** Rarotonga, Papua Stream, Te Rua Manga Track, 21°14'S 159°47'W, 220 m, 13 July 2014, P.J. de Lange CK196, T.J.P. de Lange, & F.J.T. de Lange (NSW); **New Zealand: Kermadec Islands:** 1956, R.C. Cooper 44227 (AK 321102); Kermadec Ecological Region and District, Kermadec Islands Nature Reserve, Raoul Island, Moumoukai Track, 29°16'00"S 177°54'00"E, 336 m, 8 May 2009, P.J. de Lange K212 & D.C. Havell (AK 313957); Moumoukai Track, summit ridge, 29°16'S 177°54'E, 511 m, 8 May 2009, P.J. de Lange K250 & D.C. Havell (AK 305205); Moumoukai Track, 29°16'S 177°54'E, 384 m, 8 May 2009, P.J. de Lange K219 & D.C. Havell (AK 305199).

***Plagiochila* sect. *Duræ*** Carl, Annales Bryologici, Supplement 2: 123 (1931)

Type: *Plagiochila dura* De Not.

*Plagiochila dura* the type species, was resolved sister to sect. *Glaucescentes* by Heinrichs *et al.* (2005), along with an individual of *P. ramosissima* (as *P. deltoidea*). Subsequently a range of morphologically disparate species have been placed into this section based on molecular evidence, including *P. colensoi* and *P. monospiris* (as *P. sp. nov.*) (Renner *et al.* 2017a). This lineage contains a small number of species, perhaps 10 or 15, distributed in southern temperate regions of New Zealand, South America, and the Wet Tropics of north east Queensland, and tropical montane forests of east Malesia including Papua New Guinea and the Solomon Islands.

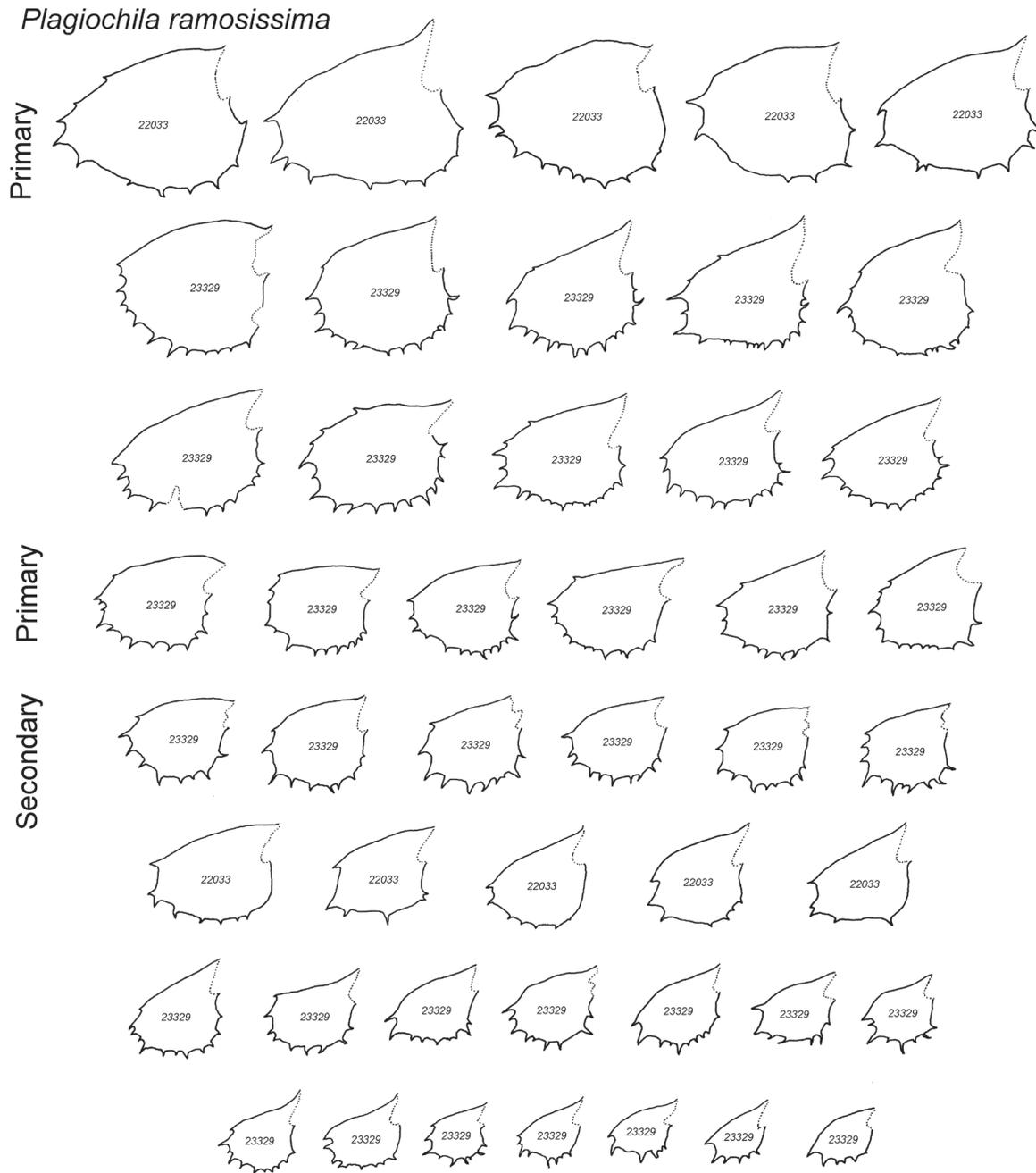
***Plagiochila ramosissima* (Hook.) Lindenb., Species Hepaticarum 2-4: 87 (1840)**Basionym: *Jungermannia ramosissima* Hook. Musci Exotici 1: 92 (1818)*Type citation*: Hab. In sinu Dusky bay dicto, apud Novam Zeelandiam. *D. Menzies*, 1791.*Type*: New Zealand: Dusky Bay, 1791, *Dr Menzies* (FH 00284130! BM! ex herb. Stephani BM!)**Etymology**: with the most branches.

**Description**: Plants with erect fasciculately branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; shoot systems to 100 mm long and 40 mm wide, dimorphic; primary shoots 3–4 mm wide, branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 600 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 to 6 layers, cortical cell walls strongly and continuously thickened, outer layer of cells slightly larger, but walls, including free external wall, thickened to same degree as inner cortical cell layers, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and transversely orientated, primary shoot leaves rotund to asymmetrically ovate, 1210–2120 µm long × 1000–1720 µm wide, with a shallowly ampliate base, ventral margin curved, apex truncate or broadly rounded, dorsal margin shallowly curved; margins with 6–16 triangular teeth distributed around apex and ventral margin, teeth variable in stature, large and small teeth admixed, often two teeth at leaf apex larger; secondary shoot leaves rotund to ovate, 660–1425 µm long × 485–1055 µm wide, with 5–12 teeth distributed around apex and on ventral margin; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with bulging to nodulose trigones and weak continuous thickening; medial leaf cells isodiametric to ovoid, 14–20 µm long × 12–17 µm wide, walls unpigmented, with bulging trigones, medial thickenings present or absent, cells in leaf base rectangular, 30–55 µm long × 13–20 µm wide, walls with bulging to nodulose trigones, medial thickening present or absent, trigones not confluent. Cell surfaces smooth. Oil-bodies 2–6 per median cell, coarsely botryoidal. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on secondary or shoots that continue vegetative growth, scattered or in loose fascicles of three or more, arising by *Frullania*-type or lateral-intercalary branching, ventral-intercalary branches not associated with male branches; bracts in 4–10 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, with 5–12 teeth, epistatic, antheridia 1 per bract; stem among bracts smooth. Gynoecia at apices of short secondary or tertiary shoots; bracts oblong-ovate or broadly ovate, similar in size to leaves; female bracteole absent. Subfloral innovations one or two produced by lateral-intercalary branching from between the female bracts. Perianth ovate oblong, to 2400 µm long and 1600 µm wide at mouth, dorsal keel with a narrow to sometimes broad and spinose wing, ventral keel unwinged; laterally compressed but with an inflated base, lateral walls plane; labia shallowly curved, each with irregular spinose-dentate teeth. Fig. 37.

**Recognition**: Shoots of *Plagiochila ramosissima* have a characteristic dendroid form, where long spreading secondary branches arise from a robust erect primary shoot in a single plane. The secondary branches all arise by lateral-intercalary branching, and result in a fasciculate shoot systems. The leaves are ovate, transversely orientated, contiguous to imbricate, and weakly spreading, the leaves bear small evenly-sized triangular teeth on their postical and apical margins. *Plagiochila ramosissima* could be confused with *P. gigantea*, but vegetative branches in *P. ramosissima* are lateral-intercalary, not *Frullania*-type. *Plagiochila ramosissima* could be confused with *P. retrospectans* or *P. fuscella* but the shoot apex is not nodding as it is in these latter two species, and the leaf marginal teeth are triangular and coarse, not numerous and fine. *Plagiochila ramosissima* could be confused with *P. colensoi*, but does not have small underleaves on the shoots.

**Distribution and Ecology**: *Plagiochila ramosissima* is endemic to New Zealand, where it is widely distributed in hyperhumid habitats from near sea level to around 1000 m elevation, throughout all three main islands, though *P. ramosissima* is restricted to cloud forests on higher elevation mountain tops in the North Island. *Plagiochila ramosissima* occurs in a range of vegetation types, from tall, closed, lowland forest, to broken subalpine scrub, and inhabits a range of microsites, encompassing epiphytic, lithophytic and terrestrial substrates. *Plagiochila ramosissima* has been collected as an epiphyte on the base of *Nothofagus menziesii*, on rotting logs within *Nothofagus* forest, forming masses on the ground under *Nothofagus menziesii*, on rock faces, and at the edge of pools alongside streams. *Plagiochila ramosissima* has been recorded from Tasmania, but these reports are based on misidentifications of other species.



**Fig 37.** *Plagiochila ramosissima* leaves, from *J.J. Engel* 22033 (F 1141444), and *J.J. Engel* 23329 (F 1141186).

**Representative specimens examined:** **New Zealand:** **North Island:** South Auckland, Mt. Te Aroha, 37°32'S 175°45'E, 900–940 m, 12 Mar 1995, *J.J. Engel* 22110 (F 1141445); Urewera National Park, Panekiri Range, summit area of Pukenui in vicinity of Pukenui Bluff, S of Lake Waikaremoana, 38°47'S 177°04'E, 1180 m, 24 Mar 1997, *J.J. Engel* 23329 (F 1141186); Taranaki, Mt Taranaki above plateau, Curtis Track, 39°18'S 174°05'E, 20 Oct 1965, *M. Barr* (AK 125548); **South Island:** North Westland, Ngakawau, Stockton mine area, Upper Deep Stream, 41°42'52"S 171°50'31"E, 850 m, 6 Dec 2006, *J.E. Braggins* 06/292G (AK 302420); North Westland, Blackball, Sewell Peak, near top of road to first peak, 42°24'32"S 171°20'24"E, 780 m, 6 Dec 2000, *J.E. Braggins* (AK 287129); Boundary of Westland and Canterbury Province, Arthurs Pass National Park, Dobson Nature Walk, summit area of Arthurs Pass, 42°54'S 171°33'E, 920 m, 5 Mar 1995, *J.J. Engel* 22033 (F 1141444); South Westland, Cascade Ecological Region, end of Jacksons River Road, Martyr River, 44°06'29"S 171°32'06"E, 30 m, 7 Dec 2000, *J.E. Braggins* (AK 287167); Fiordland, Secretary Island, 26 Jan 1987, *J. Ogden* 2#9 (AK 315778); **Rakiura (Stewart Island):** 1909, *L. Cockayne* 8310 (AK 18659).

***Plagiochila colensoi*** Hook.f. & Taylor, London Journal of Botany 5: 269 (1846)

*Type citation:* New Zealand. n. 159. *Colenso, Hook. Herb.*

*Type:* New Zealand W. *Colenso* No. 159, Hook[er] Herb., (holotype: FH 00458010!)

=*Plagiochila lyallii* Mitt. in Hooker, Flora Novae Zelandiae 2(2): 132 (1855)

*Type citation:* Northern and Middle Islands: Auckland, *Sinclair*. Wairarapa valley, *Colenso*, Port Preservation and Milford Sound, *Lyall*.

*Type:* New Zealand, Port Preservation, *Dr Lyall*, (NY! BM!)

=*Plagiochila pallescens* Colenso, Transactions and Proceedings of the New Zealand Institute 21: 47 (1889)

*Type citation:* Forests near Lake Waikare, County of Whakatane; 1888: *Mr. A. Hamilton*.

*Type:* Forests near Lake Waikare, County of Whakatane; 1888: *Mr. A. Hamilton*. sine loco, *Hep. a.1338* (BM! G!)

=*Plagiochila exilis* Colenso, Transactions and Proceedings of the New Zealand Institute 19: 282 (1887)

*Type citation:* On wet logs, etc., forming closely-growing loose tangled masses; low wet woods near Norsewood, County of Waipawa; 1886: *W.C.*

*Type:* ex herb. Pearson as *P. exilis Colenso* (BM 00067529!)

**Etymology:** of the Rev. William Colenso, missionary botanist.

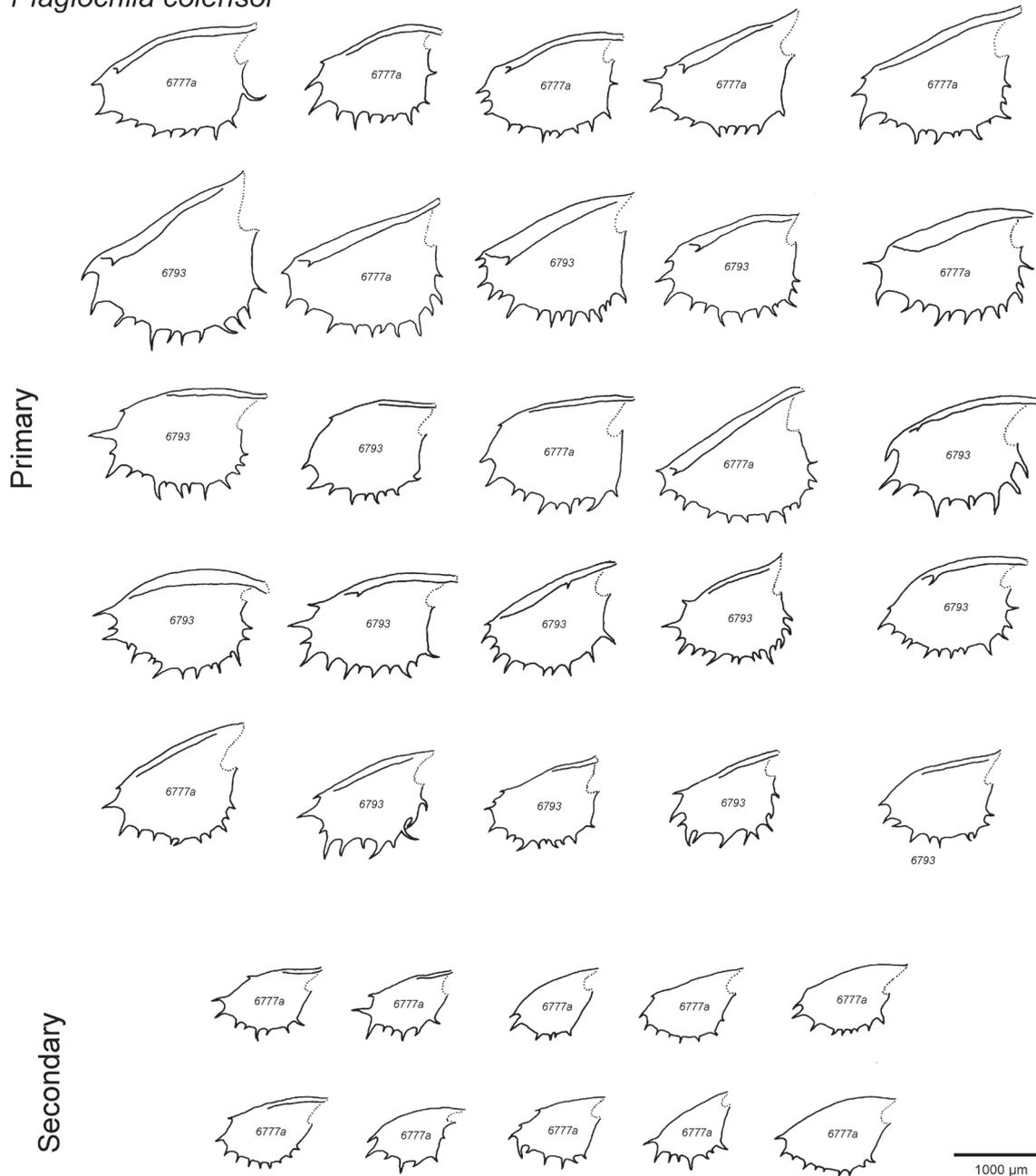
**Description:** Plants with erect pinnately branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; shoot systems to 50 mm long and 20 mm wide, dimorphic; primary shoots 3–4 mm wide, branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 400 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 3 to 6 layers, cortical cell walls strongly and continuously thickened, all cortical cells smaller than medulla cells; medulla cell walls hyaline. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves contiguous to imbricate, succubously inserted and orientated, primary shoot leaves asymmetrically ovate, 1195–2020 µm long × 930–1550 µm wide, dorsal margin straight or shallowly curved, apex truncate or broadly rounded, ventral margin curved, not ampliate, straight at base; apex and ventral margins with 10–17 triangular teeth, teeth variable in stature, large and small teeth admixed, often two teeth at leaf apex larger; secondary shoot leaves obovate, 910–1190 µm long × 530–850 µm wide, with 6–10 teeth distributed around apex and on ventral margin, again two teeth at apex usually larger; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, walls with bulging trigones and weak continuous thickening; medial leaf cells isodiametric to ovoid, 9–16 µm long × 7–13 µm wide, walls unpigmented, with bulging trigones, medial thickenings present or absent, cells in leaf base rectangular, 30–55 µm long × 13–20 µm wide walls with bulging to nodulose trigones, medial thickening present or absent, trigones not confluent. Cell surfaces smooth. Oil-bodies 3–5 per median cell, coarsely botryoidal. Underleaves present, vestigial, triangular. Asexual reproduction absent.

Dioicous. Androecia intercalary on secondary or shoots that continue vegetative growth, scattered or in fascicles of three to five, arising by *Frullania*-type branching, rarely by lateral-intercalary branching, ventral-intercalary branches not associated with male branches; bracts in 6–11 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, with 3–6 teeth, epistatic, margin of dorsal lobe with prominent lacinate tooth, antheridia 1 per bract; stem among bracts smooth. Gynoecia at apices of primary or secondary shoots; bracts oblong-ovate or ovate, larger than adjacent leaves, 1800–2300 µm long × 1300–1500 µm wide; female bracteole absent. Subfloral innovations one to three produced by lateral-intercalary branching from between the female bracts in the absence of fertilization. Perianth oblong, to 2500 µm long and 1700 µm wide at mouth, dorsal keel with a narrow wing, ventral keel unwinged; laterally compressed but with an inflated base, lateral walls plane; labia shallowly curved, each with coarse triangular teeth. Fig. 38.

**Recognition:** *Plagiochila colensoi* can be recognized by the combination of branches almost all lateral-intercalary, the lateral intercalary branches spreading at around 60° to the primary shoot; the small narrow-triangular or ciliiform underleaves on vegetative shoots; leaves with two large curved triangular-dentate teeth at the apex, and 4–5(–7) smaller, straight, triangular-dentate teeth on the ventral margin, the leaves remote

and rolled when dry, the presence of small underleaves on vegetative shoots and among male bracts, androecia usually solitary, intercalary, male bracts in 4–5 and up to 12 pairs, but sometimes in pairs and up to fours with the second and subsequent branches originating by *Frullania*-type branch from the base of first; the male bracts with an accessory spine on the upper bract margin; and the dentate-denticulate perianth mouth with small evenly sized teeth on labia.

*Plagiochila colensoi*



**Fig 38.** *Plagiochila colensoi* leaves, from M.A.M. Renner 6793 (NSW 900040), and M.A.M. Renner 6777a (NSW 900148).

*Plagiochila colensoi* could be confused with *P. incurvicolla* but the male bracts of *P. colensoi* have an accessory spine on the upper bract margin, the upper bract margins of *P. incurvicolla* are not so armed. The oil-bodies of *P. colensoi* are 'coarsely botryoidal' (Inoue and Schuster 1971 p. 86), while those of *P. incurvicolla* are homogenous.

**Distribution and Ecology:** *Plagiochila colensoi* is endemic to New Zealand where it occurs from Northland, to Rakiura and everywhere wet in between including Taranaki, the Central Plateau, Wellington, NW Nelson, the West Coast and Fiordland. *Plagiochila colensoi* inhabits a wide range of podocarp-broadleaf forest types, including those on level, poorly drained, relatively infertile sites dominated by *Lepidothamnus intermedius*, *Ixerba brexioides*, *Weinmannia silvicola*, *Quintinia serrata*, *Archeria racemosa*, and *Coprosma dodonaeifolia*, and also secondary successional forests on mudstone dominated by *Prumnopitys taxifolia*, *P. ferruginea*, *Pseudopanax crassifolius*, *Podocarpus totara*, *Elaeocarpus dentatus*, *Weinmannia racemosa* in a canopy 9 m tall, with *Dicksonia squarrosa*, *Myrsine salicifolia*, *Pseudowintera colorata*, *Carpodetus serratus*, *Griselinia littoralis* in the subcanopy, and *Blechnum novae-zelandiae* and *Astelia fragrans* on forest floor. At higher elevations in the North Island *P. colensoi* grows in forests with emergent *Libocedrus bidwillii* over *Nothofagus solandri* var. *cliffortioides* with *Halocarpus bififormis*, *Phyllocladus alpinus*, *Myrsine divaricata*, *Raukaua anomala*, *R. simplex*, *Coprosma foetidissima* and other *Coprosma* spp. Within these diverse forest types, *P. colensoi* occupies a range of microsites where corticolous substrates are available, including on the trunks of living trees, on dead standing trees, and on the sides of rotting logs.

*Plagiochila colensoi* (as *P. lyallii*) has been reported from Queensland and Tasmania, but all Australian records are based on misidentifications of other species.

**Representative specimens examined: New Zealand:** *Hooker* ex herb. Kew (G 00115855); **North Island:** Northland, Waima Forest, Hauturu Highpoint track in vicinity of Hauturu trig, 35°31'S 173°28'E, 650–680 m, 23 Feb 1997, *J.J. Engel* 22600 (F 1141181); Little Barrier Island (Hauturu), Awaroa stream, c 150 m from the sea, 36°14'S 175°5'E, 27 Jan 1980, *J.E. Braggins* 80/944 & *J.E. Beever* (AK 312410); Coromandel Ecological Region, Thames Ecological District, Mt Rowe summit area; 37°02'16"S 175°40'19"E, 790 m, 14 Feb 2007, *M.A.M. Renner* 2572a (AK 298571); Coromandel State Forest Park, summit of Table Mountain, 37°03'S 175°40'E, 835 m, 14 Feb 1997, *J.J. Engel* 22361, (F 1141585); South Auckland, Mt. Te Aroha, 37°32'S 175°45'E, 900–940 m, 12 Mar 1995, *J.J. Engel* 22145 (F 1141476); Urewera National Park, crest trail from State Highway 38 toward Whakataka summit, 38°42'S 177°03'E, 930–1030 m, 29 Jan 1995, *J.J. Engel* 20647 (F 1142369); Urewera National Park, Panekiri Range, near summit area of Pukenui near Panekiri Bluff, 38°47'S 177°04'E, 1050 m, 24 Mar 1997, *J.J. Engel* 23353 (F 1141138); Central Plateau, Maunganuioteao River catchment, Erua Forest, track Tapapakurua Falls, 39°10'48"S 175°22'23"E, 850 m, 24 Nov 2013, *M.A.M. Renner* 6793 (NSW 900040); Central Plateau, Tongariro National Park, Ruapehu, Mangawhero River catchment, Ohakune Mountain Road, E1814054 N5642623, 1048 m, 23 Nov 2013, *M.A.M. Renner* 6777a (NSW 900148); Taranaki, Mt Taranaki above Plateau, Curtis track, 39°18'S 174°05'E, 21 Jan 1965, *M. Barr* (AK 125560); **South Island:** Canterbury, Arthur's Pass National Park, Scotts Track to Avalanche Peak, west of Arthurs Pass township, 42°56'S 171°33'E, 950 m, 5 Mar 1995, *J.J. Engel* 22079 (F 1141173).

Representative misidentified specimens examined:

*Plagiochila fasciculata*

Tasmania, South West District, Wanderer River, c. 5 km from mouth, 20 m, 42°43'S 145°27'E, 8 Mar 1985, *A. Moscal* 10063C (HO 99662); *ibid.*, *A. Moscal* 10066C (HO 548793); Gordon River, 42°30'S 145°40'E, 1 Jan 1914, *W.A. Weymouth* 1458 (HO 87619); Tasmania, 1901, *F.R.M. Wilson* (MEL 2278365); West Coast, North Pedder River, 41°24'S 144°51'E, 25 m, 7 Feb 1991, *A. Moscal* 21267 (HO 301767).

*Plagiochila hartziana*

Tasmania, Russell Falls, 42°41'S 146°43'E, Nov 1914, s.d. (HO 87621); Central Highlands, Brumbys Creek, 41°45'S 146°51'E, 810 m, 24 Dec 1989, *A. Moscal* 18670 (HO 548794).

***Plagiochila monospiris*** Inoue & Grolle, *Journal of the Hattori Botanical Laboratory* 36: 489 (1972)

*Type citation:* New Guinea: Goodenough Isl., east slope, 1600 m, alt., leg. Brass no. 24834 (TNS duplicates in FH, JE).

*Type:* New Guinea: Goodenough Isl., east slope, 1600 m, alt., Brass 24834 (holotype: TNS; isotypes: FH, JE)

**Etymology:** with one spiral, referring to the single band of thickening present on the elaters.

**Description:** Plants with erect irregularly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; shoot systems to 20 mm long, monomorphic; primary shoots 1.6–2.4 mm wide, branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, to 200 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 2 layers, cortical cell walls strongly and continuously thickened, cortical cells smaller than medulla cells; medulla cell

walls with small triangular trigones, hyaline. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves remote to contiguous, succubously inserted and orientated, obovate, 580–1060  $\mu\text{m}$  long  $\times$  280–650  $\mu\text{m}$  wide, dorsal margin straight or shallowly arched, apex broadly rounded, ventral margin curved in outer half and straight at base, not ampliate; apex and ventral margins with 3–8 sharp triangular teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, not attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, long axis parallel or perpendicular to leaf margin, 14–25  $\mu\text{m}$  long  $\times$  12–20  $\mu\text{m}$ , walls with bulging trigones; medial leaf cells isodiametric to ovoid, 20–35  $\mu\text{m}$  long  $\times$  17–30  $\mu\text{m}$  wide, walls unpigmented, with bulging trigones, and occasional medial thickenings, cells in leaf base ovoid, 22–45  $\mu\text{m}$  long  $\times$  17–24  $\mu\text{m}$  wide walls with bulging trigones and occasional medial thickening, trigones not confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, singly or in loose series, androecial branching absent, *Frullania*-type, lateral-intercalary, and ventral-intercalary branches not associated with male branches; bracts in 10–17 pairs, contiguous, bract-lobe reduced and smaller than adjacent leaves, with 3–6 teeth, epistatic, margin of dorsal lobe with prominent lacinate tooth, antheridia 1 per bract; stem among bracts smooth. Gynoecia at shoot apices; bracts obovate, larger than adjacent leaves, 1620–1950  $\mu\text{m}$  long  $\times$  660–720  $\mu\text{m}$  wide; female bracteole absent. One subfloral innovation produced by lateral-intercalary branching from between the female bracts. Perianth campanulate, to 2000  $\mu\text{m}$  long and 1300  $\mu\text{m}$  wide at mouth, dorsal keel longer than ventral keel, dorsal and ventral keels unwinged; laterally compressed, lateral walls plane; labia curved, each with 10–15 lacinate teeth. Figs 39, 40.

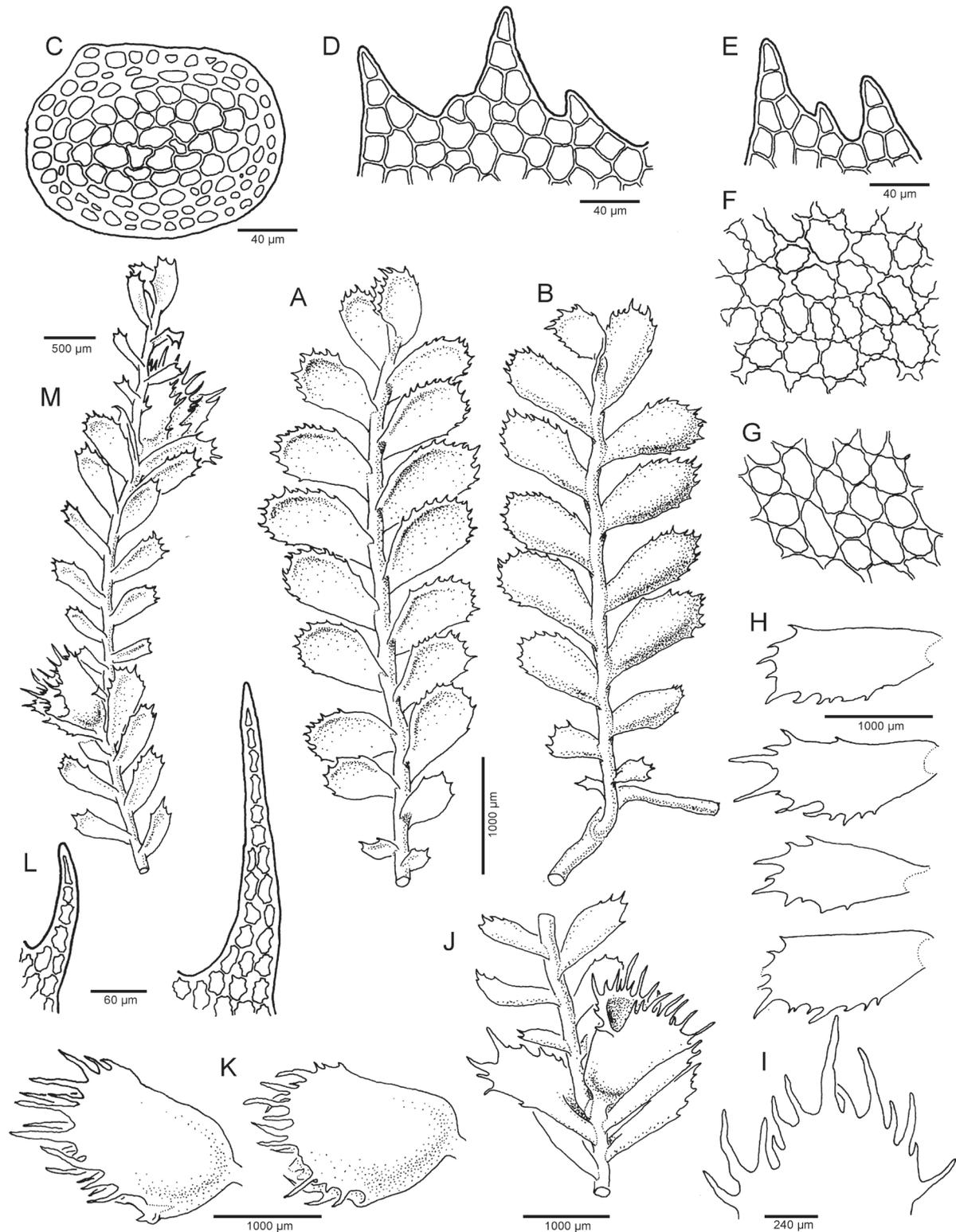
**Recognition:** *Plagiochila monospiris* can be recognized by its small size relative to other *Plagiochila* species, the leaves obovate *in situ* with 3–8 triangular teeth around their apex, and the persistent, not caducous, leaves.

*Plagiochila monospiris* differs from *P. vernicosa* by the paucity of branching within leafy shoot sectors, by the more numerous, smaller and more evenly sized teeth on the leaf and female bract margins, and by the obovate, rather than oblong to oblong-lanceolate leaf shape (Inoue 1972).

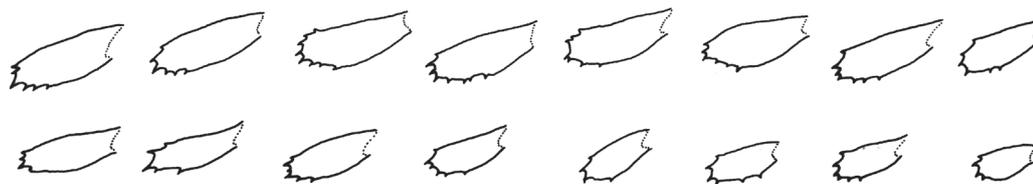
*Plagiochila monospiris* is also similar to *P. minutissima*, for characters differentiating these two species see the recognition section of the latter, below.

**Distribution and Ecology:** *Plagiochila monospiris* occurs in Papua New Guinea and Australia. In Papua New Guinea, *P. monospiris* was initially reported from Goodenough Island, on the northeastern side of the mainland, and Rossel Island at the eastern end of the Louisade Archipelago, it has since been reported from the Papua New Guinean mainland. In Australia *Plagiochila monospiris* is widely distributed through the Wet Tropics Bioregion of north-east Queensland in tropical montane forests above 800 m from Mt Finnegan in the north to the Paluma Range in the south. *Plagiochila monospiris* often grows on decaying logs on the forest floor or on the bases and lower trunks of trees with other corticolous species including *Acroscyphella*, *Radula ornata*, *R. ocellata*, and *Telaranea* spp.

**Representative specimens examined:** **Papua New Guinea:** Milne Bay District, Mt Wadimana ridge, NE from Mt Simpson, 10°02'S 149°40'E, 1770 m, 22 Jul 1969, R. Pullen 7856 (CANB 224093); Eastern Highlands Province, near Hogabi Village, 6 km SW of Lufa, 6°21'S 145°16'E, 1850 m, 14 Apr 1982, H. Streimann 18601 (CANB 8204381); *ibid.*, H. Streimann 18622 (CANB 8204402). **Australia: Queensland:** Cook, Mt Finnegan, Cedar Bay National Park, 39 km S of Cooktown, 15°49'S 145°16'E, 1110 m, 20 Oct 1995, H. Streimann 57217 (CANB 9606102); Cook, Dinden National Park, Kahlpalim Rock, vicinity of summit, 17°01'04"S 145°38'02"E, 1200 m, 5 May 2014, M.A.M. Renner 6920a & T.C. Wilson, (NSW 855499); Cook, Mt Bellenden Ker, under cable way, creek bed W of 3<sup>rd</sup> Pylon, 17°16'00"S 145°51'45"E, 1120 m, 9 Aug 1995, E.A. Brown 95/269, B.M. Weicek & K.L. Radford (NSW 390529); Cook, Wooroonooran National Park, Bartle Frere, between North West summit and Bartle Frere summit, 17°23'36.3"S 145°48'54.3"E, 1510 m, 2 Sep 2014, M.A.M. Renner 7302 & L.J. Gray (NSW 880473); Cook, Wooroonooran National Park, Bartle Frere, North West summit, 17°23'07"S 145°48'03"E, 1422 m, 1 Sep 2014, M.A.M. Renner 7294 & L.J. Gray (NSW 880570); North Kennedy, Paluma Range National Park, road to Paluma Dam and Mount Spec, 18°57'55"S 146°09'39"E, 845 m, 7 May 2014, M.A.M. Renner 6882 & T.C. Wilson (NSW 859317); Birthday Creek, Mt Spec State Forest, 37 km S of Ingham, 18°59'S 146°11'E, 800 m, 29 Oct 1995, H. Streimann 58038 (CANB 9607543); North Kennedy Paluma Range National Park, Paluma, Cloudy Creek, 19°00'02"S 146°12'03"E, 820 m, 8 May 2014, M.A.M. Renner 6898 & T.C. Wilson (NSW 859318).



**Fig 39.** *Plagiochila monospiris*. A: shoot ventral view. B: shoot dorsal view. C: stem transverse section. D, E: teeth around leaf apex. F: leaf medial cells. G: leaf basal cells. H: four female bracts. I: perianth mouth. J: gynoecium with immature perianth and subfloral innovation, dorsal view. K: two perianths in lateral view. L: two teeth from the perianth mouth. All from *M.A.M. Renner 7294 & L.J. Gray (NSW 880570)*.

*Plagiochila monospiris**Plagiochila minutissima*

**Fig 40.** *Plagiochila monospiris* and *P. minutissima* leaves, from M.A.M. Renner 7294 & L.J. Gray (NSW 880570) and M.A.M. Renner 7312 & L.J. Gray (NSW 880483) respectively.

Misidentified specimens examined.

*Plagiochila vernicosa* Inoue

Papua New Guinea, Milne Bay District, Mt Wadimana ridge, NE from Mt Simpson, 10°00'S 149°40'E, 1830 m, 22 Jul 1969, R. Pullen 7872, (CANB 223621).

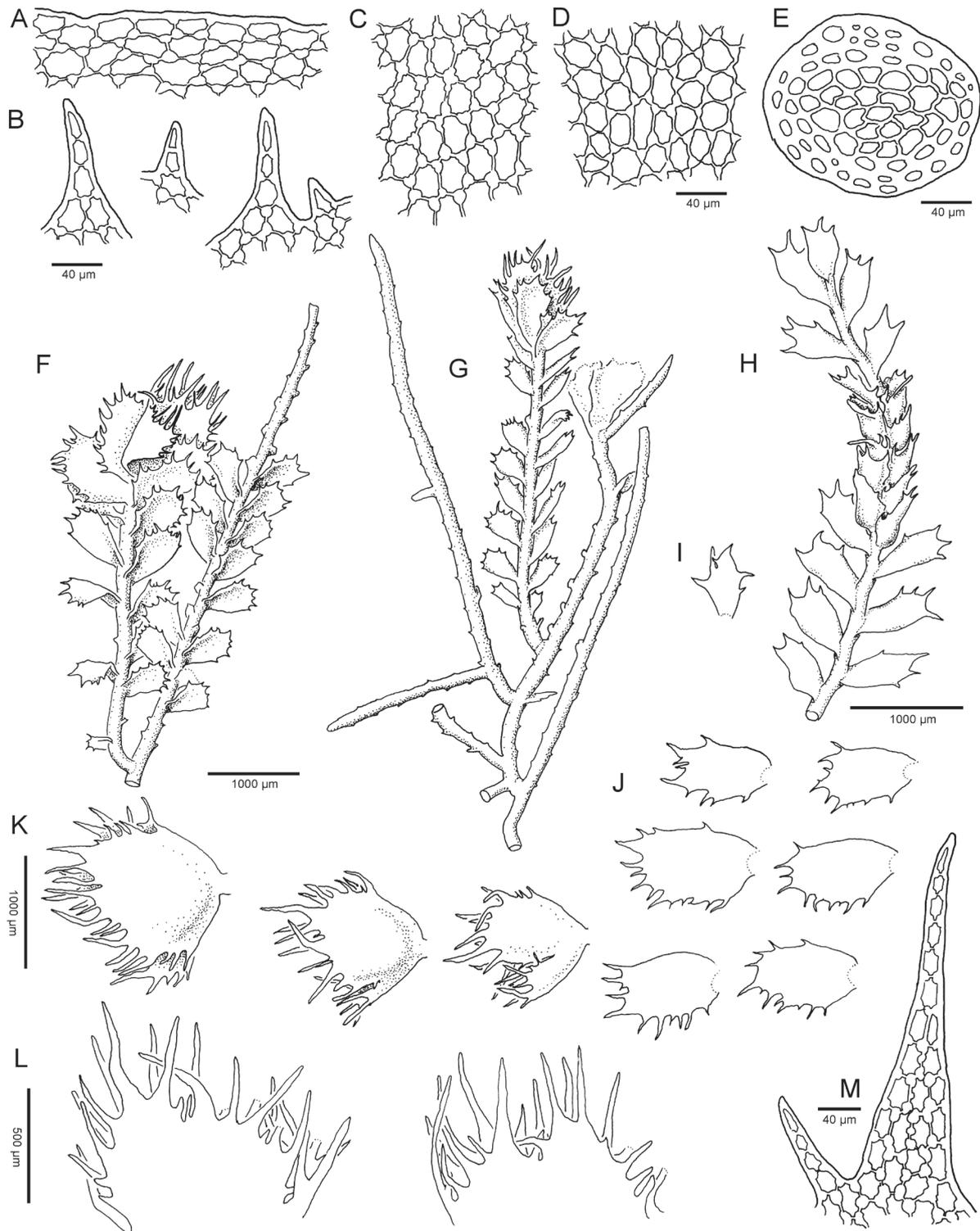
*Plagiochila minutissima* M.A.M. Renner *sp. nov.*

**Diagnosis:** *Plagiochila minutissima* can be distinguished from all other *Plagiochila* species by its small stature, with monomorphic shoots 0.8–1.3 mm wide; exclusively lateral-intercalary vegetative branching; obovate leaves with a truncate apex, ventral margin not ampliate at the base, and apex and ventral margin bearing 3–6 sharp triangular teeth; and the caducous leaves that dislocate in their entirety along their stem insertion line, leaving mature shoot sectors devoid of leaves.

**Type:** Australia, Queensland, Cook, Wooroonooran National Park, Bartle Frere, stream flowing past Western Summit camp from summit ridge north of Bartle Frere, 17°23'45"S 145°48'55"E, 1459 m, 2 Sep 2014, M.A.M. Renner 7312 & L.J. Gray (holotype: NSW 880483; isotypes: BRI, CANB, G, LAE, SUVA).

**Etymology:** smallest, in reference to the plant size.

**Description:** Plants with erect irregularly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; shoot systems to 20 mm long, monomorphic; primary shoots 0.8–1.3 mm wide, branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, to 175 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 2 or 3 layers, cortical cell walls strongly and continuously thickened, cortical cells smaller than medulla cells; medulla cell walls with small triangular trigones, hyaline. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves remote to contiguous, succubously inserted and orientated, obovate, 350–725 µm long × 190–350 µm wide, dorsal margin shallowly curved, apex truncate to rounded, ventral margin curved in outer half and straight at base, not ampliate; apex and ventral margins with 3–6 sharp triangular teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, not attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells oblong, long axis parallel to leaf margin, 23–32 µm long × 13–19 µm, walls with bulging trigones, free external wall continuously thickened; medial leaf cells isodiametric to ovoid, 22–39 µm long × 13–19 µm wide, walls unpigmented, with bulging trigones, and occasional medial thickenings, cells in leaf base ovoid, 19–41 µm long × 14–24 µm wide walls with bulging trigones and occasional medial thickening, trigones not confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction by caducous leaves that dislocate along their insertion line in entirety.



**Fig 41.** *Plagiochila minutissima*. A: leaf marginal cells. B: teeth from leaf margin. C: leaf medial cells. D: leaf basal cells. E: stem transverse section from leafy shoot. F: ventral view of shoot with gynoecium. G: dorsal view of shoot system with gynoecium. H: male branch in dorsal view. I: female bracteole. J: six female bracts. K: three perianths of varying maturity in lateral view. L: two lateral views of perianth mouth showing teeth. M: detail of tooth from perianth mouth. All from NSW 880483.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, singly or in loose series, androecial branching absent, *Frullania*-type, lateral-intercalary, and ventral-intercalary branches not associated with male branches; bracts in 4–6 pairs, contiguous, bract-lobe reduced and smaller than adjacent leaves, with 3–6 teeth, epistatic, margin of dorsal lobe with one or two prominent lacinate teeth, antheridia 1 per bract; stem among bracts smooth. Gynoecia at shoot apices; bracts obovate, larger than adjacent leaves,

915–1200 µm long × 470–640 µm wide; female bracteole present or absent. Subfloral innovations one produced by lateral-intercalary branching from between the female bracts. Perianth campanulate, to 1500 µm long and 1500 µm wide at mouth, dorsal keel longer than ventral keel, dorsal and ventral keels unwinged; laterally compressed, lateral walls plane; labia curved, each with 10–20 lacinate teeth. Figs 40, 41.

**Recognition:** With leafy shoots around 1 mm wide *Plagiochila minutissima* is the smallest species of *Plagiochila* in Australia. The leaves are caducous and fragment in their entirety from the leaf base, leaving some shoot sectors entirely devoid of leaves, it is one of only two species of *Plagiochila* in Australasia to exhibit this mode of asexual reproduction, the other is *P. spinulosa*. In other *Plagiochila* species with caducous leaves, the leaves progressively disarticulate into pieces, typically from the outermost portion inward. The leaf shape, size, and dentition of *P. minutissima* are all distinctive, the leaves are small, oblong to slightly obovate, and bear 3–6 triangular teeth around the leaf apex. *Plagiochila minutissima* never produces *Frullania*-type vegetative branches, indeed terminal branching has not been observed in this species.

In Australia *P. minutissima* is similar only to *P. monospiris*, from which it may be distinguished by its smaller plant size with shoots 0.8–1.3 mm wide (1.6–2.4 mm wide in *P. monospiris*); the production of caducous leaves (not present in *P. monospiris*); and the presence of vegetative branching within leafy shoot sectors (not found in *P. monospiris*).

*Plagiochila minutissima* differs from the Malesian *P. vernicosa* by the smaller shoots and leaves, and the leaves are caducous, disarticulating at their base, rather than persistent.

**Distribution and Ecology:** *Plagiochila minutissima* is endemic to the Wet Tropics Bioregion of north east Queensland, where it occurs in tropical montane forests above 1000 m elevation as an epiphyte on tree trunks. To date this species has been collected on Bartle Frere and Thornton Peak.

**Specimen examined: Australia: Queensland:** Cook, North Kennedy, Bellenden Ker Range, Wooroonooran National Park, Mulgrave River catchment, track to Choirichillum from end of Gourka Road, 17°22'56"S 145°47'44"E, 1310 m, 30 Mar 2012, M.A.M. Renner 6416, V.C. Linis & E.A. Brown (NSW 896955, BRI, F)

### ***Plagiochila* sect. *Abietinae* Schiffn., Die Hepaticae der Flora von Buitenzorg: 106 (1900)**

Type: *Plagiochila abietina* (Nees) Montagne

*Plagiochila* sect. *Abietinae* is a section of perhaps around 20 species distributed in Malesia, Australasia, and Oceania. Many species have pinnate shoots with *Frullania*-type vegetative branching and bear paraphyllia on stems. Other species have one or other, or neither of these characters, making elusive an effective morphological circumscription.

*Plagiochila* sect. *Abietinae* was reinstated from synonymy of *P. sect. Vagae* by Jamy *et al.* (2016), who noted that *Abietinae* had been considered one of the morphologically best circumscribed sections of *Plagiochila*, given the pinnate shoots, the postically secund leaves with spinose marginal teeth, a basal vitta and distinct, bulging trigones. However, morphological homoplasy complicates section circumscription across all of *Plagiochila* (Heinrichs *et al.* 2004, 2005; Söderström *et al.*, 2015), and this is emphasized yet again by the membership of the new species *P. vampira* M.A.M. Renner, described below, which has neither terminal branching nor paraphyllia, to *P. sect. Abietinae*. *Plagiochila vampira* was resolved sister to an indeterminate species with terminal branching and again no paraphyllia from Fiji in Renner *et al.* (2017a). However, the limited sampling within molecular phylogenetic investigations completed to date means the limits of section *Abietinae* have not been adequately addressed. The relationships between sections *Abietinae*, *Peculiares* and *Poeltiae* fluctuate among analyses on the basis of the same markers but different terminal sampling (compare Jamy *et al.* 2016 with Renner *et al.* 2017a). Should species with and without stem paraphyllia currently assigned to sect. *Abietinae* prove reciprocally monophyletic it may be possible to narrow the circumscription of sect. *Abietinae* to the former.

### ***Plagiochila abietina* (Nees) Nees & Mont., Voy. Amer. Merid. Bot. 81 (1839)**

Basionym: *Jungermannia abietina* Nees, Enumeratio Plantarum Cryptogamicarum Javae 76 (1830)

Type citation: n.v.

Type: n.v.

**Notes:** As circumscribed here *Plagiochila abietina* is a complex encompassing two closely related but consistently different morphological forms. Plants from Australia have elliptic to obovate leaves with short triangular teeth on the margins of the outer half of the leaf, the base of the ventral margin is often entire, and rarely reflexed. The dorsal stem surface bears numerous close-set spinose paraphyllia. Plants from Fiji, which

form a supported monophylum sister to Australian plants (Renner *et al.* 2017a), have ovate leaves with long spinose-ciliate teeth around the apex and along the whole of the ventral margin, including the base which is often reflexed. The dorsal stem surface of Fijian plants also bears short spinose paraphyllia but these are sparse in comparison to Australian plants. However, my sample size is fairly limited, and have not had opportunity to investigate the application of the name *Plagiochila abietina*, the typification of species within sect. *Abietinae* needs work, as discussed below under *P. hampeana*. For these reasons, and the fact that Australian and Fijian plants both fall within *P. abietina* as it is currently circumscribed, I use the name *P. abietina* for Australian plants while acknowledging that this species may constitute a complex requiring further study.

**Etymology:** in reference to *Abies*, genus of conifer.

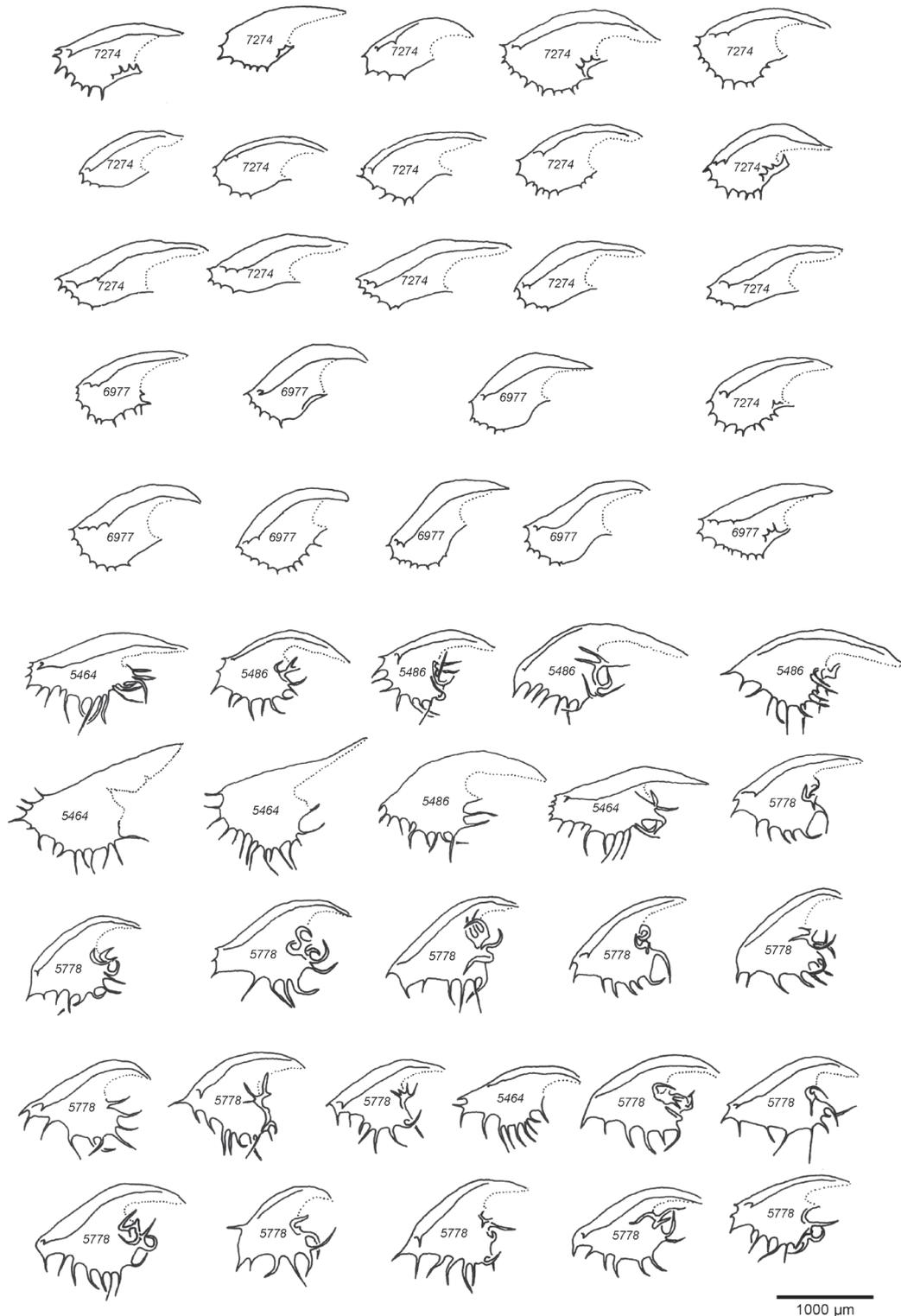
**Description:** Plants with erect pinnately to irregularly bipinnately branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; shoot systems to 50 mm long and 20 mm wide, di- to tri-morphic; primary shoots around 1 mm wide, branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems with numerous, scattered uniseriate to biseriate paraphyllia on the dorsal and lateral stem surfaces; lamellae and paraphyses absent; stem reddish-brown, in primary shoots to 500 µm diameter, transversely elliptic; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, constricting lumen which appears compressed, all cortical cells smaller than medulla cells; medulla cell walls hyaline, with small triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves on primary shoots remote to contiguous, succubously inserted and orientated, primary shoot leaves asymmetrically ovate, 620–1050 µm long × 550–840 µm wide, dorsal margin curved, inrolled, entire, apex rounded, ventral margin arched, not ampliate, sometimes reflexed; apex and ventral margins with 5–19 triangular teeth, teeth 2–4 cells broad and 2–4 tiers high, capped by a slightly elongate triangular cell; secondary shoot leaves smaller; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells subquadrate to rectangular or oblong 11–19 µm long × 7–14 µm wide, long axis parallel or perpendicular to leaf margin, walls with bulging trigones and heavy, irregular, continuous thickening, tan-brown pigmented; medial leaf cells isodiametric to oblong, 13–21 µm long × 10–16 µm wide, walls tan-brown pigmented, with bulging trigones, medial thickenings, and often strong, irregular, continuous thickenings between trigones, cells in leaf base rectangular, 19–32 µm long × 9–24 µm wide walls with bulging trigones and even continuous thickening, trigones confluent or not. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction absent.

Dioicous. Androecia not seen. Gynoecia at apices of secondary shoots; bracts asymmetrically ovate, similar to but larger than adjacent leaves; female bracteole absent. Subfloral innovations absent. Perianth broadly obtriangular to transversely obtrullate, to 900–1300 µm long and 1200–1800 µm wide at mouth, dorsal keel and ventral keel without wings; laterally compressed but with an inflated base, lateral walls plane; labia shallowly curved, each with 15–20 triangular acuminate to lacinate teeth. Fig. 42.

**Recognition:** *Plagiochila abietina* can be recognized by the erect regularly pinnate (to bipinnate) shoot systems with *Frullania*-type vegetative branching, stems with paraphyllia, and asymmetrically ovate leaves with a reflexed dorsal margin and arched ventral margin. *Plagiochila abietina* is the only *Plagiochila* in Australasia with this combination of characters and is not likely to be confused with any other species.

**Distribution and Ecology:** In Australia *Plagiochila abietina* occurs in the Wet Tropics Bioregion of north-east Queensland in tropical montane forests above 800 m elevation as an epiphyte on tree trunks and branches, or as a lithophyte on granite boulders and outcrops. *Plagiochila abietina* is not common in Australia and is currently known from 3 sites, but where it occurs it may form extensive tall near pure turfs. *Plagiochila abietina* co-occurs with other *Plagiochila* including *P. conturbata* and *P. aenea*, as well as a range of other large bryophyte species.

**Representative specimens examined:** Australia: Queensland: Cook, Cedar Bay National Park, Mt Finnegan, shrubberies of summit, 7 Sep 1948, *L.J. Brass 20141* (MEL 1039222); Daintree National Park, track to Manjal Jimalji, between coral fern patch and split rock, 16°23'32"S 145°17'31"E, 1136 m, 30 Aug 2014, *M.A.M. Renner 7274* & *L.J. Gray* (NSW 848776); *ibid.*, *M.A.M. Renner 7275* & *L.J. Gray* (NSW 998794); *ibid.*, 16°23'29"S 145°17'29"E, 1025 m 19 May 2014, *M.A.M. Renner 6977* & *T.C. Wilson* (NSW 848775). Fiji: *M.A.M. Renner 5464* NSW 890131; *M.A.M. Renner 5486* NSW 890173; *M.A.M. Renner 5778* NSW 895657 [or NSW 895637 ?? – check].

*Plagiochila abietina*

**Fig 42.** *Plagiochila abietina* leaves, showing variation among Australian individuals (above) and Fijian individuals (below) in leaf shape and dentition. Australian individual's leaves illustrated from M.A.M. Renner 7274 & L.J. Gray (NSW 848776) and M.A.M. Renner 6977 & T.C. Wilson (NSW 848775); Fijian individual's leaves illustrated from M.A.M. Renner 5464 (NSW 890131); M.A.M. Renner 5486 (NSW 890173); and M.A.M. Renner 5778 (NSW 895657).

***Plagiochila vampira* M.A.M. Renner sp. nov.**

**Diagnosis:** *Plagiochila vampira* can be distinguished from all other Australasian *Plagiochila* species by its sparingly branched monomorphic leafy shoot systems 2.3–3.8 mm wide; exclusively lateral-intercalary vegetative branching; triangular-oblong leaves with apex and ventral margin bearing 9–15 evenly sized and spaced sharp triangular teeth; and leaves with long axis nearly perpendicular to the stem.

**Type:** Australia, Queensland, Cook, Dinden National Park, Kahlpali Rock, between summit and junction with Ridge Track, 17°0'59"S 145°37'49"E, 1200 m, 12 May 2014, M.A.M. Renner 6929 & T.C. Wilson (holotype: NSW 855503; isotypes: BRI, CANB, G)

**Etymology:** in reference to both the inhabitation of lofty and often foreboding mountainous crags, and the chiropteran outline of the leaf silhouette.

**Description:** Plants with irregularly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; shoot systems to 20 mm long, monomorphic; shoots 2.3–3.8 mm wide, branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, to 250 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 2 layers, cortical cell walls continuously thickened and brown-pigmented, cortical cells smaller than medulla cells; medulla cell walls with small triangular trigones, hyaline. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves contiguous to imbricate, succubously inserted and orientated, triangular-oblong, 1250–1700 µm long × 550–780 µm wide, dorsal margin straight to shallowly arched, apex truncate to rounded, ventral margin straight in outer three quarters and curved at base, not or only shallowly amplified; outer dorsal margin, apex and ventral margins with 9–15 sharp triangular teeth, evenly sized and spaced; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells oblong, long axis parallel to leaf margin, 18–26 µm long × 10–21 µm, walls with bulging trigones, free external wall continuously thickened; medial leaf cells isodiametric to ovoid, 19–32 µm long × 16–23 µm wide, walls unpigmented, with bulging trigones, cells in leaf base ovoid to oblong, 20–41 µm long × 13–25 µm wide walls with bulging trigones, trigones not confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction absent.

Diocious. Male plants not seen. Gynoecia at shoot apices; bracts triangular-oblong, larger than adjacent leaves, 1700–2050 µm long × 750–1200 µm wide, margins with coarse triangular teeth of variable size; female bracteole absent. Subfloral innovations one produced by lateral-intercalary branching from between the female bracts. Perianth campanulate, 2050–2500 µm long and 1700–2000 µm wide at mouth, dorsal keel longer than ventral keel, dorsal and ventral keels unwinged; laterally compressed, lateral walls plane; labia curved, each with 15–22 spinose dentate teeth. Figs 43, 44.

**Recognition:** *Plagiochila vampira* can be recognized by the combination of sparingly branched, monomorphic shoots with lateral-intercalary vegetative branching, the spreading, triangular-oblong leaves with 9–15 evenly spaced triangular teeth, and stem surfaces lacking lamellae or paraphyllia.

*Plagiochila vampira* is similar to some of the varieties of *Plagiochila rutilans* (see for example Heinrichs *et al.* 2002), but *P. rutilans* is not closely related to *P. vampira* and the distribution of *P. rutilans* is Neotropical.

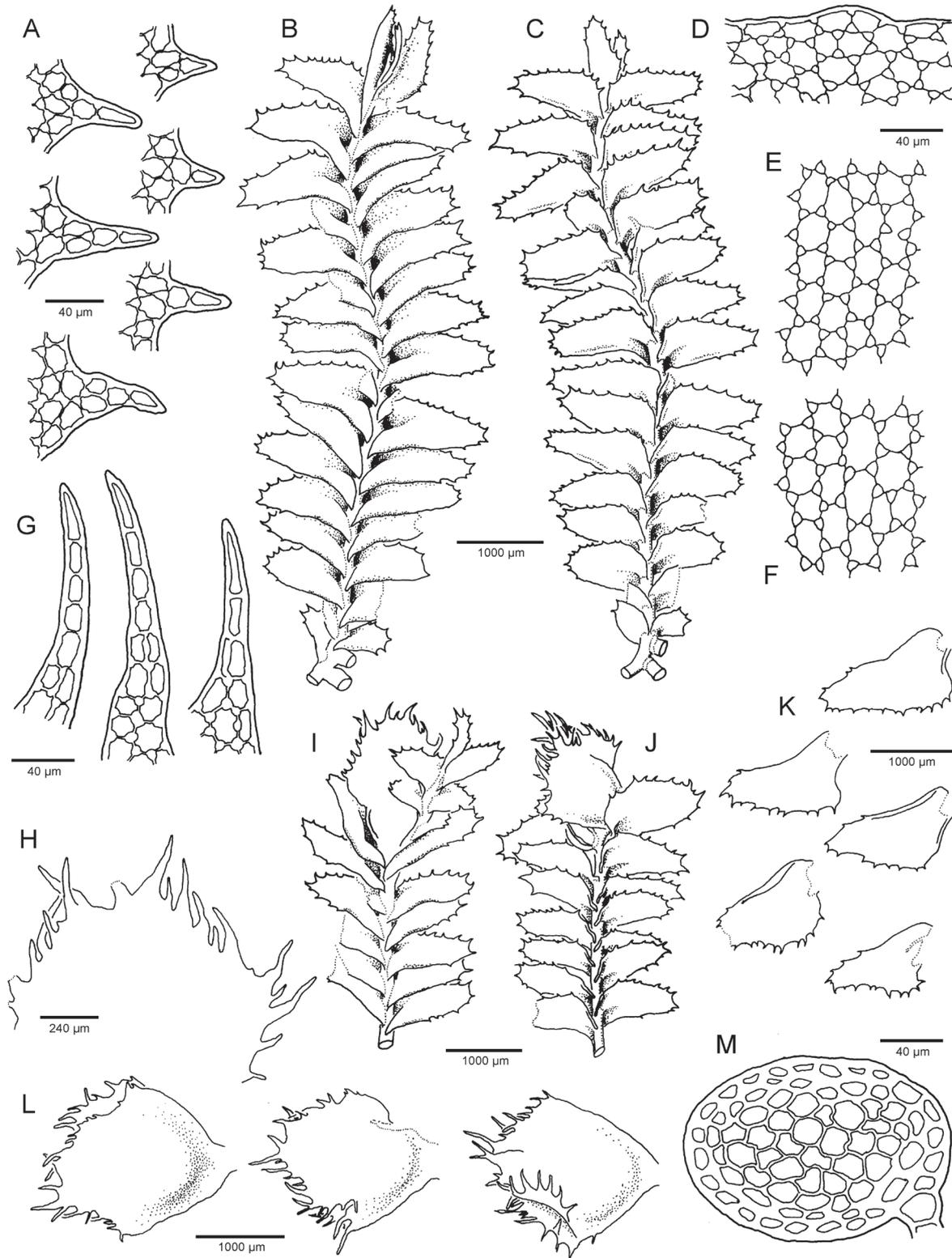
**Distribution and Ecology:** *Plagiochila vampira* is known only by the type gathering, which was made at 1200 m on the summit ridge of Kahlpalim Rock in simple notophyll montane rainforest. Here *P. vampira* grew as a trunk epiphyte in a mixed short turf with *Chiastocaulon dendroides*.

**Notes on other species in *Plagiochila* sect. *Abietinae***

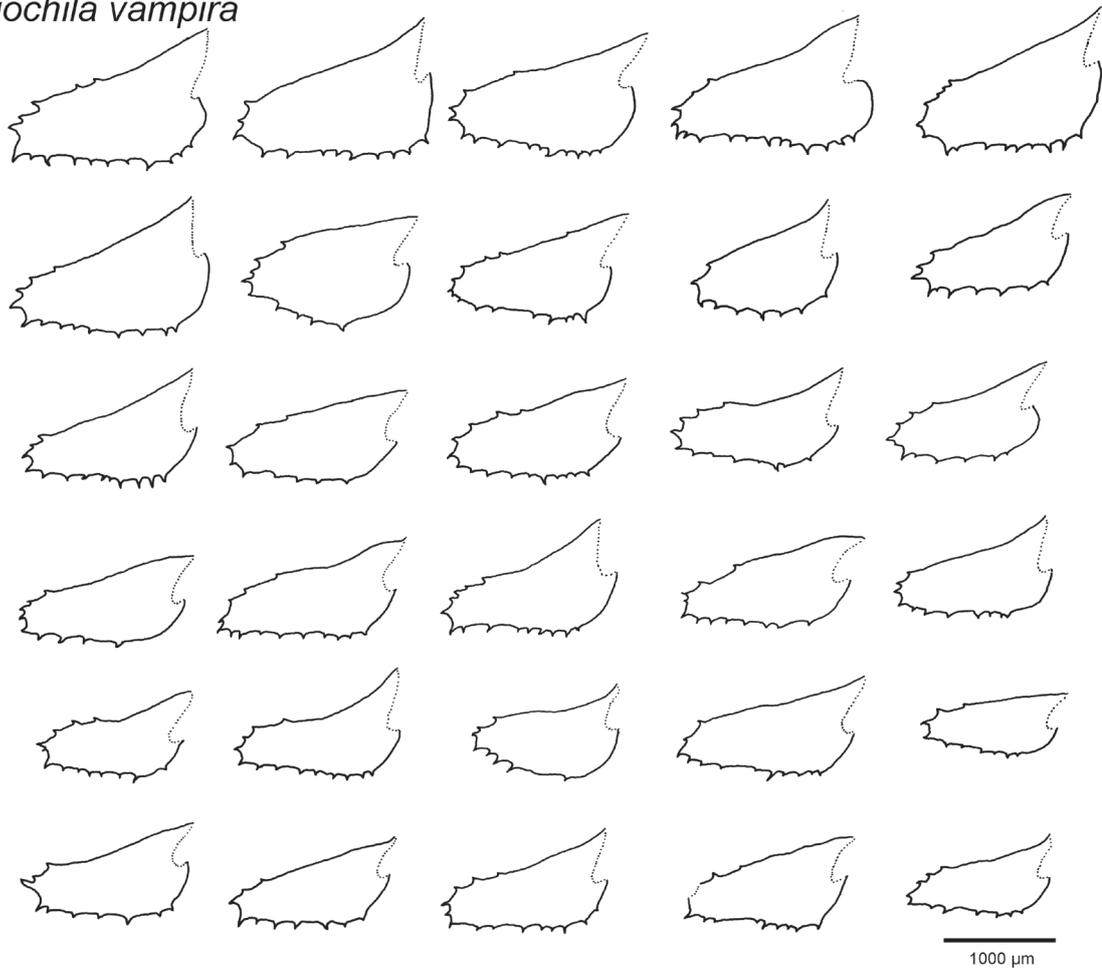
***Plagiochila hampeana*** Gottsche, Botanische Zeitung, Berlin, Beilage 16: 38 (1858)

**Type citation:** *Plagiochila abietina* V. der Sande Lacoste in Hb. Hampeano

**Type:** Java. 1894, 2920 m, Kjellerup, Herb. Gottsche, 'Gottsche's original' (lectotype designated by Inoue (1984) but here rejected: G 00264701!)



**Fig 43.** *Plagiochila vampira*. A: teeth from leaf margin. B: shoot in dorsal view. C: shoot in ventral view. D: leaf marginal cells. E: leaf medial cells. F: leaf basal cells. G: three teeth from the perianth mouth. H: perianth mouth. I: dorsal view of gynoecium with perianth on shoot. J: ventral view of gynoecium with perianth on shoot. K: four female bracts. L: three perianths in lateral view. M: stem transverse section from leafy shoot. All from M.A.M. Renner 6929 & T.C. Wilson (NSW 855503).

*Plagiochila vampira*

**Fig 44.** *Plagiochila vampira* leaves, all from *M.A.M. Renner 6929* & *T.C. Wilson (NSW 855503)*.

**Notes:** Inoue's lectotype of *P. hampeana* has ovate, imbricate leaves with evenly sized and spaced, reasonably close-set teeth round the entire postical leaf margin. The paraphyllia are long linear things resembling the paralamellae on *P. homomalla* – they are broad based, low, and triangular. However, details in the protologue of *P. hampeana* are pertinent to lectotypification. Firstly, Gottsche based his new species on specimen(s) from Sande Lacoste in herb. Hampe under the name *P. abietina*. A lectotype should be selected from among the specimens in or derived from herb. Hampe. Secondly, Gottsche stated 'A *Plagiochila abietina* N. ab Es. (Synops. Hepat. p. 57. n. 88) differ caule nudo glabro, nec hirsuto' (Gottsche 1858 p. 38) which can be roughly translated as 'from *P. abietina* differs by the stems glabrous naked, and not hirsute', given 'nec' is being used as a conjunction. Gottsche's species had glabrous stems without paraphyllia, and any lectotype should agree with the protologue in this detail. Other data from the protologue emphasize this character, in particular the section where Gottsche expands on his decision to recognize *P. hampeana* as distinct from *P. abietina*, explaining '*Plag. abietina*. Die von v. d. Sde. Lacoste geschickte Pflanze ist nicht *Plag. abietina* N. ab Es., weil der Stengel glatt ist, während der Stengel der wirklichen *Pl. abietina* durch kien 3gliedrige dicht stehende Haare rah is und die Pflanze daher in eine eigene Gruppe wit *Plag. acanthocaulis* Sullivant und *Plag. hirta* Taylor (Ldbg.) gehört.' [roughly: v. d. Sde. Lacoste's skillful plant is not *P. abietina* N. ab Es., because the stalk is smooth, while the stem of the actual *P. abietina* is characterized by clusters of 3-membered dense-standing hairs, and therefore the plant belongs in its own group with *P. acanthocaulis* Sullivant and *P. hirta* Taylor (Ldbg.)]. The lectotype proposed by Inoue (1984) has hirsute stems, though the density of paraphyllia is not as great as in his *P. abietina*. On this critical character Inoue's lectotype is in conflict with the protologue and must be rejected (Article 9.19b).

***Plagiochila gedeana*** Schiffn., *Die Hepaticae der Flora von Buitenzorg*: 146 (1900)

*Type citation*: n.v.

*Type*: Java, Prov. Preanger, in regione superiore montis ignivomi Gedeh, regio alpina, 2500 m, 10 Jul 1894, *V. Schiffner Iter Indicum 1893/94 No. 1028* (FH! G 00064462!)

**Notes:** The type of *P. gedearna* contains two *Plagiochila* elements, one with lateral intercalary branches, rhizoids copious and scattered on ventral stem surface within leafy shoot sectors, large contiguous to imbricate leaves with prominent cnemis, this plant is a *Peculiares*. The other element has *Frullania*-type branches only, remote to contiguous leaves, and paraphyllia on the dorsal stem surface, also prominent cnemis but ovate-long-triangular leaves. The paraphyllia are triangular, low, long, and restricted to two lines down the dorsal stem surface, except at branches where they occur on the lateral side of the stem postical to the branch. Lectotypification within the type specimen is required.

### ***Plagiochila* sect. *Plagiochila***

Type: *Plagiochila asplenioides* (L.) Dum.

The sole Australasian representative of sect. *Plagiochila* is *P. lamellata*, a species here segregated from the *P. trapezoidea* Lindenb. complex. The limits of sect. *Plagiochila* have not been fully assessed, the section is currently circumscribed by the tubular perianth, the exclusively lateral-intercalary vegetative branching, and the low spore ornamentation. *Plagiochila trapezoidea* (including *P. lamellata*) was resolved sister to the remainder of sect. *Plagiochila* by Renner *et al.* (2017a), and although *P. trapezoidea* has a thin-walled capsule epidermis, a feature not found in species of sect. *Plagiochila* (Heinrichs 2002), it was conservatively placed in sect. *Plagiochila*. In addition to the unusual capsule epidermis, *P. trapezoidea* and its likely allied species, including *P. innovans* and *P. lamellata*, have dorsal stem lamellae, another feature not found in sect. *Plagiochila*, but it remains to be seen whether a case for segregating these species can be made once relationships have been reconstructed on the basis of a comprehensive species sample.

In addition to the European species *P. asplenioides* and *P. porelloides* and their hybrid *P. x britannica* (Barbulescu *et al.* 2017), *P.* sect. *Plagiochila* species occur in central and south eastern Asia, Malesia, and the Pacific, but the exact number of species belonging to this lineage is not yet known. Söderström *et al.* (2016) placed 27 species here, and though membership of most species has been confirmed by molecular data, one New Zealand species listed here, *P. circumdentata* Steph., belongs in sect. *Deflexifoliae*.

### ***Plagiochila lamellata* M.A.M. Renner *sp. nov.***

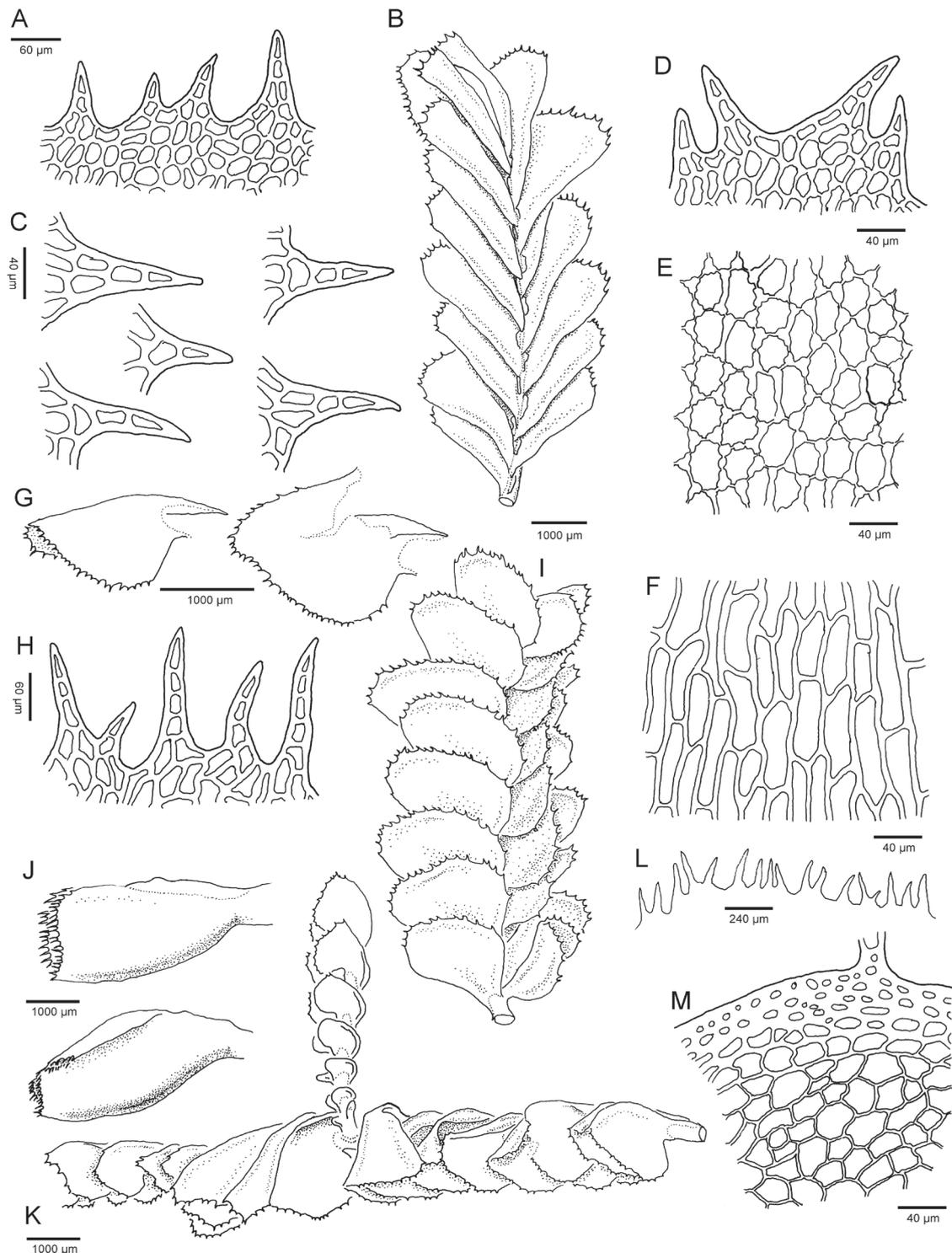
**Diagnosis:** *Plagiochila lamellata* shares with *P. trapezoidea* and *P. innovans* the distinctive single longitudinal lamella adjacent to and parallel with each leaf on the dorsal stem surface; but *P. lamellata* differs from *P. trapezoidea* by its smaller size, closely imbricate leaves whose margins bear 14–24 teeth, rather than contiguous leaves with more than 50 teeth; *P. lamellata* differs from *P. innovans* by the presence of a wing on the perianth dorsal keel, and the asymmetrically ovate leaves, rather than perianth dorsal keel without a wing and triangular-ovate leaves.

**Type:** Australia, Queensland, Daintree National Park, track to Manjal Jimalji, between coral fern patch and split rock, 16°23'29"S 145°17'29"S, 1025 m, 19 May 2014, M.A.M. Renner 6976 & T.C. Wilson (holotype: NSW 858927; iso types: BRI, CANB, G, SUVA)

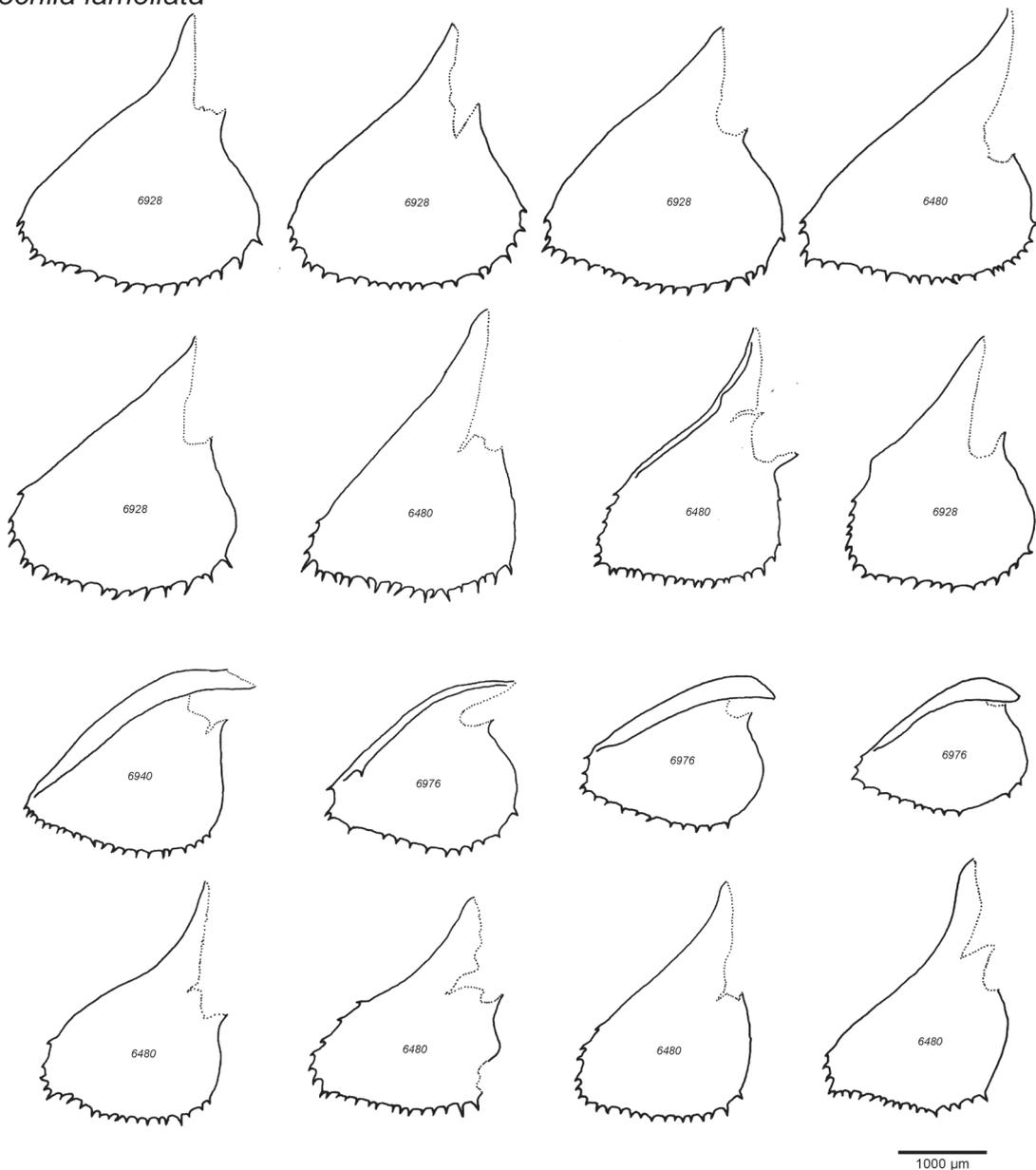
**Etymology:** in reference to the lamellae on the dorsal stem surface.

**Description:** Plants with procumbent, irregularly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; shoot systems to 50 mm long, monomorphic; primary shoots 3.0–4.2 mm wide, branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems with one linear, entire, lamella per leaf, inserted parallel with and on the outside of each dorsal leaf insertion line, without paraphyllia or paraphyses; reddish-brown, in primary shoots to 450 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, red-brown pigmented, all cortical cells smaller than medulla cells; beneath the cortex proper a single subcortical tier of large cells with continuously thickened walls separates the cortex and medulla; medulla cell walls hyaline, without thickening. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and subtransversely orientated, primary shoot leaves asymmetrically ovate, 1950–2850 µm long × 1550–2450 µm wide, dorsal margin straight, revolute, apex broadly rounded, ventral margin shallowly curved, base ampliate, then arched at very base; apex and ventral margins with 14–24 spinose teeth, teeth evenly sized, one to three cells broad at base, uniseriate above, up to four cell tiers tall, cells rectangular or oblong; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, or irregular polyhedral, long axis parallel or perpendicular to leaf margin, 14–25 µm long × 10–24 µm wide, walls with strong continuous thickening, sometimes more pronounced along the middle of cell walls; medial leaf cells oblong to elliptic, 29–44 µm long × 20–33 µm wide, walls unpigmented, with coarse

bulging or triradiate trigones that often extend along medial walls and may be confluent, some longitudinal walls continuously thickened between trigones, cells in leaf base long oblong and sometimes slightly sinuous, with truncate or less often tapering ends, 55–115  $\mu\text{m}$  long  $\times$  12–20  $\mu\text{m}$  wide, longitudinal walls continuously and evenly thickened, transverse walls less thickened. Cell surfaces smooth. Oil-bodies unknown. Underleaves absent. Asexual reproduction absent.



**Fig 45.** *Plagiochila lamellata*. A: leaf marginal cells. B: dorsal view of primary shoot. C: five teeth from leaf margin. D: cells at leaf apex. E: leaf medial cells. F: leaf basal cells. G: two female bracts. H: detail of teeth from perianth mouth. I: ventral view of primary shoot. J: two perianths in lateral view. K: lateral view of perianth bearing shoot showing subfloral innovation. L: perianth mouth. M: dorsal sector of transverse section through stem from leafy shoot. All from M.A.M. Renner 6976 & T.C. Wilson (NSW 858927).

*Plagiochila lamellata*

**Fig 46.** *Plagiochila lamellata* leaves, from M.A.M. Renner 6928 & T.C. Wilson (NSW 855092), M.A.M. Renner 6976 & T.C. Wilson (NSW 858927) and M.A.M. Renner 6480, V.C. Linis & E.A. Brown (NSW 897031).

Dioicous. Androecia not seen. Gynoecia at apices of shoots; bracts asymmetrically ovate, larger than adjacent leaves, 4200–4600  $\mu\text{m}$  long  $\times$  2500–3000  $\mu\text{m}$  wide, margins with spinulose teeth; female bracteole absent. One subfloral innovation produced by lateral-intercalary branching from between the female bracts. Perianth oblong, to 5000  $\mu\text{m}$  long and 1800  $\mu\text{m}$  wide at mouth, dorsal keel with a broad wing near the base, ventral keel unwinged; laterally compressed but with an inflated base, lateral walls plane; labia shallowly curved, each with numerous spinulose teeth. Figs 45, 46.

**Recognition:** *Plagiochila lamellata* is the only species in Australia with one lamella per leaf on the dorsal stem surface, located on the outside of the leaf insertion line. *Plagiochila lamellata* is bronze-green in life, often grows on granite boulders in tropical montane forest, has up to 24 small spinose teeth on the apical and ventral margin of its triangular-ovate leaves, the long basal leaf cells with continuously thickened walls, and elliptic medial leaf cells with discrete trigones; vegetative branching exclusively lateral-intercalary, the perianths are ligulate, and have a dorsal wing on the basal third, and the leaves have an indistinct basal vitta of long rectangular cells.

*Plagiochila trapezoidea* differs from *P. lamellata* by its more numerous teeth on the leaf margin, usually more than 50 distributed on all margins (but not in the type plant) compared with 14–24 around the apex and on the ventral margin in *P. lamellata*, and the smaller teeth on the perianth mouth, 2 or 3 cells long compared with 3–5 cells long in *P. lamellata*. The leaf cell walls of *P. trapezoidea* bear less pronounced secondary wall thickenings than *P. lamellata*, but whether this is the result of environmentally induced variation or inter-species difference is not known. *Plagiochila trapezoidea* is a larger plant, and has contiguous leaves.

*Plagiochila innovans* is distinct from *Plagiochila lamellata* in the absence of a dorsal wing on the perianth, and in the triangular leaf shape. *Plagiochila lamellata* perianths have a dorsal wing, and the leaves are ovate-triangular. However, these two species seem, on the basis of the protologue of *P. innovans* at least, very similar and further work to clarify their circumscription is required.

**Distribution and Ecology:** *Plagiochila lamellata* is apparently endemic to Australia, where it is confined to tropical montane rainforests above 900 m elevation in the Wet Tropics Bioregion of north-east Queensland. *Plagiochila lamellata* is usually found growing as a lithophyte on granite outcrops and exposed boulders within the forest interior. Here it may form extensive near pure turfs, or mixed turfs including other *Plagiochila* species including *P. abietina*, *P. aenea* and *P. conturbata*.

**Representative specimens examined:** Australia: Queensland: Cook, Daintree National Park, Manjal Jimalji, track to summit, vicinity of split rock, 16°23'25"S 145°17'28"E, 966 m, 19 May 2014, *M.A.M. Renner 6982* & *T.C. Wilson* (NSW 858928); Daintree National Park, track to Manjal Jimalji, between coral fern patch and split rock, 16°23'32"S 145°17'31"S, 1136 m, 30 Aug 2014, *M.A.M. Renner 7273* & *L.J. Gray* (NSW 849294); Mount Lewis Road, c. 30.5 km from intersection with Mossman-Mount Molloy Road, c. 50 m up small stream, State Forest 143, 16°30'50"S 145°16'10"E, 16 Jul 1994, *E.A. Brown 94/502b*, *R.G. Coveny* & *B. Tan* (NSW 298151); Cook, Dinden Natinal Park, Kahlpalim Rock, between summit and junction with Ridge track, 17°0'59"S 145°37'49"E, 1200 m, 12 May 2014, *M.A.M. Renner 6928* & *T.C. Wilson* (NSW 855092); Cook, Bellenden Ker Range, Wooroonooran National Park, Mulgrave River catchment, track between Choorichillum and Bartle Frere (South Peak), 17°23'55"S 145°49'00"E, 1545 m, 31 Mar 2012, *M.A.M. Renner 6480*, *V.C. Linis* & *E.A. Brown* (NSW 897031).

#### Excluded from the Australasian flora

***Plagiochila renitens*** (Nees) Lindenb., Species Hepaticarum 2-4: 90 (1840)

Basionym: *Jungermannia renitens* Nees, Enumeratio plantarum cryptogamicarum Javae: 76 (1830)

Type citation: in Java insula. (Blume et Reinwardt.)

Type: Java (G 00115160!)

**Notes:** The presumed type of *P. renitens* (G 00115160) has spinose-dentate teeth around two thirds of the leaf. The leaf has a distinct cnemis, there are rhizoids scattered continuously on the ventral stem surface, there are no paraphyllia on either dorsal or ventral stem surfaces, and no Australian plants agree in all details with the type.

***Plagiochila trapezoidea*** Lindenb., Species Hepaticarum 2-4: 112 (1840)

Basionym: *Jungermannia asplenioides* *australis* Nees, Enumeratio plantarum cryptogamicarum Javae: 73 (1830)

Type citation: in Java insula ad terram

Type: (So & Grolle 2000): Indonesia. Java. "mis. Nees ab Es. 1832". (holotypes *vide* So & Grolle (2000): W Lindenberg Hep. 851)

=*Plagiochila intercedens* Schiffn., Die Hepaticae der Flora von Buitenzorg: 151 (1900)

Type citation: *n.v.*

Type: Indonesia. Sumatra occid., Mt. Singalang, 2390 m, 1894, *Schiffner 1083* (Lectotype designated by Inoue 1984a: FH); residual syntypes: Indonesia. Sumatra occid., Mt. Singalang, 2440 m, 1894, *Schiffner 1084* (G00128872! G00128873! G00128874!)

=*Plagiochila vinkii* Inoue et Grolle, Studies on the Cryptogams of Papua New Guinea: 14 (1979)

Type citation: *n.v.*

Type: Papua New Guinea. Southern Highlands Distr. Mt. Né, Tari Subdistr., 2730 m, in *Nothofagus* forest, Vink 17332/b (holotype: L, isotypes: JE, TNS)

=*Plagiochila winteri* Steph., Species Hepaticarum 6: 241 (1922)

*Type citation:* Java (Winter legit)

*Type:* Cameroons, Buea, 1500 m, 14 Oct 1891, *Preuss 1075*, ex herb. Berlin (G)

**Notes:** The residual syntypes of *P. intercedens* have long perianths with ciliate-denticulate labia, and male bracts that are inflated and loosely imbricated. Branching is wholly lateral-intercalary. On the ventral leaf insertion line is recurved and decurrent to the extent that a continuous low wing of tissue runs between adjacent leaves.

No Australian specimens corresponding with the type of *P. trapezoidea* have been seen, possibly *P. trapezoidea* has been reported as a result of confusion with *P. lamellata*.

**Representative specimens examined:** Papua New Guinea: Western Highlands, Tabibuga Road, Jimi Valley, 14 km N of Banz, 5°41'S 144°38'E, 1950 m, 25 Jun 1982, *H. Streimann 20846* (CANB 8400484); Southern Highlands, Munia Logging Area, 14 km NW of Ialibu, 6°11'S 153°55'E, 2300 m, 8 Sep 1982, *H. Streimann 23223* (CANB 8405928); Morobe Province, Ekuti Divide, Bulolo-Aseki Road, 33 km WSW of Bulolo, 7°19'S 146°23'E, 2260 m, 16 Jun 1982, *H. Streimann 20060* (CANB 8212037); Morobe Province, Mt Kaindi, 5 km W of Wau, 7°19'S 146°44'E, 2300 m, 26 Jul 1982, *H. Streimann 22444* (CANB 8403607); *ibid.*, *H. Streimann 22453* (CANB 8403616); *ibid.*, *H. Streimann 22454* (CANB 8403617); Morobe Province, track to Mt Kaindi, 4 km W of Wau, 7°21'S 146°41'E, 2230 m, 22 May 1982, *H. Streimann 19868* (CANB 8211182).

***Plagiochila* sect. *Peculiares*** Schiffn., Hep. Fl. Buitenzorg: 107 (1900)

*Type:* *Plagiochila peculiaris* Schiffn.

Section *Peculiares* contains five species distributed throughout Malesia and extending east to Fiji and Samoa and south to the Australian Wet Tropics. Section *Peculiares* is characterized by the unusual vermicular secondary thickenings on leaf cell walls (Inoue 1984). Inoue (1984) stated that sect. *Peculiares* shared characters with both sect. *Plagiochila* and sect. *Zonatae*, the latter was synonymized with sect. *Peculiares* by Söderström *et al.* (2015) who cited molecular evidence from *P. magna* Inoue a putative relative of the type species, *Plagiochila zonata* Steph., which has not yet been included in molecular phylogenetic analyses. Section *Zonatae* is resolved polyphyletic in some analyses (J. Heinrichs unpublished data), so whether this synonymy is appropriate remains to be tested.

**Key to species of *Plagiochila* sect. *Peculiares*, adapted from Inoue (1969).**

1. Ventral leaf base often strongly incurved (subsect. *Zantenii* Inoue) ..... 2
1. Ventral leaf base not incurved. (subsect. *Peculiares*) ..... 4
2. Leaves reniform. .... *P. zantenii* Inoue
2. Leaves triangular-ovate. .... 3
3. Leaves entire or with 2 or 3 teeth at apex, margins plane. .... *P. huerlimannii* Inoue
3. Leaves with 0–8 teeth around apex and onto dorsal margin, ventral margin undulate. .... *P. aenea* M.A.M. Renner
4. Teeth present around all leaf margins. .... 5
4. Teeth absent from dorsal leaf margin. .... *P. crassitexta* Steph.
5. Cells at mid-leaf 55–75 × 25–30 µm, teeth on dorsal leaf margin 12–19, toothed to base of dorsal margin; plants large, usually 5–8 cm long; known from Sumatra, Java, Borneo ..... *P. peculiaris* Schiffn.
5. Cells at mid-leaf 21–27 × 14–18 µm, teeth on dorsal leaf margin 2–6, toothed in outer half only; plants small, usually 4–6 cm long; known only from the Philippines ..... *P. philippinensis* Steph.

Some individuals of *Plagiochila aenea* will key above to *P. crassitexta* in subsect. *Peculiares*. The morphological variation exhibited by *P. aenea* suggests subsection *Peculiares* may be polyphyletic, and the subsectional classification requires further investigation on the basis of a study including all species. As noted below, it also suggests that the circumscription of *P. aenea* requires further investigation.

***Plagiochila aenea* M.A.M. Renner *sp. nov.***

**Diagnosis:** *Plagiochila aenea* can be distinguished by the nitid, monomorphic, sparingly branched shoots with lateral-intercalary vegetative branching, the imbricate, transversely oriented triangular ovate leaves with (typically) a few triangular teeth around the leaf apex and outer half of the ventral margin only and a reflexed auricle at the base of the broad ampliate leaf base, leaf cell walls with nodular trigones and conspicuous bulging medial thickenings, 2 or more on each wall face, the perianths with labia bearing bidentate spinose-dentate teeth, smaller lateral teeth projecting from the sides of larger teeth in a fractal pattern.

**Type:** Australia: Queensland: Cook, Daintree National Park, track to Manjal Jimalji, between coral fern patch and split rock, 16°23'29"S 145°17'29"E, 1025 m, M.A.M. Renner 6975 & T.C. Wilson (holotype: NSW 858925; isotypes: BRI, CANB, MEL, SUVA).

**Etymology:** *aenea* bronzed, in reference to the colour of living plants.

**Description:** Plants with procumbent, irregularly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; shoot systems to 70 mm long, monomorphic; primary shoots 4.0–4.7 mm wide, branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without lamellae, paraphyllia or paraphyses; stem reddish-brown, in primary shoots to 450 µm diameter, transversely elliptic, surfaces ridged by projecting cortical cell profiles; cortical cells in 3 or 4 layers, cortical cell walls strongly and continuously thickened, red-brown pigmented, all cortical cells smaller than medulla cells; medulla cell walls hyaline, without some continuous thickening on cell walls and small triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, triangular, 1550–2850 µm long × 1500–2500 µm wide, dorsal margin straight, revolute, apex obtuse to acute, ventral margin straight in outer half, base ampliate, sometimes with one or two undulations, often with the extreme base reflexed in a semicircular flange; apex with 0–9 spinose dentate teeth, evenly sized, two to four cells broad at base, uniseriate toward the apex, four to six cell tiers tall, cells rectangular or oblong, apical cell slightly elongate; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, and attaining the ventral stem midline. Marginal leaf cells short to long rectangular, long axis parallel to leaf margin, 18–43 µm long × 8–22 µm wide, walls with one or two prominent, rounded medial thickenings on each face, either in opposing pairs or not, with smaller bulging trigones at wall junctions, free external wall continuously thickened, medial cells oblong to long oblong, 48–91 µm long × 14–24 µm wide, two to four prominent, rounded medial thickenings on each face, either in opposing pairs or not, with smaller bulging trigones at wall junctions, cells in leaf base oblong to long oblong, with truncate ends, 65–130 µm long × 14–21 µm wide, longitudinal walls with two to four prominent, rounded medial thickenings on each face, either in opposing pairs or not, or continuously and evenly thickened, transverse walls unthickened. Cell surfaces smooth. Oil-bodies unknown. Underleaves absent. Asexual reproduction absent.

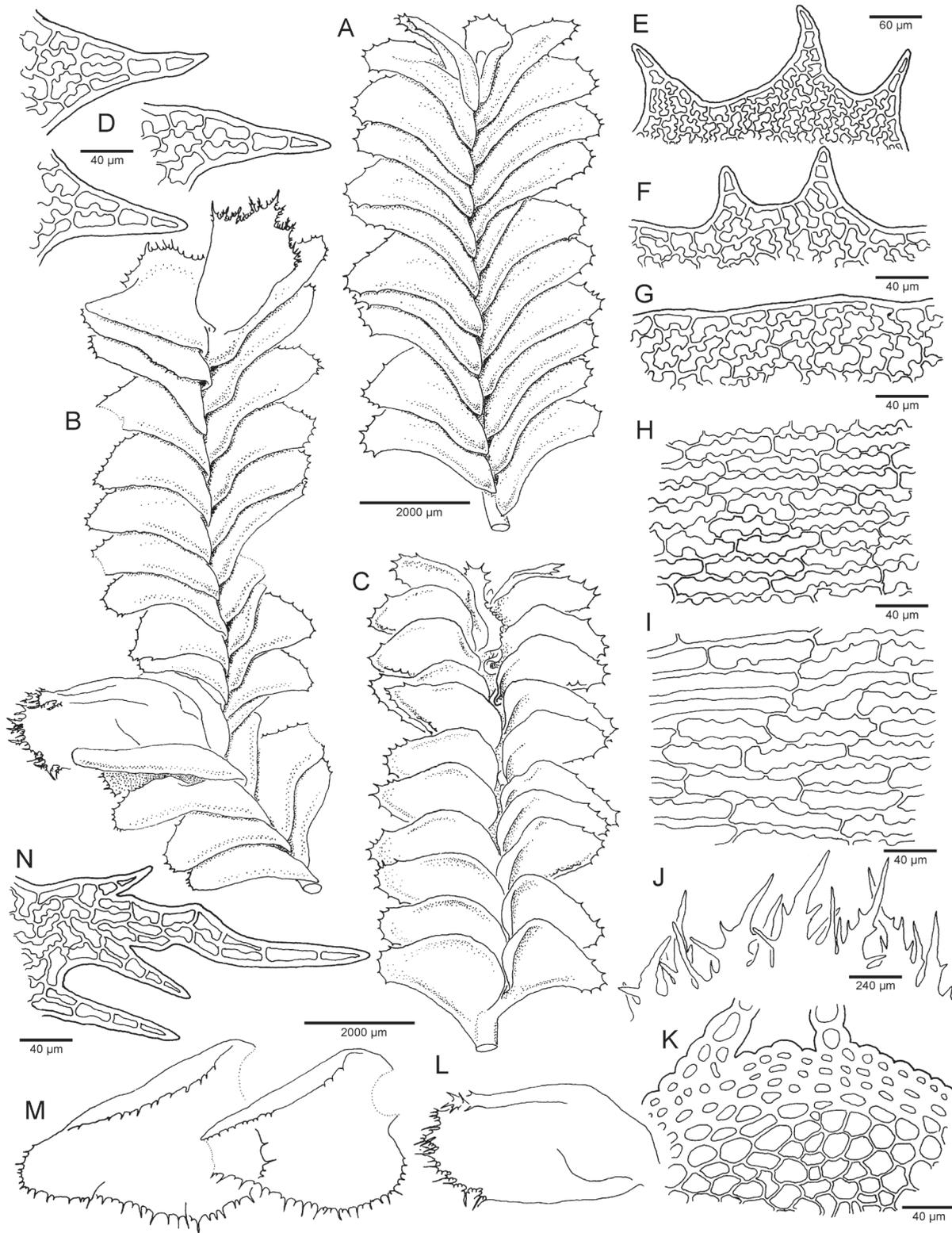
Dioicous. Androecia not seen. Gynoecia at apices of shoots; bracts triangular ovate, larger than adjacent leaves, 3500–4200 µm long × 2600–2900 µm wide, margins with spinulose teeth; female bracteole absent. One subfloral innovation produced by lateral-intercalary branching from between the female bracts. Perianth oblong, to 4700 µm long and 2200 µm wide at mouth, dorsal keel unwinged, ventral keel unwinged; laterally compressed but with an inflated base, lateral walls plane; labia shallowly curved, each with fractal spinulose dentition. Figs 47–49.

**Recognition:** *Plagiochila aenea* can be recognized by the broad triangular leaves with a broad ampliate base, the nearly entire leaf margins save a few triangular teeth scattered around the leaf apex, the bronze-green colour, and the vermicular thickenings on the leaf cell walls. In addition, vegetative branching is exclusively lateral-intercalary, the shoot systems are monomorphic, and the plants grow as lithophytes on exposed granite outcrops and boulders in montane rainforests of the Wet Tropics Bioregion of north-east Queensland.

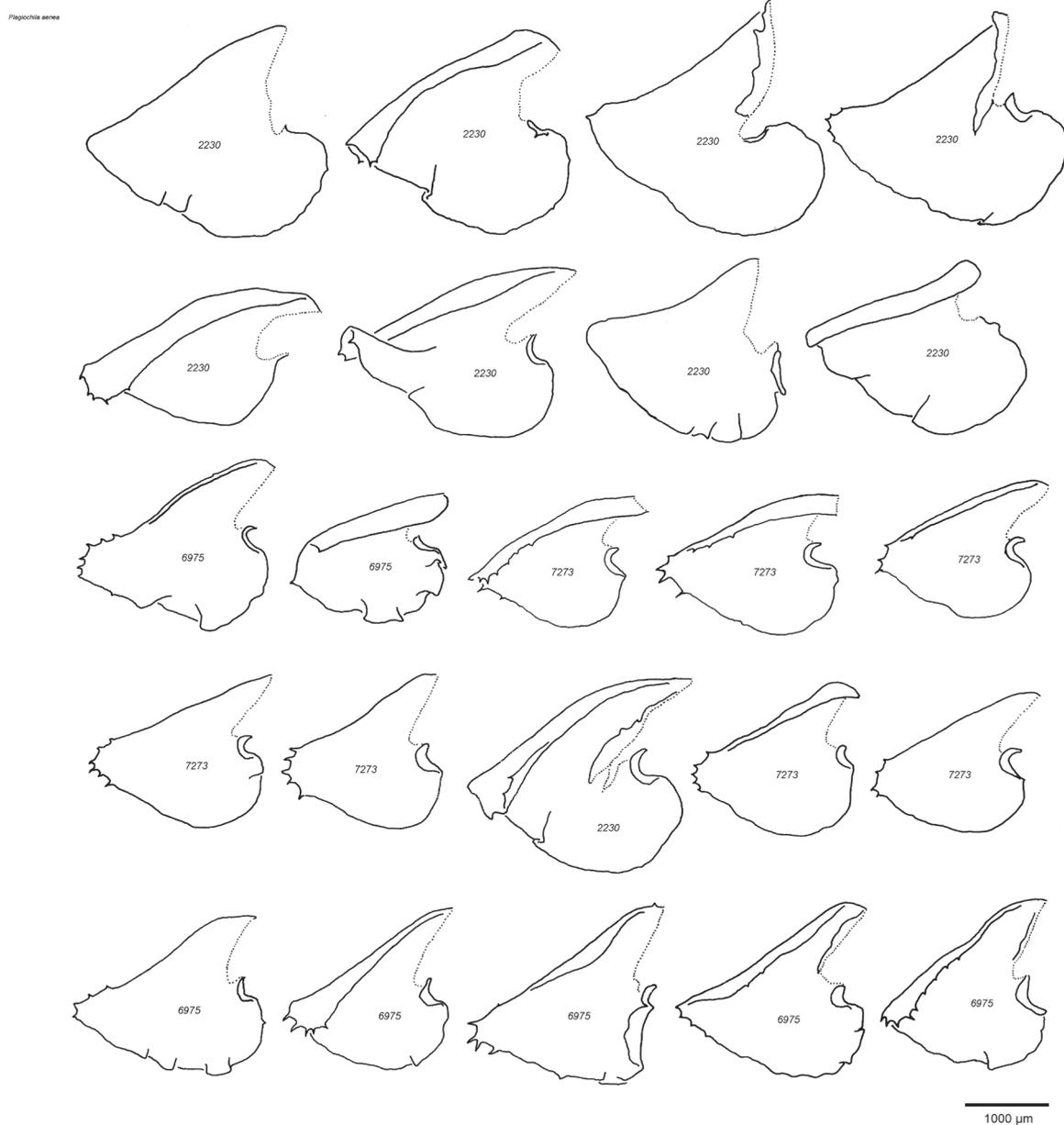
Within Australia *P. aenea* is similar to *P. lamellata* in the monomorphic shoots, exclusively lateral-intercalary vegetative branching, bronze colour, and occupancy of granite, but can be distinguished by the absence of lamellae on the dorsal stem surface and the few triangular teeth around the leaf apex only, and the vermiculately thickened leaf cell walls.

*Plagiochila aenea* differs from *P. zantenii* by triangular-ovate leaf shape and presence of teeth on leaf margins (versus leaves reniform and entire).

*Plagiochila aenea* differs from *P. huerlimannii* by having the teeth around the leaf apex only, the undulate ventral margin, and broad ampliate leaf base; and the closely imbricate leaves obscure stem in dorsal view (versus leaves entire, ventral margin plane, base moderately ampliate, leaves contiguous with stem visible in dorsal view).



**Fig 47.** *Plagiochila aenea*. A: shoot dorsal view. B: perianth bearing shoot dorsal view. C: shoot ventral view. D: leaf marginal teeth. E: leaf apex. F: leaf margin near apex. G: leaf ventral margin. H: leaf medial cells. I: leaf basal cells. J: perianth mouth. K: dorsal part of transverse stem section from leafy shoot. L: perianth in lateral view. M: two female bracts. N: teeth from perianth mouth. A, C-I, K from M.A.M. Renner 7273 & L.J. Gray (NSW 849269); B, J, L-N from M.A.M. Renner 7106 & T.C. Wilson (NSW 852983).

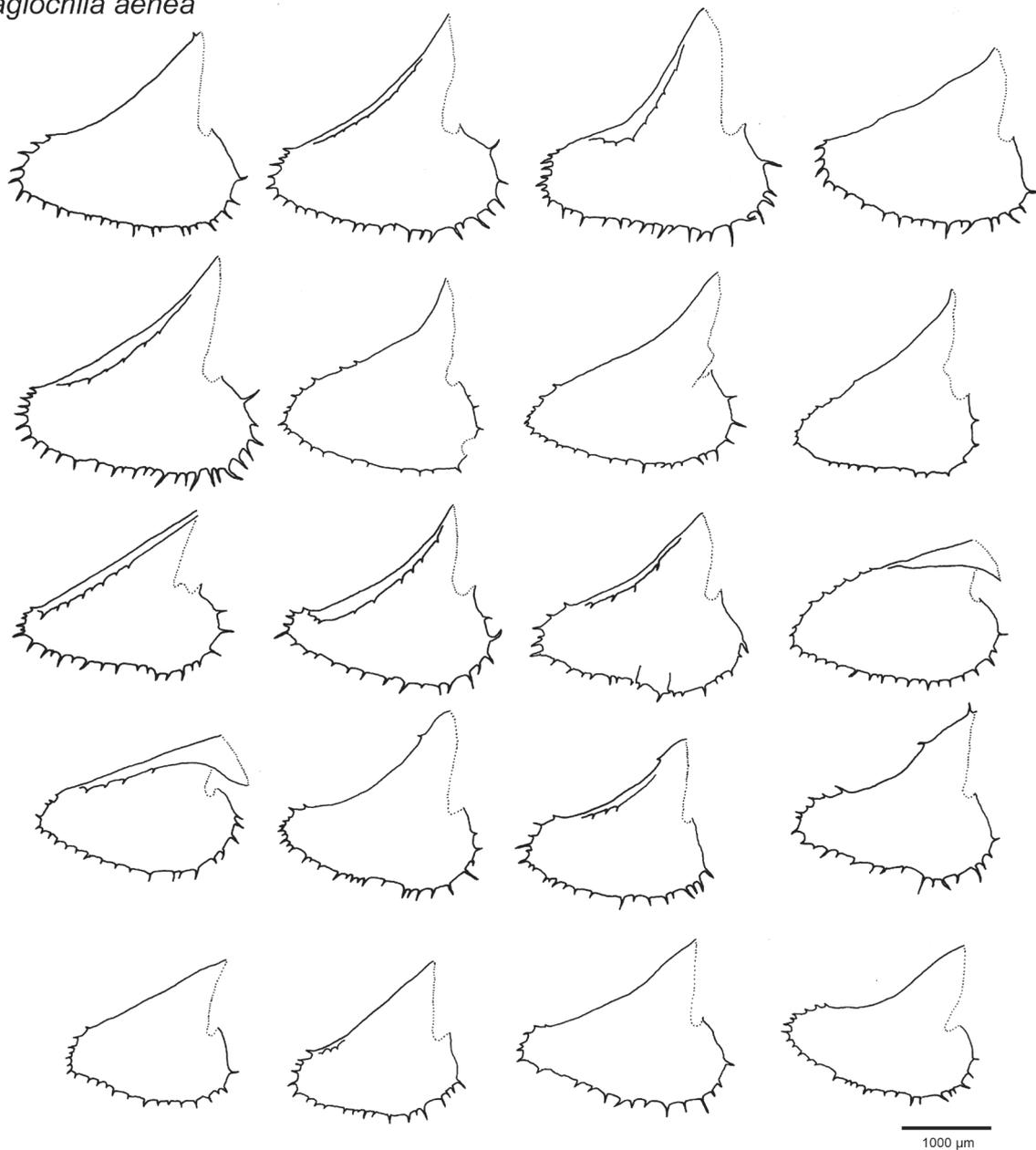


**Fig 48.** *Plagiochila aenea* leaves, from M.A.M. Renner 2230 & E.A. Brown (NSW 980513), M.A.M. Renner 6975 & T.C. Wilson (NSW 858925), and M.A.M. Renner 7273 & L.J. Gray (NSW 849269).

*Plagiochila aenea* differs from *P. peculiaris* by the triangular-ovate leaf shape, restriction of teeth to the leaf apex, and the teeth narrow triangular (versus leaves rotund, teeth ciliform and distributed all around the leaf margin).

*Plagiochila aenea* differs from *P. philippinensis* by having the leaf base incurved, rather than plane.

**Variation:** Individuals exhibit variation in leaf shape and dentition. One individual included in this study (NSW 852983) differed from others in colour, leaf shape and dentition, having leaves without a broadly amplate base, and up to 35 marginal teeth (Fig. 49). In the field this plant was a mid-green colour, and was mistaken for a member of sect. *Cucullatae*, such was its field-aspect. This individual was included in the molecular phylogeny of Renner *et al.* (2017a) and was resolved sister to the other *P. aenea* individuals, but without strong support. Further study of additional specimens is warranted to fully resolve its status, given the significant differences in leaf shape, dentition, and microsite occupancy.

*Plagiochila aenea*

**Fig 49.** *Plagiochila aenea* leaves, all from *M.A.M. Renner 7106 & T.C. Wilson*, (NSW 852983).

**Distribution and Ecology:** *Plagiochila aenea* is known only from Australia, where it is confined to tropical montane rainforests above 900 m elevation in the Wet Tropics Bioregion of north-east Queensland. *Plagiochila aenea* is usually found growing as a lithophyte on granite outcrops and exposed boulders within the forest interior. Here it may form extensive near pure turfs, or mixed turfs including other *Plagiochila* species including *P. abietina*, *P. conturbata*, and *P. lamellata*. The morphologically deviant form of *P. aenea*, noted above, was collected as an epiphyte on a tree-trunk base at Charmillan Creek near Ravenshoe where it grew with *P. bantamensis*.

**Representative specimens examined:** Australia: Queensland: Cook, Daintree National Park, track to Manjal Jimalji, between coral fern patch and split rock, 16°23'32"S 145°17'31"E, 1136 m, 30 Aug 2014, *M.A.M. Renner 7273 & L.J. Gray* (NSW 849269); Wooroonooran National Park, Mount Bartle Frere centre peak, 17°23'19"S 145°48'30"E, 1525 m, 15 Jul 2005, *M.A.M. Renner 2230 & E.A. Brown* (NSW 980513); North Kennedy, Tully Falls National Park, Tully Falls Road, track to Rhyolite Pinnacle from Charmillan Creek, 17°42'40"S 145°33'12"E, 1085 m, *M.A.M. Renner 7106 & T.C. Wilson*, (NSW 852983).

**Notes on other species of *Plagiochila* sect. *Peculiares*.**

***Plagiochila peculiaris*** Schiffn., Die Hepaticae der Flora von Buitenzorg: 157 (1900)

*Type:* Indonesia. Sumatra occid. in cacumine montis Singalang, 2800 m, 25 Jul 1894, V. Schiffner *Iter Indicum* 1893/94 No. 1102 (lectotype designated by Inoue (1984): FH, isolectotypes: G 00264755! G 00264754! G 00264753! JE)

**Notes:** In the strict sense, *Plagiochila peculiaris* is a large plant in comparison with other *Plagiochila* species; when hydrated the shoots in the isolectotypes are nearly 10 mm across, the leaves are nearly isosceles triangles with the hypotenuse adjacent the stem, the interior leaf margin is broadly ampliate and imbricate over the ventral stem surface, and bears long spinose-ciliate teeth. The shoots are nitid, and the unusually shaped and thickened cells are apparent under the dissecting microscope.

**Representative specimens examined:** Thailand, Nakornsrihamarat, granitic massive Khao (Mt.) Luang, 8°30'N 99°45'E, 1740 m, 5 Feb 1966, A. Touw 11801 (CANB 225337); Malaysia: Pahang, Cameron Highland, Brinchang, trail to Irau Mountain, 2000 m, 14 Mar 2004, A. Ilkiu-Borges, S.R. Gradstein, K.T. Yong & M. Ponniah 3027 (CANB 00669804).

***Plagiochila* sect. *Vagae*** Lindenb., Monographia hepaticarum generis *Plagiochilae*: xv. (1844) [1843]

*Type:* (lectotype designated by Heinrichs *et al.* 2002) *Plagiochila patula* (Sw.) Lindenb.

This speciose section has a circumtropical distribution, with centres of diversity in the Neotropics especially the Andes, and Malesia, and around 100 species are currently attributed to it (Söderström *et al.* 2016). *Plagiochila* sect. *Vagae* can be recognized by their combination of pseudodichotomous *Frullania*-type vegetative branching, shoot systems that are hierarchically structured with two, three or four or more shoot orders in which leaf size decreases with increasing shoot order, and leaf shape and dentition may also change among shoot orders. Leaf teeth are typically triangular, not spinose. Asexual reproduction by leaf-borne propagules occurs in many species, but not necessarily all individuals. Underleaves and or ventral stem paraphyllia are present in some species. Most species are yellow-green in life. Perianths are transversely broadly ovate in lateral view, and often have a wing on the dorsal keel. Eleven species of sect. *Vagae* are here recognized for Australia, four of these are new species, and two are new records. Section *Vagae* is among the more challenging lineages within *Plagiochila* in terms of species circumscription. In Malesia and Australasia many problems remain, which will best be addressed on the basis of a greater sampling of individuals from across this region.

***Plagiochila daviesiana*** Steph., Bulletin de l'Herbier Boissier, sér. 2, 3: 105 (1903) = Species Hepaticarum 2: 285 (1903)

*Type citation:* Pacific Isles (?) Georges Davies.

*Type:* Pacific Isles, herb. Georges Davies, 1889 (G 00067757!)

=*Plagiochila bellenderiensis* Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 601 (1904) = Species Hepaticarum 2: 452 (1904)

*Type citation:* Queensland (Bailey)

*Type:* Australia: Queensland: Bellenden Ker Range, 1889, F.M. Bailey (ex herb. Brotherus 648 ?) (holotype: G 00064210! isotype: BM! (as *P. mittenii* det Steph.))

**Notes:** The type of *P. daviesiana* in G is a single ramified shoot system with pseudodichotomous *Frullania*-type vegetative branching, and numerous gynoecia. The shoots bear leaves corresponding with those of tertiary and quaternary shoots in Australian plants, having a deeply bilobed apex and 1–3 teeth on the postical margin that is inclined toward the stem when hydrated. The female bracts are similarly dentate as in Australian plants. The perianth mouth is lacerate, with 6–10 long teeth per labium.

The type of *P. junghuniana* comprises several ramified shoots with pseudodichotomous *Frullania*-type vegetative branching, and several gynoecia. The leaves are broader than in *P. daviesiana*, with a shallowly bifid apex, and 4–8 small triangular teeth on the postical margin, which is perpendicular to the stem when hydrated. The perianth mouth is denticulate, with ca. 15–20 short teeth on each labium.

The Bonner lectotype of *Plagiochila pulchra* Steph. from New Caledonia is different again. This plant, though only nine or ten shoot systems are present in the type, exhibits no dichotomous branching. The leaves are apparently caducous about one-third from the leaf base. The leaf apex is shallowly bifid and there is one or two additional teeth on the postical margin of leaves on primary shoots, but no any additional teeth on tertiary and quaternary shoot leaves. Additional research into the identity of *P. pulchra* is required, but the differences in size,

branching, leaf shape and leaf dentition all suggest that it is not conspecific with the Malesian *P. junghuhniana*. No plants corresponding in morphology with the Bonner lectotype of *P. pulchra* are known from Australia. The Philippine paralectotype of *P. pulchra* is a good match with *P. junghuhniana*.

The type of *P. bellenderiensis* is *P. daviesiana*, not *P. paucidens* or *P. metcalfeii*, in whose synonymy *P. bellenderiensis* was placed by So (2000). *Plagiochila daviesiana* needs to be critically compared to *Plagiochila didyma* Inoue and *Plagiochila padangensis* Schiffn., both species similar to *P. junghuhniana* but differentiated from it by the same characters as is *P. daviesiana* here (Inoue 1974).

**Etymology:** dedicated to Georges Davies, who gathered the type material.

**Description:** Plants with pseudodichotomously branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 70 mm long and 40 mm wide, trimorphic; primary shoots 2.3–3.0 mm wide, secondary shoots c. 1.5–2.4 mm wide; branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 450  $\mu\text{m}$  diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 or 5 layers dorsally, 5 or 6 layers ventrally, cortical cell walls heavily and continuously thickened, red-brown pigmented, walls on all internal cortical cells heavily thickened to same degree, walls on external cortical cell tier thickened but not so heavily, cell lumen quadrate in cross section, not so constricted as internal cortical cell lumina, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, walls with irregular bulging trigones and continuous medial wall thickening. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves oblong-triangular, 1490–1730  $\mu\text{m}$  long  $\times$  900–1080  $\mu\text{m}$  wide, dorsal margin straight or arched, apex truncate, ventral margin straight to arched in outer two thirds, and curved and ampliate at base; with 6–10 sharp triangular teeth distributed around the apex and along ventral margin, scattered and irregularly spaced, often with a break along the median part of the ventral margin, teeth around the leaf apex often slightly larger and prominent, ampliate margin with two or three teeth, dorsal margin entire, teeth two to four cells broad at base, cells oblong, capped by an oblong-triangular cell with obtuse to rounded apex; secondary shoot leaves triangular-oblong, 1140–1265  $\mu\text{m}$  long  $\times$  525–720  $\mu\text{m}$  wide, base not ampliate, with 5–7 teeth; tertiary shoot leaves smaller again, usually narrow oblong, without basal ampliation, and with teeth confined to the apex; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells subquadrate to long rectangular, 11–24  $\mu\text{m}$  long  $\times$  7–13  $\mu\text{m}$  wide, long axis parallel to leaf margin, walls with bulging trigones, some internal walls continuously thickened; medial leaf cells isodiametric to oblong, 12–24  $\mu\text{m}$  long  $\times$  9–17  $\mu\text{m}$  wide, walls faint yellow pigmented, with bulging trigones somewhat elongate, rarely confluent, medial thickenings rare, cells in leaf base polyhedral to oblong, 16–31  $\mu\text{m}$  long  $\times$  11–18  $\mu\text{m}$  wide walls with bulging to nodulose trigones, medial thickening present on most longitudinal walls, some walls continuously thickened, trigones sometimes confluent, many walls with irregular continuous thickening. Cell surfaces smooth. Oil-bodies not known. Underleaves present or absent, persistent, triangular to filiform, with two or three filiform lobes. Asexual reproduction by leaf-borne cladia produced from the ventral surface of leaf cells.

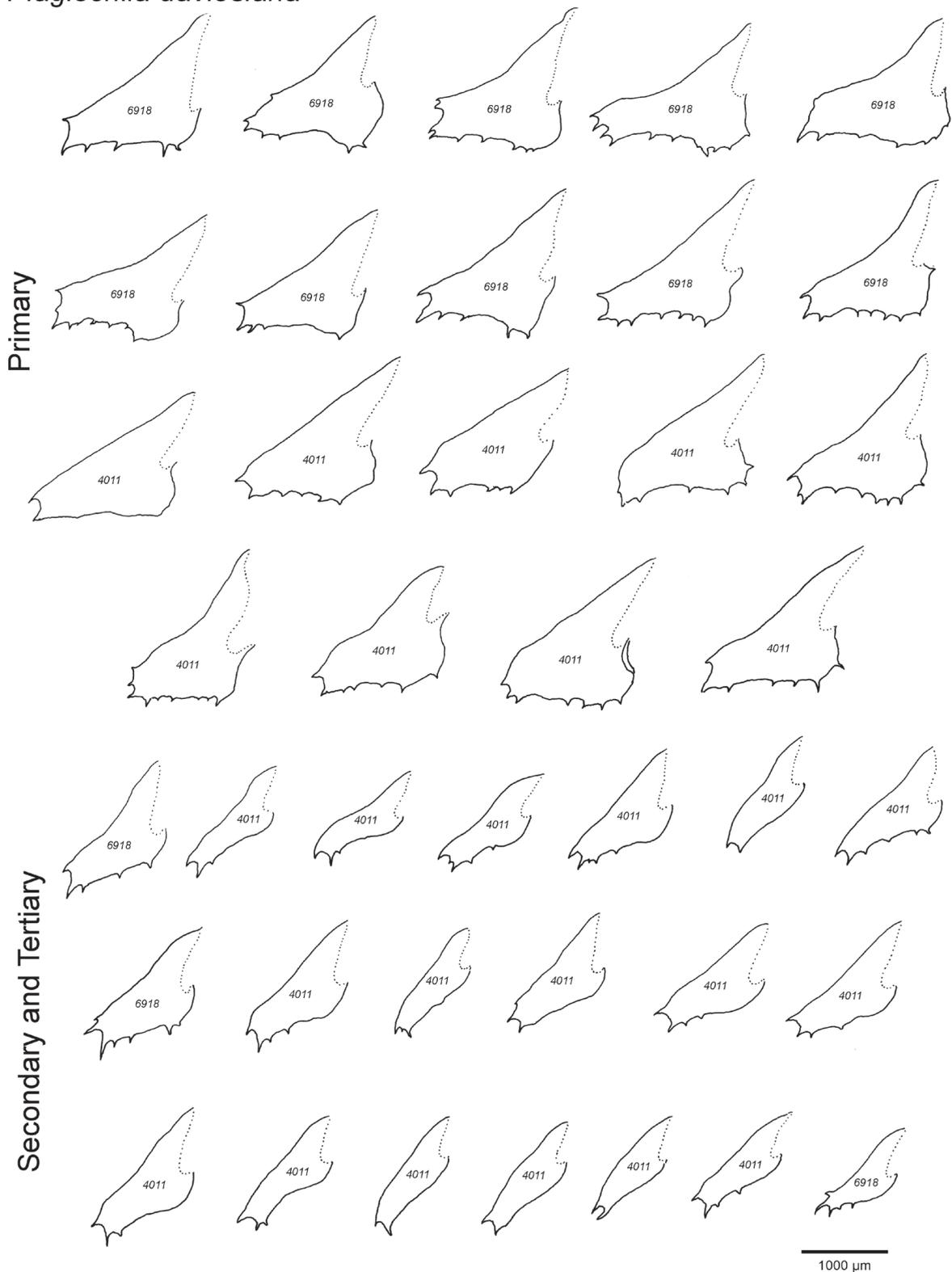
Dioicous. Androecia intercalary on secondary, tertiary, or quaternary shoots that continue vegetative growth, singly or in opposing pairs produced by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 3–4 pairs, imbricate, closely packed, bract-lobe spreading, oblong, leaf-like, narrowing to a truncate apex bearing two prominent and one or more smaller teeth, eaves. Gynoecia not seen. Fig. 50.

**Recognition:** *Plagiochila daviesiana* can be recognized by the combination of pseudodichotomous vegetative branching, hierarchically structured shoots wherein leaf stature and dentition reduces with increasing shoot order, the cultriform primary shoot leaves whose apex bears two or three teeth, and whose postical leaf margin bears 0–4 widely spaced acicular teeth, and straight or slightly concave dorsal leaf margin.

Small bifid underleaves are present on vegetative shoots, and the first branch underleaf on *Frullania*-type vegetative branches is particularly conspicuous, and sometimes has a longitudinal insertion line. The perianth base inflated, mouth bilabiate, and labia are lacinate.

*Plagiochila daviesiana* has been regarded as a synonym of *P. junghuhniana*, but *P. junghuhniana* has a shallower sinus separating the prominent teeth at leaf apex and wider leaves, and the perianth labia each bear 15–20 short triangular teeth whereas in *P. daviesiana* the perianth labia each bear 6–10 lacinate teeth. The significance of these differences has not been assessed against data capable of substantiating the separate species status of these morphological forms and further investigation is required. Until this is completed I use the name *P. daviesiana* for Australian plants due to the closer match on morphological grounds between them and the Tahitian type.

*Plagiochila daviesiana*



**Fig 50.** *Plagiochila daviesiana* leaves, from M.A.M. Renner 6918 & T.C. Wilson (NSW 858917), and J.A. Curnow 4011 (CANB 9500795).

**Distribution and Ecology:** *Plagiochila daviesiana* is known from the island of Tahiti in the central Pacific and the Wet Tropics of north-east Australia. In Australia *P. daviesiana* occurs in complex mesophyll-vine rainforest below 400 m with subcanopy and ground layers dominated by *Rhodamnia*, *Dendrocnide*, *Freycinetia*, *Archontophoenix*, *Allocasia*, and *Pandanus*, within which it grow as a weft-forming epiphyte on twigs and branches of riparian vegetation.

**Specimens examined:** **Australia: Queensland:** Mulgrave River Forestry Road, Goldsborough Valley, 18 km S of Gordonvale, 17°16'S 145°47'E, 80 m, 15 Dec 1990, *J.A. Curnow 4011* (CANB 9500795, NSW 428923); *ibid*, *J.A. Curnow 4021* (CANB 9500805); North Kennedy, Tully Gorge National Park, Tully River, Cochable Creek catchment, Cannabullen Creek walking track, Whispy Falls, 17°43'34"S 145°37'22"E, 234 m, 11 May 2014, *M.A.M. Renner 6916 & T.C. Wilson* (NSW 858878); *ibid*, *M.A.M. Renner 6918 & T.C. Wilson* (NSW 858917); Tully Gorge National Park, Cochable Creek campground, 17°44'42"S 145°37'51"E, 165 m, 11 May 2014, *M.A.M. Renner 6914 & T.C. Wilson* (NSW 870829); **Tahiti:** District of Papara, 14 Oct 1909, *Miss J.E. Tilden* (BM 000576204).

***Plagiochila minax* M.A.M. Renner *sp. nov.***

**Diagnosis:** *Plagiochila minax* is distinctive among Australasian *Plagiochila* in the pseudodichotomous, *Frullania*-type vegetative branching, the relatively large shoots with primary shoots 4.6–5.2 mm wide; the contiguous triangular ovate leaves with a broad ampliate base, rounded to truncate apex and straight to arched dorsal margin, bearing 10–16 sharp triangular teeth often the two or three teeth around the apex larger and conspicuous; the absence of underleaves; the spinose dentate female bracts; and the perianths with broad wings on the dorsal and ventral keels.

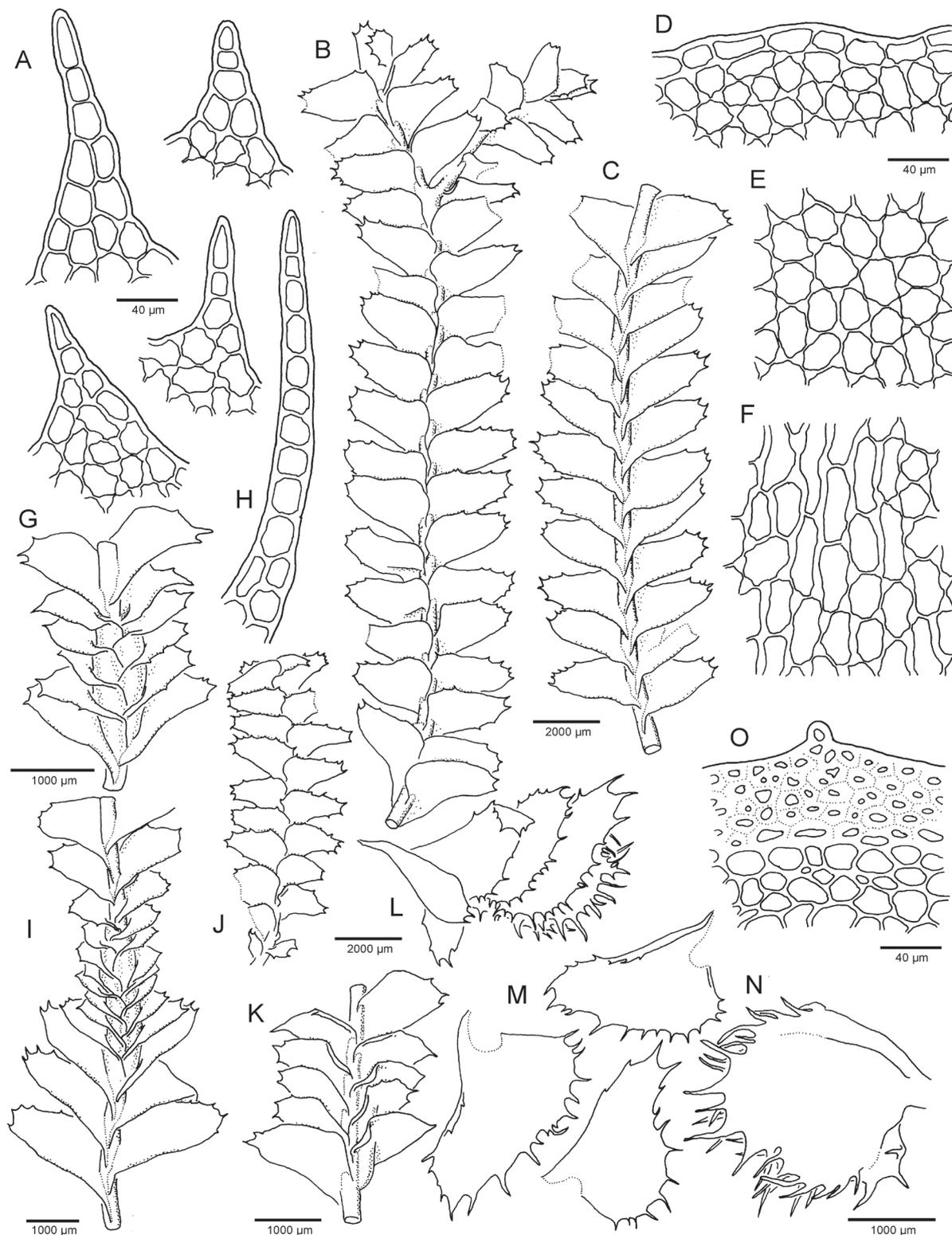
**Type:** Australia, Queensland, North Kennedy, Tully Gorge National Park, Tully River, Cochable Creek catchment, Cannabullen Creek walking track, Whispy Falls, 17°43'34"S 145°37'22"E, 234 m, 11 May 2014, *M.A.M. Renner 6958 & T.C. Wilson* (holotype: NSW 858855; isotypes: BRI, CANB, G, LAE, MEL, SUVA).

**Etymology:** *minax*, projecting or overhanging (Latin) in reference to the pendant-procumbent shoots.

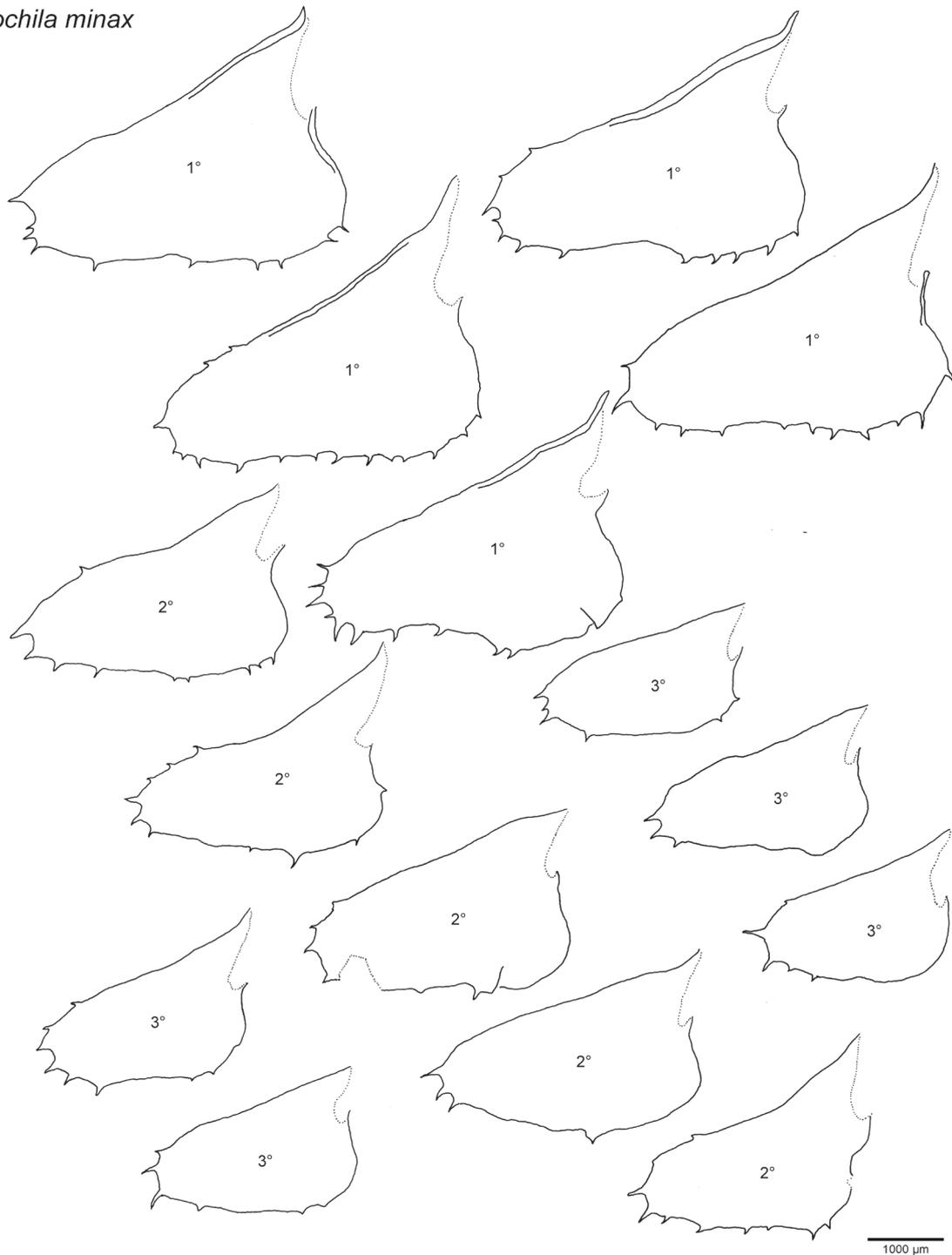
**Description:** Plants with pseudodichotomously branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 90 mm long and 60 mm wide, trimorphic; primary shoots 4.6–5.2 mm wide, secondary shoots c. 2.9–3.7 mm wide; branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; reddish-brown, in primary shoots to 700 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 or 5 layers, cortical cell walls strongly and continuously thickened, all walls including free external wall thickened to same degree, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, walls with triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves oblong-triangular, 2980–3250 µm long × 1850–1990 µm wide, dorsal margin straight or arched, apex rounded, ventral margin straight to arched in outer two thirds, and curved and ampliate at base; with 10–16 sharp triangular teeth distributed around the apex and along ventral margin, scattered and irregularly spaced, often with a break along the median part of the ventral margin, teeth around the leaf apex often slightly larger and prominent, ampliate margin with two or three teeth, dorsal margin entire, teeth two to four cells broad at base, cells oblong, capped by an oblong-triangular cell with obtuse to rounded apex; secondary shoot leaves triangular-oblong, 2380–2700 µm long × 1220–1530 µm wide, with 4–10 teeth; tertiary shoot leaves 1840–2080 µm long × 990–1205 µm wide, with 3–7 teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to oblong, 19–34 µm long × 11–17 µm wide, long axis parallel to leaf margin, walls with bulging to nodulose trigones, some walls continuously thickened; medial leaf cells isodiametric to ovoid, 23–40 µm long × 17–28 µm wide, walls unpigmented, with bulging trigones, medial thickenings rare, cells in leaf base polyhedral to long and slightly sinuous oblong, 28–55 µm long × 11–24 µm wide walls with bulging to nodulose trigones, medial thickening present or absent, some walls continuously thickened, trigones sometimes confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction by leaf-borne cladia produced from the ventral surface of leaf cells.

Dioicous. Androecia intercalary on secondary, tertiary, or quaternary shoots that continue vegetative growth, usually in opposing pairs produced by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 3–7 pairs, imbricate, closely packed, bract-lobe spreading, reduced and smaller than adjacent leaves, with zero to three spinose teeth apex acute, epistatic, bract margin broadly rounded, weakly ampliate, entire; stem among bracts smooth. Gynoecia at apices of shoots; bracts triangular-ovate, 2500–3300 µm long and 1400–2000 µm wide; dorsal margin curved, inrolled, ventral margin ampliate; apex truncate, ventral margin straight in outer half and ampliate at base; dorsal margin, apex and ventral margins all with 20–30 long triangular to lacinate teeth, unequal in size, longer around ampliate base; bract cells as for leaf cells; cell surfaces smooth; female bracteole present. Subfloral innovations absent, or one or two produced by lateral-intercalary branching from between the female bracts. Perianth campanulate, to 2500 µm long and 2500 µm wide at mouth, dorsal keel with a wing

along its whole length, with a few lacinate teeth along the outer half, ventral keel with a wing also bearing 3 or 4 lacinate teeth; laterally compressed but with an inflated base, lateral walls plane; labia curved, each with around 20 lacinate teeth. Figs 51, 52.



**Fig 51.** *Plagiochila minax*. A: teeth from leaf margin and apex. B: primary shoot sector in ventral view. C: primary shoot sector in dorsal view. D: leaf marginal cells. E: leaf medial cells. F: leaf basal cells. G: male branch in dorsal view. H: tooth from the perianth mouth. I: male branch in dorsal view. J: secondary shoot in ventral view. K: male branch in ventral view. L: lateral view of gynoecium. M: three female bracts. N: perianth in lateral view showing wings on dorsal and ventral keels. All from *M.A.M. Renner 6958 & T.C. Wilson (NSW 858855)*.

*Plagiochila minax*

**Fig 52.** *Plagiochila minax* leaves, all from M.A.M. Renner 7113 & T.C. Wilson (NSW 853008).

**Recognition:** *Plagiochila minax* can be recognized by the mid-green, pseudodichotomously branched shoots with *Frullania*-type vegetative branching, two characters which place the species into sect. *Vagae*, the relatively large primary shoots 4.6–5.2 mm wide, the contiguous triangular ovate leaves with a broad ampliate base, rounded apex and straight to arched dorsal margin, bearing 10–16 sharp triangular teeth often the two or three teeth around the apex larger and conspicuous, particularly in living material where leaves may appear narrowly bi- or tri-dentate at their apex, with the teeth projecting outwards perpendicular to the stem.

*Plagiochila minax* is readily distinguished from both *P. obtusa* and *P. streimannii* by the lack of stem ventral paraphyllia.

*Plagiochila minax* is a larger plant than many of the other sect. *Vagae* that lack ventral stem paraphyllia in the Wet Tropics, including *P. acutifolia*, *P. apatila*, *P. daviesiana*, and *P. nebulosa*, and from these four species can be distinguished by the contiguous, not imbricate leaves and several additional characters. It differs from *P. apatila* and *P. nebulosa* by the lack of spinose teeth and the rounded, not truncate, leaf apex. *Plagiochila nebulosa* differs from *P. minax* further in the elongate cells of the leaf teeth, and the smaller male bracts which are entire-margined and have an obtuse to acute apex, as opposed to the leaf-like bracts with two or more teeth around the apex in *P. minax*. *Plagiochila apatila* differs from *P. minax* in the male bracts having subcrenulate male bract lobes, rather than entire, and spinose-dentate perianth labia, rather than dentate-lacerate. *Plagiochila daviesiana* differs from *P. minax* by the narrow oblong leaves developed on tertiary and quaternary shoots.

*Plagiochila minax* approaches *P. teysmannii* in size, and both share rounded leaf apices with spinose teeth at their apex. However, *P. teysmannii* has numerous sharp triangular teeth on apex and ventral leaf margin (Fig. 61).

Where *P. minax* co-occurs with other species of *Plagiochila* sect. *Vagae*, microsite provides the first clues to identity as *P. minax* tends to occur as a lithophyte, while all the other species are predominantly epiphytes. However, *P. minax* will also grow as an epiphyte, so this is a guide only.

*Plagiochila minax* is, superficially at least, similar to *P. aspera* Steph. from New Caledonia (So 2000), though it is difficult to draw any firm conclusions about *P. aspera* given the attribution of this species to a grossly polyphyletic section, the paucity of type material, and resulting superficial description and illustration. Comparison between Australian and New Caledonian plants should be conducted on the basis of detailed morphological and molecular study.

**Distribution and Ecology:** In Australia *Plagiochila minax* occurs in tropical rainforests of north east Queensland and is currently known to occur from Mossman Gorge in the north to Wallaman Falls in the south. *Plagiochila minax* occurs across a wide elevational range, from 80 to more than 1000 m above sea level, in a wide range of forest types, including complex mesophyll vine forest, complex notophyll forest, and notophyll-vine forest. Most collections of *P. minax* have been made from on rocks within or near streams. At Wallaman Falls *P. minax* grew on rhyolite boulders at the base of a talus slope within dry rainforest at the bottom of a steep-sided gully near the river. At Whispy Falls, *P. minax* grew on the downstream sides of large rhyolite boulders within the streambed where it formed pendant-procumbent dull-green fans. At Rex Creek *P. minax* formed pseudodichotomously branched pendants on the side of a rhyolite boulder on the forest floor in a gully head with WSW aspect. *Plagiochila minax* may also grow as an epiphyte on tree trunks, as at Charmillan Creek where it formed wefts mixed with *Plagiochila nebulosa* and other bryophytes on the trunk of a large canopy tree c. 40 cm diameter, between 1 and 5 metres above ground, on the edge of a forest gap.

**Specimens examined: Australia: Queensland:** 1883 misit Bailey ex herb. Kidz 217 as *P. fasciculata* (BM); Cook, Daintree National Park, Mossman Gorge, Rex Creek, at water intake, 16°28'26"S 145°19'21"E, 160 m, 17 May 2014, M.A.M. Renner 6951 & T.C. Wilson (NSW 858862); *ibid.*, M.A.M. Renner 6954 & T.C. Wilson (NSW 858922); Daintree National Park, Mossman Gorge, Rex Creek, 16°28'S 145°19'E, 80 m, 5 Dec 1990, J.A. Curnow 3792 (CANB 9409746); North Kennedy, Wright Creek, Lake Eacham, 16 km E of Atherton, 17°17'S 145°38'E, 800 m, 28 Feb 1983, H. Streimann 16872 (CANB 8302505); North Kennedy, Mount Hypipamee National Park, Dinner Creek Falls, 17°24'53"S 145°30'19"E, 1130 m, 31 May 2014, M.A.M. Renner 7066 & T.C. Wilson (NSW 858864); *ibid.*, M.A.M. Renner 7067 & T.C. Wilson (NSW 858866); *ibid.*, M.A.M. Renner 7075 & T.C. Wilson (NSW 858867); North Kennedy, Tully Falls National Park, Tully Falls Road, track to Rhyolite Pinnacle from Charmillan Creek, 17°42'20"S 145°32'48"E, 1005 m, 1 Jun 2014, M.A.M. Renner 7113 & T.C. Wilson (NSW 853008); North Kennedy, Wooroonooran National Park, South Johnston River catchment, Maple Creek, Maple Creek Road, 17°42'28"S 145°41'16"E, 720 m, 5 Apr 2012, M.A.M. Renner 6533, E.A. Brown & V.C. Linis (NSW 898868); North Kennedy, Girringun National Park, Wallaman Falls, Djinda track to base of falls from Wallaman Lookout, 18°35'28"S 145°47'58"E, 464 m, 9 May 2014, M.A.M. Renner 6899 & T.C. Wilson (NSW 858850); *ibid.*, M.A.M. Renner 6900 & T.C. Wilson (NSW 858853); Wallaman Falls, W of Ingham, 18°36'S 145°48'E, 3 Jul 1983, W.B. Schofield 80341 & M.I. Schofield (NSW 734773).

***Plagiochila obtusa*** Lindenb., Species Hepaticarum 2-4: 42 (1840)

*Type citation:* in montosis Javae insulae ad terram rarior. Legerunt clar. viri Blume et Reinwardt.

*Type:* Indonesia. Java. Blume & Reinwardt s.n. (holotype: W isotypes: FH, S, STR)

=*Plagiochila eberhardtii* Steph., Revue Bryologique 34: 49 (1907)

*Type citation:* 'se sont retrouvées dans le second envoi de M. le Dr Eberhardt' and 'Epiphyte dans les forêts sur la route de Djirin, aux bords de L'Arroyo, 1,450 m.'

*Type:* Vietnam, Annam, Djirin, auxbords de l'Arroyo, 1450 m, 1906, *Eberhardt* 75 (holotype: G-5305)

=*Plagiochila hispida* Steph., Bulletin de l'Herbier Boissier, sér. 2 3: 881 (1903) = Species Hepaticarum 2: 366 (1903)

*Type citation:* Sumatra (Ferd. v. Müller) Java (*Fleischer*).

*Type:* Indonesia. Java. Am Gedeh, 13-1500 m, *Fleischer s.n.* (lectotype designated by Inoue (1984): G-12781)

=*Plagiochila villosa* Steph., Species Hepaticarum 6: 239 (1921)

*Type citation:* Java (*Fleischer* legit).

*Type:* Indonesia: Java. Salak, 1200-1400 m, 15 August 1909, *Fleischer* (?holotype: G00069839!)

=*Plagiochila obtusa* f. *villosa* (Steph.) Herzog, Annalen des Naturhistorischen Museums in Wien 53: 362 (1943)

**Notes:** The plant that is the type of *P. villosa* is huge, and has long cilia continuous along the ventral stem margin, and ciliform teeth at the base of the interior leaf margin. The plant appears to be covered in propagules, and I think I can make out a cellular origin for these from the ventral surface of the leaf. Propagules also appear to arise from the cilia on the ventral stem surface, which is unusual. I really doubt that this is conspecific with *P. obtusa*, at least as it occurs in Australia, but more work on the relationships between the plant represented in the type of *P. villosa* and others in this complex is required, on the basis of a greater sampling of both species.

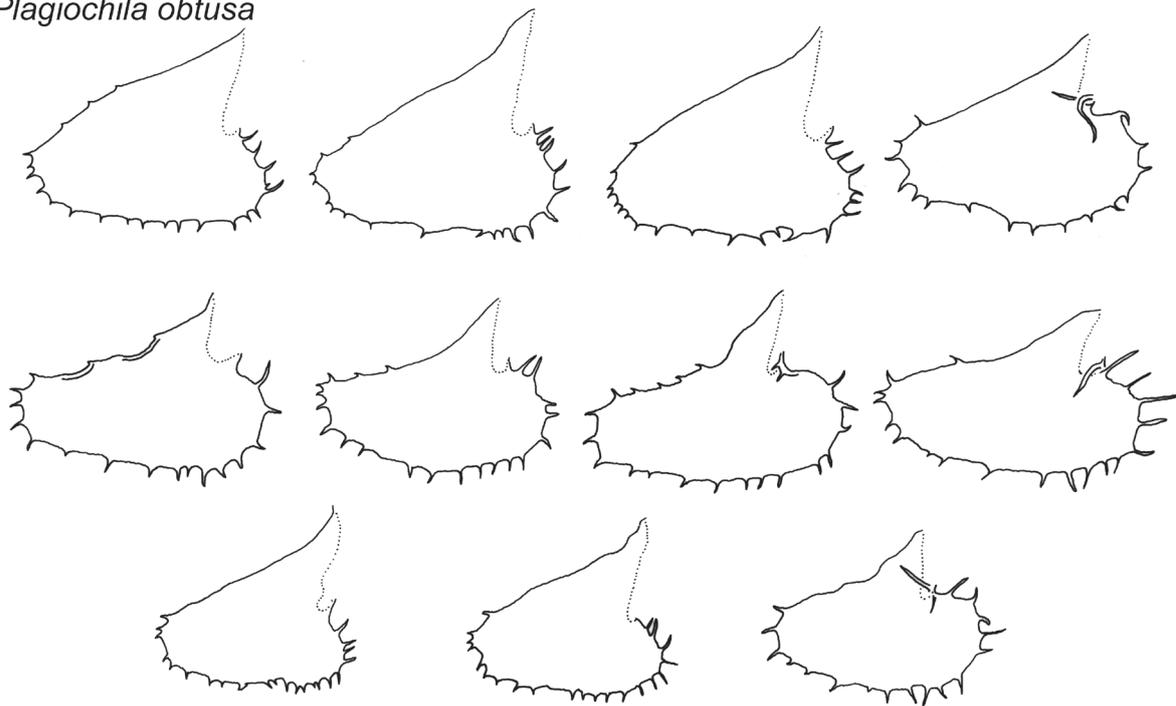
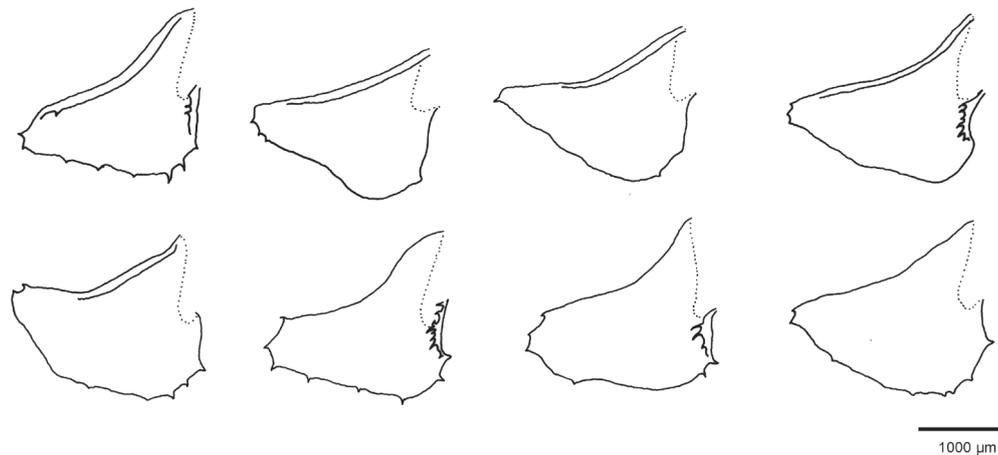
**Etymology:** *obtusa* – obtuse, possibly in reference to the leaf apex.

**Description:** Plants with pseudodichotomously branched leafy shoots arising from a basal creeping stolon, branches offsetting primary shoot by as little as 15–20°; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 50 mm long and 30 mm wide, di- or trimorphic depending on stature; primary shoots 4.5–5.5 mm wide, secondary shoots smaller; branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 450 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 3 to 5 layers, cortical cell walls strongly and continuously thickened, all walls including free external wall thickened to same degree, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, walls with small triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves elliptic-ovate, 2190–2460 µm long × 1750–1820 µm wide, dorsal margin straight or arched, apex truncate to rounded, ventral margin continuously curved, shallowly in outer two thirds, and deeply at the ampliate base; with 20–23 spinose ciliate teeth distributed around the apex and along ventral margin, sometimes on the dorsal margin as well, fairly regularly spaced, teeth around the leaf apex more triangular and slightly shorter than the long ciliate teeth on the leaf base, teeth two to four cells broad at base, cells oblong, capped by an oblong-triangular cell with obtuse to rounded apex; secondary shoot leaves ovate, smaller than primary shoot leaves; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells rectangular, 14–20 µm long × 6–10 µm wide, long axis parallel to leaf margin, walls with bulging to nodulose trigones, medial thickenings present, some walls continuously thickened; medial leaf cells isodiametric to ovoid, 12–20 µm long × 8–14 µm wide, walls yellow-pigmented, with bulging trigones, medial thickenings rare, cells in leaf base polyhedral to long and slightly sinuous oblong, 19–20 µm long × 10–16 µm wide walls with bulging to nodulose trigones somewhat elongated, medial thickening present or absent, trigones sometimes confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves present, persistent, ciliate. Asexual reproduction by leaf-borne cladia produced from the ventral surface of leaf cells.

Fertile material not seen. Fig. 53.

**Recognition:** *Plagiochila obtusa* can be recognized by the combination of yellow-green colour in life, *Frullania*-type vegetative branching, the ventral stem surface bearing dense paraphyllia but no conspicuous underleaves; the ovate triangular leaves with an ampliate base whose margin bears long spinose-ciliate teeth, and whose apex bears narrow triangular teeth (Fig. 53).

*Plagiochila obtusa* could be confused with *P. streimannii*, but *P. streimannii* has falcate leaves whose margins bear triangular teeth (Fig. 53), and conspicuous underleaves on the ventral stem surface, in addition to dense paraphyllia.

*Plagiochila obtusa**Plagiochila streimannii*

**Fig 53.** *Plagiochila obtusa* leaves and *Plagiochila streimannii* leaves, from M.A.M.Renner 6941 & T.C. Wilson (NSW 853117) and H. Streimann 29726 (CANB 8407897 p.p.) respectively.

**Distribution and Ecology:** *Plagiochila obtusa* is distributed from Vietnam through Indonesia and Malesia including Sumatra and Java, with an outlying occurrence in north-east Australia first reported by Inoue (1986). In Australia *P. obtusa* has been collected in the vicinity of Mt Spurgeon, growing corticolously on recently dead standing trunks within simple microphyll rainforest with *Agathis atropurpurea*, *Prumnopitys ladei*, and *Eucalyptus grandis* emergent over simple notophyll rainforest canopy to 20 m tall on a face with a westerly aspect, on an old tin mining site. The dead standing tree upon which *P. obtusa* was collected was overhanging Unnamed Stream at the bottom of Coopers Clearing.

**Specimens examined: Australia: Queensland:** Cook, Mt Carbine Tableland, western slopes of Mount Spurgeon, Coopers Clearing 16°26'32"S 145°11'31"E, 1180 m, 15 May 2014, M.A.M.Renner 6941 & T.C. Wilson (NSW 853117); Mt Spurgeon, west of Mossman, 23 Aug 1982, M.L. Hicks 11093 (F 1092847).

***Plagiochila streimannii*** Inoue, Journal of Japanese Botany 63: 365 (1988)

**Type citation:** Papua New Guinea: Nauti Logging Area; upper Watutu River, 10 km SW of Bulolo, ca 1400 m alt, leg. H. Streimann 17097 (TNS; duplicates in CBG, LAE, JE, NICH).

*Type:* Papua New Guinea, Morobe Province, Nauti Logging Area, Upper Watut River, 10 km SW of Bulolo, 7°16'S 146°36'E, 1400 m, 3 Mar 1982, *H. Streimann 17097* (holotype: TNS; isotype: CANB 8201226!)

**Etymology:** *streimannii* of Streimann, referencing Heinar Streimann (1938–2001) Estonian born Australian bryologist and collector of the type.

**Description:** Plants with pseudodichotomously branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 70 mm long and 50 mm wide, trimorphic; primary shoots 2.7–3.6 mm wide, secondary shoots 2.2–2.7 mm wide; branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems with numerous paraphyllia on ventral surface, paraphyllia with numerous spinose ciliate teeth, sometimes branched; lamellae and paraphyses absent; reddish-brown, in primary shoots to 500 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 or 5 layers, cortical cell walls strongly and continuously thickened, all walls including free external wall thickened to same degree, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, walls with triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves triangular-ovate, falcate, 2000–2390 µm long × 1250–1600 µm wide, dorsal margin arched, inrolled, apex obtuse, less often narrowly rounded, ventral margin straight to curved in outer half, and curved and ampliate at base; with 2–7 small triangular teeth distributed around the apex and along ventral margin, scattered and irregularly spaced, then usually with numerous closely packed spinose ciliate teeth on the basal-most portion of the ventral margin which is also reflexed; dorsal margin entire, triangular teeth two to four cells broad at base, cells quadrate to rectangular, capped by an oblong-triangular cell with rounded to obtuse apex; secondary shoot leaves smaller and with fewer teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to short rectangular, 13–21 µm long × 11–18 µm wide, long axis parallel or perpendicular to leaf margin, walls with bulging to nodulose trigones, sometimes confluent, some walls continuously thickened; medial leaf cells isodiametric to ovoid, 23–40 µm long × 17–28 µm wide, walls unpigmented, with bulging to nodulose trigones, medial thickenings present on some walls, cells in leaf base polyhedral to oblong, 24–40 µm long × 12–23 µm wide walls with nodulose trigones, medial thickening present on some walls, some walls continuously thickened, trigones sometimes elongate along medial walls and sometimes confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves present, conspicuous, persistent, bilobed, lobes lacinate, margins with numerous spinose-ciliate teeth, sometimes branched. Asexual reproduction by leaf-borne cladia produced from the ventral surface of leaf cells.

Reproductive structures not seen. Figs 53, 54.

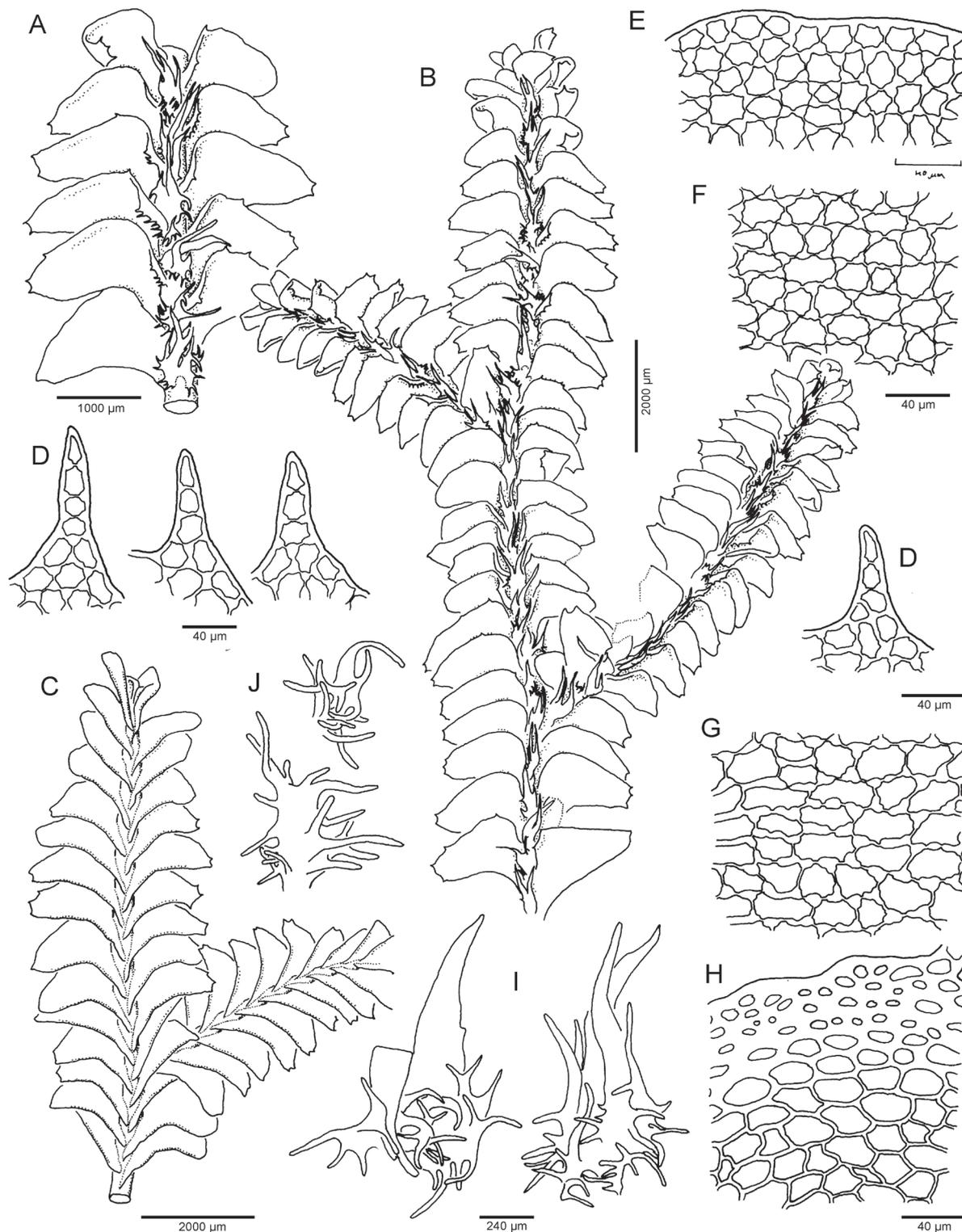
**Recognition:** *Plagiochila streimannii* can be recognized by the combination of pseudodichotomous branching, presence of numerous paraphyllia on the ventral stem surface and conspicuous underleaves with long ciliiform lobes visible between the leaves in ventral view, the falcate leaves with triangular teeth around the apex and on the margin of the ampliate leaf base, the occasionally reflexed interior margin of the leaf, which may bear several close-set spinose teeth.

*Plagiochila streimannii* could be confused with *P. obtusa*, with which it shares paraphyllia on the ventral stem surface, but the underleaves of *P. obtusa* are not so conspicuous, and the leaves are ovate-triangular, rather than falcate.

**Distribution and Ecology:** *Plagiochila streimannii* is known to occur in Papua New Guinea and Australia, and has been reported from Indonesia (Patzak *et al.* 2016). In Australia *P. streimannii* is known by a single collection made from a granite boulder on the Windsor Tableland, where it grew mixed in a tall turf with *P. nebulosa*. I have not seen the specimen of *Plagiochila streimannii* reported from Indonesia by Patzak *et al.* (2016).

**Specimens examined: Papua New Guinea:** Gulf Province, Bema-Kaintiba Road, 4 km N of Kaintiba, 7°29'S 146°01'E, 1180 m, 25 Jan 1983, *H. Streimann 33675* (CANB 9006007);

**Australia: Queensland:** Cook: Windsor Tableland 38 km NW of Mossman, 16°17'S 145°04'E, 1140 m, 26 Jun 1984, *H. Streimann 29726* (CANB 8407897 *p.p.*).



**Fig 54.** *Plagiochila streimannii*. A: ventral view of primary shoot. B: ventral view of primary and secondary shoots, showing very faint pseudodichotomous branching. C: dorsal view of primary and secondary shoot. D: four teeth from the leaf margin. E: marginal leaf cells. F: medial leaf cells. G: basal leaf cells. H: dorsal sector of transverse section through stem from primary shoot. I: two underleaves. J: two paraphyllia. All from *H. Streimann* 29726 (CANB 8407897 *p.p.*).

***Plagiochila apatila* M.A.M.Renner *sp. nov.***

*Diagnosis:* *Plagiochila apatila* is distinguished by the combination of pseudodichotomous, *Frullania*-type vegetative branching, primary shoots 2.2–3.3 mm wide, imbricate oblong-triangular leaves with a truncate apex, straight ventral margin and ampliate base, with apex and ventral margins bearing 11–15 irregularly

spaced triangular teeth, cells of the teeth not elongated, the absence of underleaves, the male bract lobule with crenulated or dentate interior margin, and the perianth with a winged dorsal keel bearing a few spinose teeth, and 20–30 spinose-ciliate teeth on each labium.

*Type:* Australia, Queensland, North Kennedy, Tully Falls National Park, Tully Falls Road, Charmill Creek, 17°42'03"S 145°31'26"E, 1000 m, 31 May 2014, M.A.M. Renner 7090 & T.C. Wilson (holotype: NSW 858920; isotypes: BRI, CANB, G).

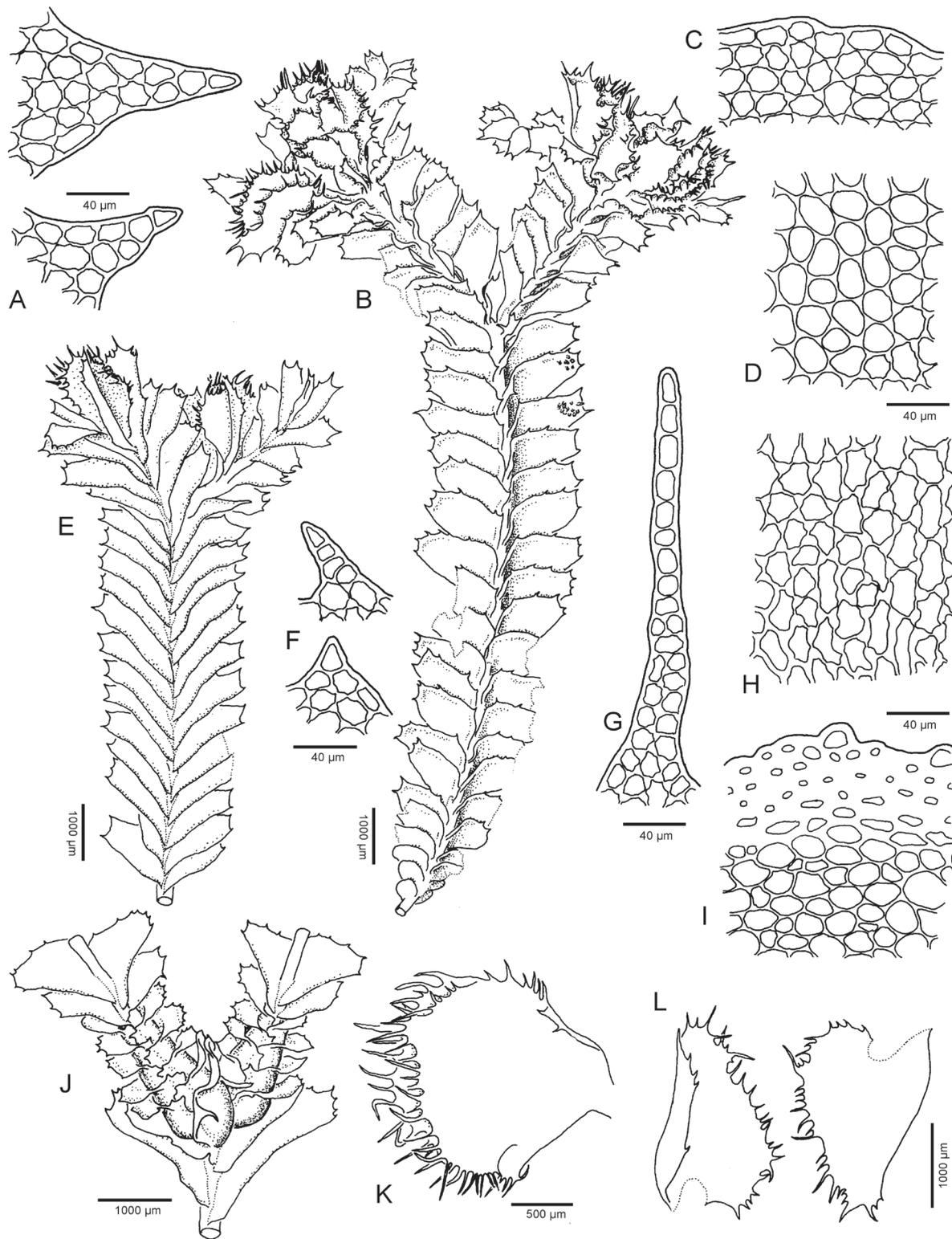
**Etymology:** Greek απατηλός *apatilos*, deceitful.

**Description:** Plants with pseudodichotomously branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 70 mm long and 40 mm wide, trimorphic; primary shoots 2.2–3.3 mm wide, branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; reddish-brown, in primary shoots to 500 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 or 5 layers, cortical cell walls strongly and continuously thickened, all walls including free external wall thickened to same degree, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, walls with triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves oblong-triangular, 1660–1925 µm long × 1055–1190 µm wide, dorsal margin straight or arched, apex truncate, ventral margin straight in outer two thirds, and curved and weakly ampliate at base; with 11–15 triangular teeth distributed around the apex and along ventral margin, scattered and irregularly spaced, ampliate margin usually without teeth, dorsal margin entire, teeth up to five cells broad at base, capped by a short triangular cell with obtuse to rounded apex; secondary shoot leaves triangular-oblong, smaller than primary shoot leaves and with fewer teeth, tertiary shoot leaves smaller again; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to oblong, 15–26 µm long × 9–17 µm wide, long axis parallel to leaf margin, walls with bulging to nodulose trigones but not continuously thickened; medial leaf cells isodiametric to ovoid, 18–32 µm long × 14–23 µm wide, walls unpigmented, with bulging trigones, medial thickenings rare, cells in leaf base polyhedral to long and slightly sinuous oblong, 19–38 µm long × 9–19 µm wide walls with bulging to nodulose trigones, medial thickening present or absent, some walls continuously thickened, trigones sometimes confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction by leaf-borne cladia produced from the ventral surface of leaf cells.

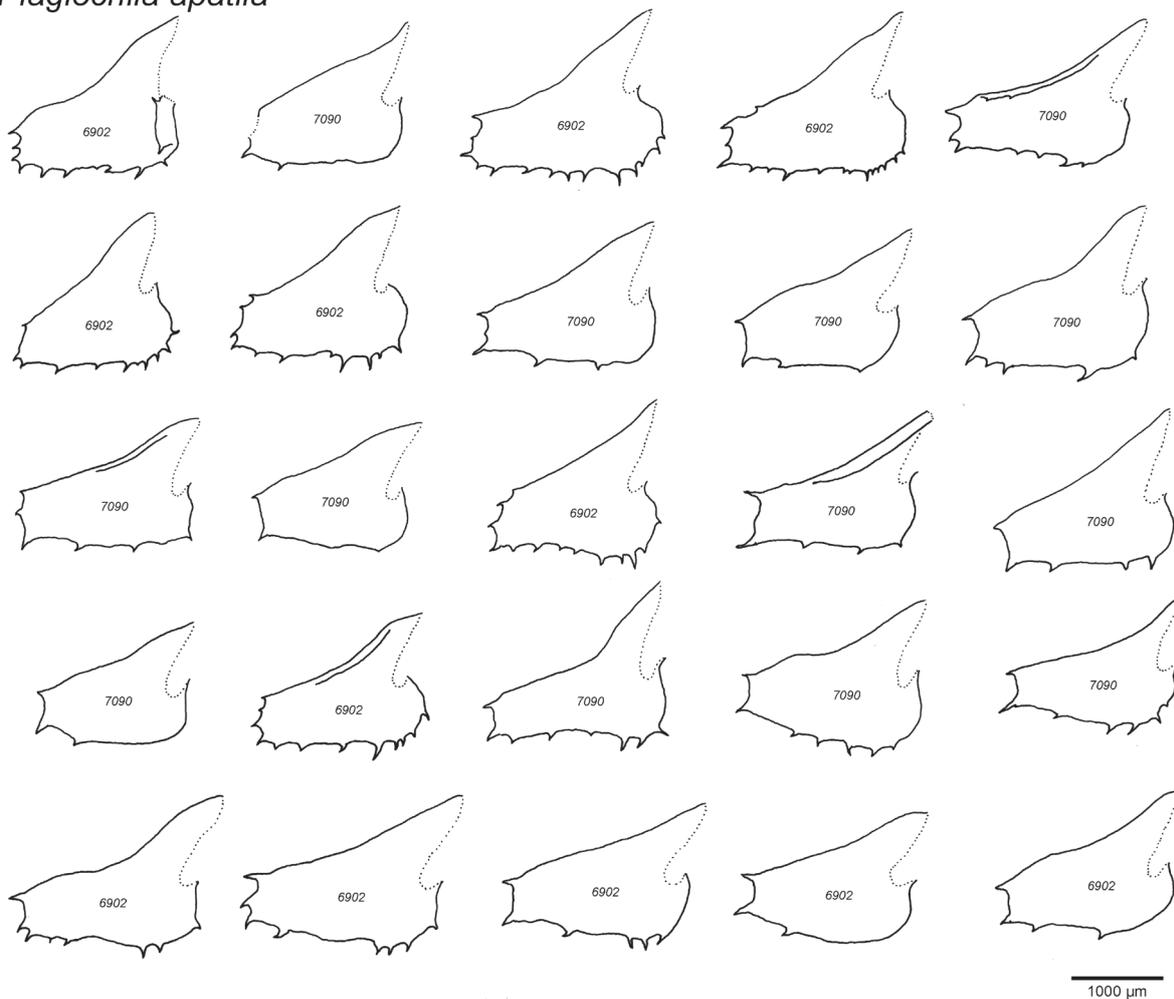
Dioicous. Androecia intercalary on secondary, tertiary, or quaternary shoots that continue vegetative growth, usually in opposing pairs produced by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 3–6 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, with four to seven three triangular teeth, epistatic, bract margin broadly and irregularly crenate to toothed on the interior margin; stem among bracts smooth. Gynoecia at apices of shoots; bracts triangular-oblong, to 2400 µm long and 1550 µm wide; dorsal margin curved, inrolled, ventral margin ampliate; apex obtuse, ventral margin straight in outer half and ampliate at base; apex and ventral margins all with around 30 short to long triangular to spinose-ciliate teeth, unequal in size; bract cells as for leaf cells; cell surfaces smooth; female bracteole present. Subfloral innovations absent, or one or two produced by lateral-intercalary branching from between the female bracts. Perianth triangular, to 2100 µm long and 1400 µm wide at mouth, dorsal keel with a wing along its whole length, with a few spinose ciliate teeth along the outer half, ventral keel unwinged; laterally compressed but with an inflated base, lateral walls plane; labia curved, each with 20–30 spinose-ciliate teeth. Figs 55, 56.

**Recognition:** *Plagiochila apatila* can be recognized by the pseudodichotomous shoot systems, with hierarchical structuring of leaves, leaves on primary shoots with a truncate apex bearing two or three triangular teeth, and the ventral margin with 1–10 additional teeth, base moderately ampliate, the small underleaves present on vegetative shoot sectors, perianths with toothed dorsal wing, mouth spinose-lacerate with teeth 15–20 cell tiers long, and the toothed male bract pouch.

*Plagiochila apatila* is similar to *Plagiochila junghuhniana* but differs by having imbricate leaves, not contiguous, and the leaves are wider at their apex, there are two or three smaller teeth at the leaf apex, and the leaf base is more ampliate than in *P. junghuhniana*. The leaf marginal teeth are triangular, comprised of more or less isodiametric cells on the leaves, not spinose teeth composed of elongated cells. Perianth mouth teeth are longer, 15–20 cells long, not triangular as in the type of *P. junghuhniana*.



**Fig 55.** *Plagiochila apatila*. A: two teeth from the leaf margin near the apex. B: ventral view of shoot bearing gynoecia at apex of secondary branches and on associated subfloral innovations. C: leaf marginal cells. D: leaf medial cells. E: dorsal view of primary shoot bearing terminal gynoecium. F: two teeth from the ventral leaf margin. G: tooth from the perianth mouth. H: leaf basal cells. I: dorsal half of transverse section through stem from primary leafy shoot. J: dorsal view of male branches. K: perianth in lateral view. L: two female bracts. All from *M.A.M. Renner 7090 & T.C. Wilson (NSW 858920)*.

*Plagiochila apatila*

**Fig 56.** *Plagiochila apatila* leaves, from M.A.M. Renner 6902 & T.C. Wilson, (NSW 858870) and M.A.M. Renner 7090 & T.C. Wilson (NSW 858920).

*Plagiochila apatila* is similar to *P. nebulosa* but *P. nebulosa* has spinose dentate teeth on the leaf margin with the teeth fairly regularly spaced, and whose cells are long rectangular; and the male bracts are obtuse at their apex but otherwise entire. *Plagiochila apatila* has triangular teeth clustered toward the leaf apex and around the ampliate base whose cells are quadrate; and the male bracts bear 4–7 teeth.

*Plagiochila apatila* is similar to *P. massalongoana* but differs by having a wing on the dorsal perianth keel, the perianths in *P. massalongoana* are unwinged.

*Plagiochila apatila* is similar to *P. daviesiana* but differs by having male bract lobes rounded, with scattered teeth, not rectangular with two prominent teeth at the apex.

*Plagiochila apatila* could be confused with *P. minax*, but *P. minax* is a larger plant with prominent teeth around the narrow apex, and scattered prominent teeth on the ventral leaf margin, and contiguous to loosely imbricate leaves. The male bract lobes of *P. minax* are large, and leaf-like particularly at the base of the male branch, and don't have the irregular lobes on the interior of the dorsal margin, as is present in *P. apatila*. These two species also inhabit different microsites, *P. apatila* is usually an epiphyte while *P. minax* is often a lithophyte, but there is overlap in the microsites occupied by these two species, and they may grow sympatrically.

*Plagiochila apatila* could be confused with *P. parviflora*, but *P. parviflora* has conspicuous bifid underleaves (see Inoue 1984) whereas *P. apatila* does not.

**Distribution and Ecology:** *Plagiochila apatila* is distributed from Malaysia and Indonesia in the west to the Solomon Islands in the east, and south to north-eastern Australia. In Australia *Plagiochila apatila* is confined to the Wet Tropics, from the Big Tableland and Thornton Beach in the north, through Mt Lewis, the Atherton Tableland, the Hugh Nelson Range, Tully Gorge, south to Blue Water Creek west of Ingham. *Plagiochila apatila* occurs between sea level and 1300 m elevation, in a range of rainforest types including littoral megaphyll rainforest, and notophyll and microphyll-vine rainforests at higher elevations. At Thornton Beach *Plagiochila apatila* grew within littoral cyclone impacted megaphyll-vine rainforest with broken canopy to 25 m tall on a flat coastal plain where it was an epiphyte on the trunk of a small Sapindaceae tree 3 cm dbh. *Plagiochila apatila* was also collected as an epiphyte on tree trunks in the Hugh Nelson Range, but may also grow on rocks as a Blue Water Creek, where it grew on a boulder in rainforest fringing the stream.

Plants conspecific with Australian *P. apatila* are present in the Solomon Islands, Indonesia, and Malaysia (J. Heinrichs unpublished data). The Solomon Island plants share the salient features of Australian *P. apatila*. I have not had opportunity to examine the closely related individuals from Indonesia and Malaysia, but assume from the closeness of their phylogenetic relationship they all belong to the same species. The specific epithet refers to the fact that these plants were previously identified as *P. parviflora*.

**Specimens examined: Australia: Queensland:** Cook: Big Tableland, 26 km S of Cooktown, 15°43'S 145°17'E, 610 m, 4 Jul 1984, *H. Streimann 30804* (CANB 781987); Daintree National Park, between Thornton Beach and Noah Creek, 16°09'04"S 145°26'28"E, 5 m, *M.A.M. Renner 6332a*, *V.C. Linis* & *E.A. Brown* (NSW 896732); Mt Lewis National Park, Brooklyn Wildlife Refuge, Ho Chi Minh trail, tailings Dam, 16°36'05"S 145°16'21"E, 1010 m, 13 May 2014, *M.A.M. Renner 6902* & *T.C. Wilson* (NSW 858882); North Kennedy: Barrine Lake, Atherton Tableland, 17°15'S 145°38'E, 29 June 1983, *W.B. Schofield 80056* & *M.I. Schofield* (CANB 00781981); North Kennedy, Mt Baldy, Great Dividing Range, 4 km SW of Atherton, 17°17'S 145°27'E, 1080 m, 25 Jun 1984, *H. Streimann 29322* (CANB 8407450); North Kennedy, Hugh Nelson Range, Crater State Forest, 19 km S of Atherton, 17°26'S 145°29'E, 1000 m, 2 Mar 1983, *H. Streimann 27192* (CANB 8302993); Hugh Nelson Range, Longland's Gap, 17°27'15"S 145°28'09"E, 1241 m, 9 Jun 2001, *D.C. Cargill 10* (CANB 640605.1); Palmerston National Park, Gooligan Creek, 17°37'S 145°48'E, 2 Jul 1983, *W.B. Schofield 80308* & *M.I. Schofield* (NSW 734501); North Kennedy, Tully Gorge National Park, Tully River, below power station, 17°46'00"S 145°34'50"E, 205 m, 10 May 2014, *M.A.M. Renner 6902* & *T.C. Wilson*, (NSW 858870); Koombooloomba Dam Road, 23 km SE of Ravenshoe, 17°49'S 145°33'E, 780 m, 23 Jun 1984, *H. Streimann 28900*, CANB 8407028); Blencoe Creek, Cardwell Range 48 km NW of Cardwell, 18°03'S 145°39'E, 740 m, *H. Streimann 36904* (CANB 781989); Blue Water Creek, Old Mill Road, 39 km WSW of Ingham, 18°45'S 145°48'E, 600 m, 19 June 1984, *H. Streimann 28438* (CANB8406248).

***Plagiochila nebulosa* M.A.M. Renner *sp. nov.***

**Diagnosis:** *Plagiochila nebulosa* is distinguished by the combination of pseudodichotomous, *Frullania*-type vegetative branching, primary shoots 2.8–3.7 mm wide, with imbricate triangular-ovate leaves with a rounded to truncate apex, straight to shallowly curved in ventral margin and ampliate base, with apex and ventral margins bearing 14–20 regularly sized and spaced spinose teeth, cells of the teeth elongated; the presence of persistent, vestigial, small triangular underleaves; the male bract lobule margin entire, and bract lobe obtuse to acute; the perianth with winged dorsal keel, and with 20–30 spinose-ciliate teeth on each labium.

**Type:** Australia, Queensland, North Kennedy, Tully Falls National Park, Tully Falls Road, track to Rhyolite Pinnacle from Charmillan Creek, 17°42'20"S 145°32'48"E, 1005 m, 1 Jun 2014, *M.A.M. Renner 7112* & *T.C. Wilson* (holotype: NSW 852994; isotypes: BRI, CANB, G, SUVA)

**Etymology:** clouded, in reference to the habitat occupied by the species.

**Description:** Plants with pseudodichotomously branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 70 mm long and 40 mm wide, trimorphic; primary shoots 2.8–3.7 mm wide, secondary shoots c. 2.3–2.6 mm wide, tertiary branches 1.6–2.0 mm wide; branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; reddish-brown, in primary shoots to 500 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 to 6 layers, cortical cell walls strongly and continuously thickened, walls of inner cortical cells thickened to same degree, walls of outer layer not as thickened as inner cells; all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, with small bulging trigones, and some walls with irregular continuous thickenings. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to

contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves triangular-ovate, 2100–2550  $\mu\text{m}$  long  $\times$  1450–1780  $\mu\text{m}$  wide, dorsal margin straight or slightly arched, inrolled, apex rounded to truncate, ventral margin straight to shallowly curved in outer two thirds and ampliate at base; with 14–20 spinose teeth distributed around the apex and along ventral margin, fairly regularly spaced and evenly sized, dorsal margin entire or with one or two teeth at outer end, teeth two to four cells broad at base, cells long rectangular, capped by an elongated triangular cell with an acute apex; secondary shoot leaves triangular-ovate, 1590–2050  $\mu\text{m}$  long  $\times$  950–1380  $\mu\text{m}$  wide, smaller than primary shoot leaves and with 11–19 teeth, tertiary shoot leaves smaller again, 1160–1750  $\mu\text{m}$  long  $\times$  700–1100  $\mu\text{m}$  wide with 9–15 teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells oblong, 16–24  $\mu\text{m}$  long  $\times$  7–14  $\mu\text{m}$  wide, long axis parallel or perpendicular to leaf margin, walls with bulging trigones and weak continuous thickening, medial thickenings present in some cells; medial leaf cells isodiametric to ovoid, 19–30  $\mu\text{m}$  long  $\times$  13–22  $\mu\text{m}$  wide, walls unpigmented, with bulging trigones, medial thickenings present on some walls, cells in leaf base polyhedral to oblong, 26–40  $\mu\text{m}$  long  $\times$  17–26  $\mu\text{m}$  wide walls with bulging to nodulose trigones, medial thickening present on some walls. Cell surfaces smooth. Oil-bodies not known. Underleaves present or absent, vestigial, persistent, triangular. Asexual reproduction by leaf-borne cladia produced from the ventral surface of leaf cells.

Dioicous. Androecia intercalary on secondary or tertiary shoots that continue vegetative growth, usually in opposing pairs produced by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 4–9 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, entire with an acute apex, epistatic, bract interior margin broadly rounded to weakly ampliate, entire; stem among bracts smooth. Gynoecia at apices of shoots; bracts triangular-oblong, 2200–2500  $\mu\text{m}$  long and 1400–1700  $\mu\text{m}$  wide; dorsal margin arched, inrolled, apex rounded to truncate, ventral margin straight in outer half and ampliate at base; apex and ventral margins with around 30 triangular to lacinate teeth, unequal in size, longer on the ampliate base, dorsal margin sometimes with a few small triangular teeth; bract cells as for leaf cells; cell surfaces smooth; female bracteole present or absent. Subfloral innovations present, one or two produced by lateral-intercalary branching from between the female bracts. Perianth triangular to campanulate, 2300–2700  $\mu\text{m}$  long and 1700–2600  $\mu\text{m}$  wide at mouth, dorsal keel with prominent wing, ventral keel unwinged; laterally compressed but with an inflated base, lateral walls plane; labia curved, each with 20–30 spinose-ciliate teeth. Figs 57–59.

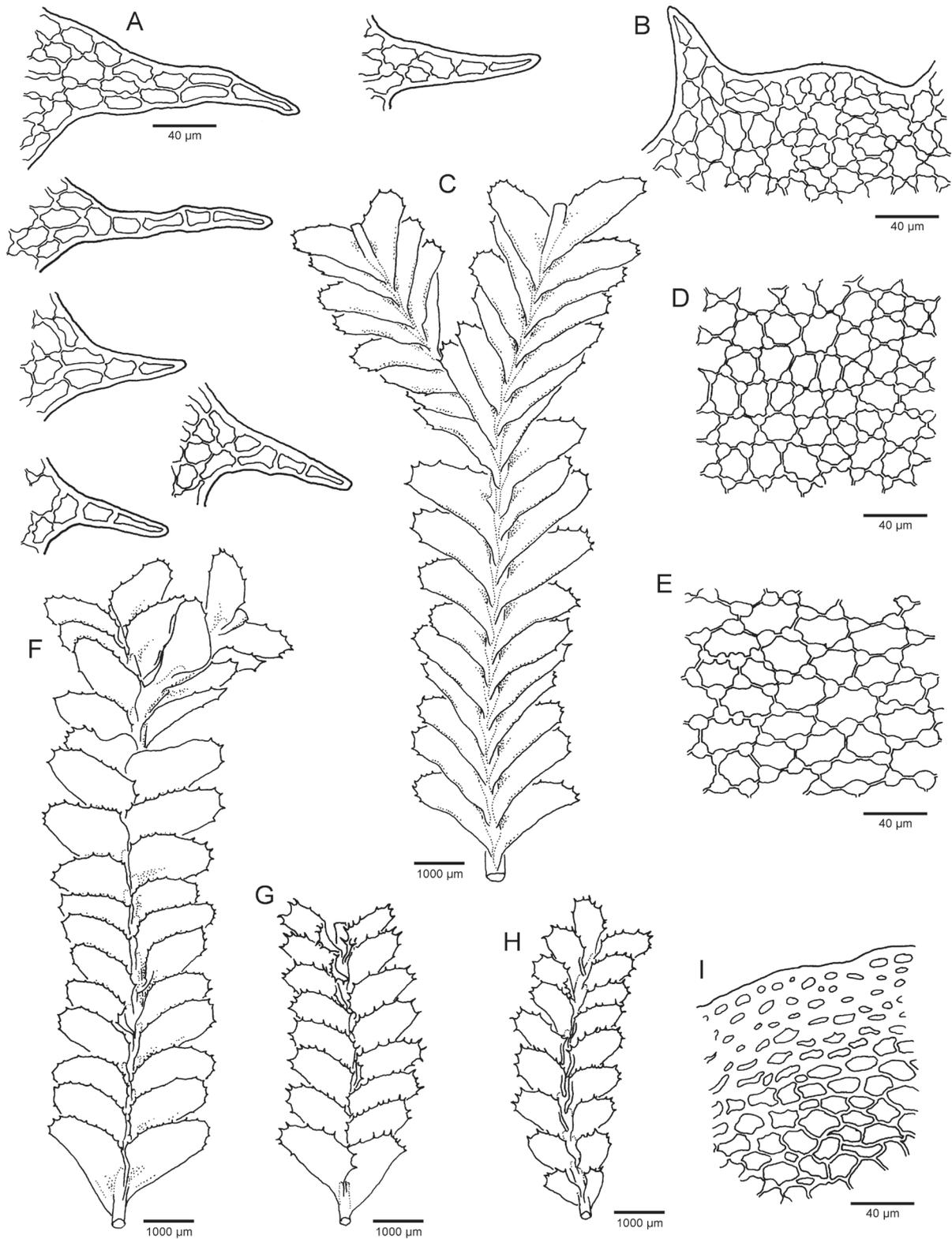
**Recognition:** *Plagiochila nebulosa* can be recognized by the combination of triangular ovate leaves with 14–20 spinose teeth, in which the teeth cells are elongate, and the apical cell is long narrow triangular with an acute apex; the dorsal leaf margin is inrolled forming a distinct cnemis; the presence of a modified first branch underleaf at the base of *Frullania*-type vegetative branches, which is often bilobed and sometimes asymmetrically so. The ventral leaf insertion line is decurrent, and bears a low wing of tissue, and there are usually small underleaves among the leaves, often close to the preceding leaf and so obscured by it. In female plants the perianth has a wing along the dorsal keel. In male plants the male bract lobes have an obtuse to acute apex, and otherwise entire margins.

*Plagiochila nebulosa* could be confused with *P. apatila* but *P. apatila* has small triangular teeth irregularly spaced along the leaf margins.

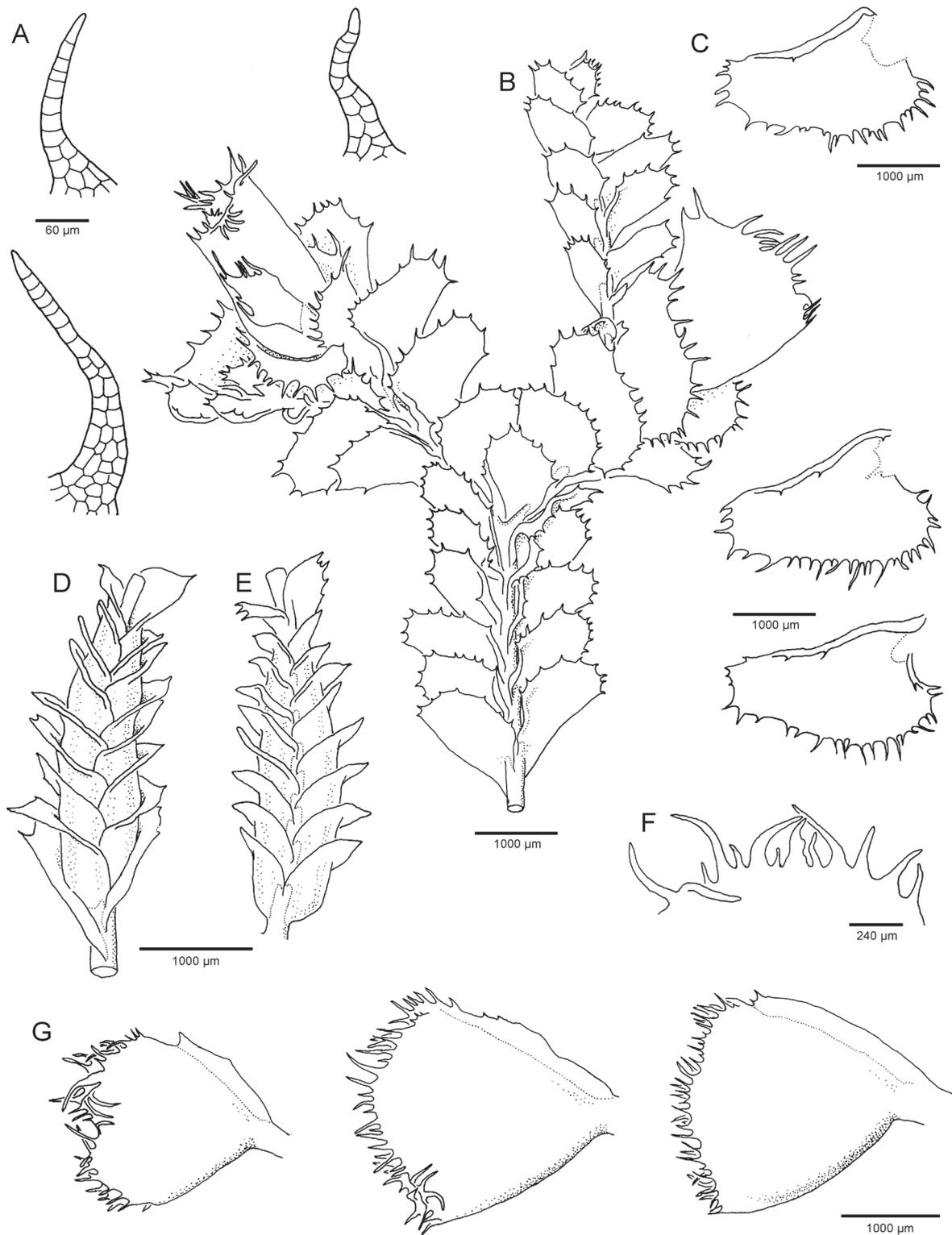
*Plagiochila nebulosa* could be confused with *P. meridionalis* but *P. meridionalis* is a larger plant with triangular teeth on leaves, no wing on the dorsal perianth keel in females, and male bract lobes rounded and bearing two or more teeth in males.

*Plagiochila nebulosa* is similar to *Plagiochila powellii* from Samoa and New Caledonia (Inoue 1981) but differs by the fewer teeth on the leaf margin (14–20 versus 18–27), the absence of medial wall thickenings and confluent trigones in cells of the leaf base, both of which are present in *P. powellii*, and the more numerous and shorter teeth on the perianth labia, the longest of which are 15 cells long, rather than a minimum of 20 cells long as in *P. powellii* (Inoue 1981).

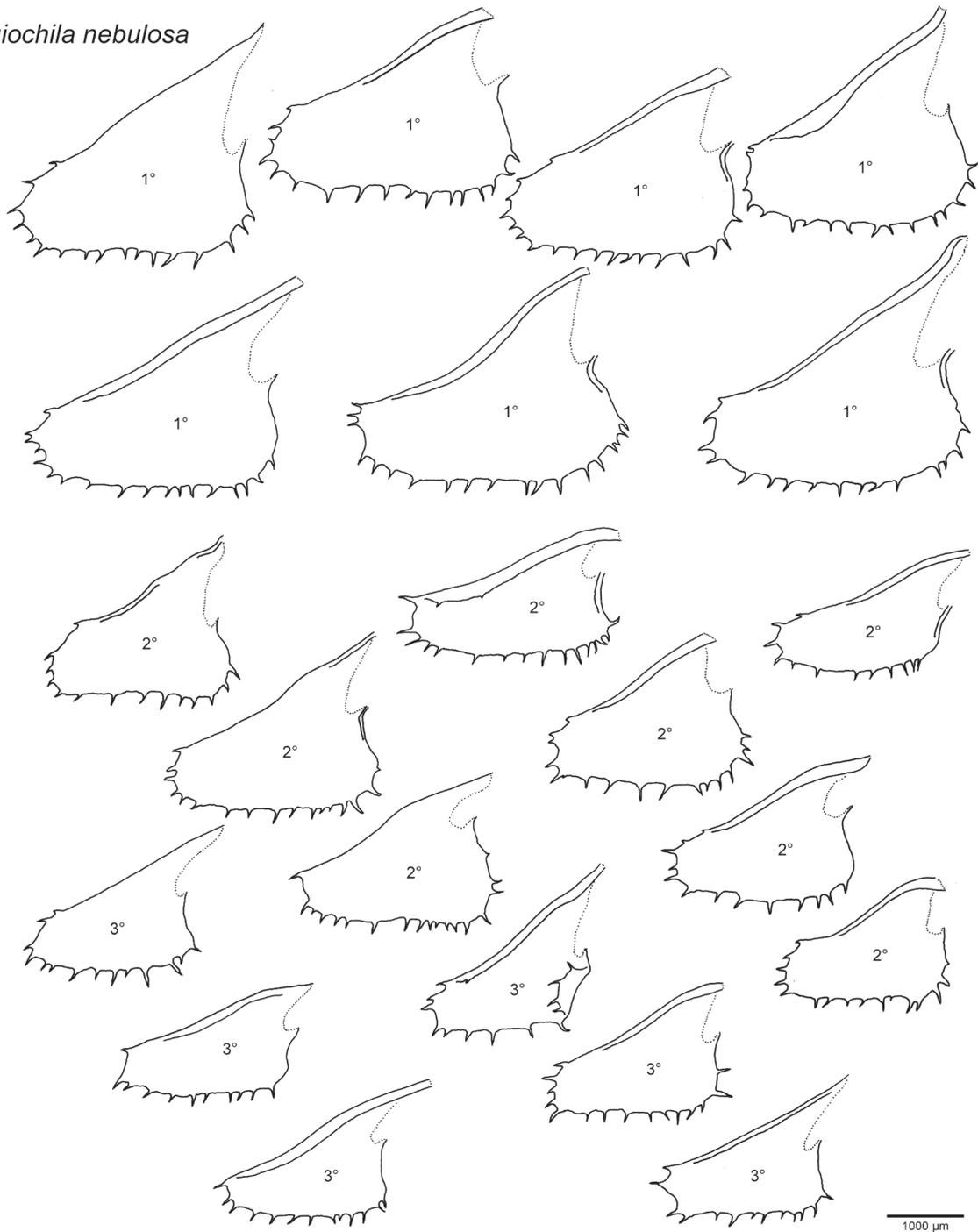
**Distribution and ecology:** *Plagiochila nebulosa* is currently known with certainty only from Australia, where it is confined to the Wet Tropics Bioregion of north-eastern Queensland, from the Windsor Tableland in the north to Tully Falls in the south. Within this region *P. nebulosa* inhabits tropical montane rainforests above 800 m elevation, and most collections have been made above 1000 m elevation. *Plagiochila nebulosa* may grow as an epiphyte, for example on saplings or on buttresses of large trees, or as a lithophyte on granite boulders, in both cases *P. nebulosa* is usually found in association with permanent waterways.



**Fig 57.** *Plagiochila nebulosa*. A: six teeth from the leaf margin. B: leaf marginal cells. C: dorsal view of primary and secondary shoot sector. D: medial leaf cells. E: basal leaf cells. F: ventral view of primary and secondary shoot sector. G: ventral view of secondary shoot. H: ventral view of tertiary shoot. I: dorsal part of transverse section through stem from primary shoot. All from *M.A.M. Renner 7112 & T.C. Wilson (NSW 852994)*.



**Fig 58.** *Plagiochila nebulosa*. A: three teeth from the perianth mouth. B: ventral view of gynoecia and perianth bearing shoot sector. C: three female bracts. D: dorsal view of male bract. E: ventral view of male bract. F: perianth mouth. G: three perianths in lateral view. All from *M.A.M. Renner 7112 & T.C. Wilson (NSW 852994)*.

*Plagiochila nebulosa*

**Fig 59.** *Plagiochila nebulosa* leaves, all from M.A.M. Renner 7112 & T.C. Wilson (NSW 852994).

**Representative specimens examined: Australia: Queensland:** Cook: Windsor Tableland, 39 km NW of Mossman, 16°16'S 145°04'E, 1080 m, 26 Jun 1984, *H. Streimann* 29669 (CANB 8407840); *ibid.*, *H. Streimann* 29666 (CANB 8407837); Windsor Tableland, 38 km NW of Mossman, 16°17'S 145°04'E, 1140 m, 26 Jun 1984, *H. Streimann* 29726 (CANB 8407897); Windsor Tableland, 38 km NW of Mossman, 16°17'S 145°04'E, 1100 m, 26 Jun 1984, *H. Streimann* 29731 (CANB 8407901); Lamb Range, near Mt Haig, 20 km SE of Mareeba, 17°05'S 145°35'E, 1100 m, 25 Oct 1995, *H. Streimann* 57648 (CANB 9607012); *ibid.*, *H. Streimann* 57651 (CANB 9607015); *ibid.*, *H. Streimann* 57657 (CANB 9607021); Kauri Creek, Mt Haig Road, Lamb Range, 22 km NE of Atherton, 17°08'S 145°36'E, 800 m, 27 Jun 1984, *H. Streimann* 29872 (CANB 8408227); *ibid.*, *H. Streimann* 29877 (CANB 8408232); *ibid.*, *H. Streimann* 29886 (CANB 8408241); North Kennedy: Mount Hypipamee National Park, Dinner Creek Falls, 17°24'53"S 145°30'19"E, 1130 m, 31 May 2014, M.A.M. Renner 7065 & T.C. Wilson (NSW 858929); *ibid.*, M.A.M. Renner 7073 & T.C. Wilson (NSW 858918); Tully Falls National Park, Tully Falls Road, Charmillan Creek, 17°42'03"S 145°31'26"E, 1000 m, 31 May 2014, M.A.M. Renner 7080 &

T.C. Wilson (NSW 858912); *ibid*, M.A.M. Renner 7084 & T.C. Wilson (NSW 858913); *ibid*, M.A.M. Renner 7094 & T.C. Wilson, (NSW 858914); North Kennedy, Tully Falls National Park, Tully Falls Road, track to Rhyolite Pinnacle from Charmillan Creek, 17°42'20"S 145°32'48"E, 1005 m, 1 Jun 2014, M.A.M. Renner 7114 & T.C. Wilson (NSW858921).

***Plagiochila queenslandica*** Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 600 (1904) = Species Hepaticarum 2: 451 (1904)

*Type citation*: Queensland (Bailey); New-South Wales (Camara, Shaw, Stephen Johnson, Watts, F. v. Müller).

*Type*: Queensland, Mt Bartle Frere, 3000', 1891, *Stephen Johnson*, ex herb. Melbourne (lectotype designated here: G 00061508! isolectotypes: sub *P. pendula* Hampe BM! MEL 1039468!); residual syntypes: Queensland, Bellenden ker District, 1889, *F.M. Bailey* (?665), (G 00061511! BM!); Queensland, Bellenden ker Range, *F.M. Bailey* ex herb. Brotherus 659 p.p. (G 00061510!); Port Denison, *Shaw*, sub *P. pendula* Hampe ms, Gottsche dedit, (G 00061514! BM! MEL 1039470!); Mt Elliot, (?) *F. Muller*, ex herb. Melbourne, olim *Plag. pendula* Hampe ms, (G 00061515! BM! MEL 103946!).

= *Plagiochila pendula* Hampe ex Gottsche, Fragmenta Phytographiae Australiae 11, suppl. 4: 55 (1880) *nom. inval.*

*Type citation*: Australia Gottsche Icon. Hep. ined., Mount Elliot, Fitzalan (Port Denisson, leg. Shaw; Tweed River, leg. Camara)

**Notes**: Stephani's protologue describes a plant with imbricate ovate leaves bearing 11 or 12 teeth on the postical margin and around the apex, and bearing a perianth with densely spinose mouth. Stephani's protologue incorrectly cites Stephen Johnson as two separate collectors, and lists his collections as originating in New South Wales, in fact they were collected in Queensland. Inoue (1986) designated as lectotype of *P. queenslandica* a specimen from the Bellenden River Range held in NY, unfortunately no such specimen is held in NY. One specimen annotated "*Plag. queenslandica* St. nsp." by Stephani was collected by Robinson on Norfolk Island, however, neither the collector nor the locality were mentioned in the protologue of *P. queenslandica*, so this specimen is not a primary syntype, even though it was probably seen by Stephani before *P. queenslandica* was published. The plant contained in this specimen matches neither the protologue nor the other syntypes because the leaves bear only three or four small triangular teeth around their apex, not 6 or 7 teeth on the postical margin and another 5 around the apex, and do not have an ampliate base. The Norfolk Island plant also bears copious propagules on the ventral leaf surface, which all other syntypes, though asexual reproductive devices or lack thereof are not mentioned in the protologue. The plant in the Robinson specimen is *P. paucidens*.

Notes on the syntypes:

- 1) Queensland, *F.M. Bailey* (?161) G 00061513 is *P. nebulosa*. The leaves do not have an ampliate base, and the leaves are remote to contiguous when dry. The plant is female.
- 2) Queensland, Mt Mistake, *F.M. Bailey* (?116) G 00061509 is also *P. nebulosa*.
- 3) Queensland, Mt Bartle Frere, 3000', 1891, *Stephen Johnson*, ex herb. Melbourne G 00061508 is the same entity as the remaining unexcluded syntypes, but has leaves whose teeth are generally not so prominent as in others, which are a better match for the protologue. The specimen is a single mixed gathering of male and female plants.
- 4) Queensland, Bellenden Ker District, 1889, *F.M. Bailey* (?665), G 00061511 agrees with the protologue, is female, but there is not much material. 665 may be the Brotherus herbarium number, as other Bailey specimens bearing the same number series have this recorded as the number's source.
- 5) Queensland, Bellenden Ker Range, *F.M. Bailey* ex herb. Brotherus 659 p.p. G 00061510 female, a range of shoots separated out. This plant is in full agreement with protologue for sterile and female description.
- 6) Australia, Port Denison, *Shaw*, sub *P. pendula* Hampe ms, Gottsche dedit, G00061514. In full agreement with protologue for sterile and female description, relatively copious and intact collection including basal plant parts, unlike G 00061510.
- 7) Australia, Mt Elliot, (?) *F. Muller*, ex herb. Melbourne, olim *Plag. pendula* Hampe ms, G00061515! is in good agreement with protologue, female.

Among the type specimens cited for *Plagiochila pendula* the Mt Elliot specimen is *P. queenslandica*; the Tweed River specimen is *P. paucidens*.

Part of the evidence considered by So (2000) when she synonymized *P. queenslandica* with *P. metcalffii* was Stephani's misidentification of *Watts* 584 from the north coast of NSW as *P. queenslandica*. So also concluded that this specimen was *P. metcalffii*, when in fact it is *P. meridionalis*.

**Etymology:** *Queenslandica* named for the Queensland, whence the syntypes were collected.

**Description:** Plants with pseudodichotomously branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 40 mm long and 40 mm wide, tri-quadrimorphic; primary shoots 2.8–3.2 mm wide, secondary shoots c. 2.0–2.8 mm wide; branches arising by *Frullania*-type branching, lateral-intercalary vegetative branching rare, from primary or secondary shoots; ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; reddish-brown, in primary shoots to 500 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 6 to 8 layers, cortical cell walls strongly and continuously thickened, all walls including free external wall thickened to same degree, all cortical cells smaller than medulla cells; medulla cell walls faintly yellow-pigmented, walls with small triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, strongly ventrally secund when dry, on primary shoot leaves asymmetrically broadly triangular ovate, 1250–18750 µm long × 900–1600 µm wide, dorsal margin straight or arched, apex rounded to truncate, ventral margin straight to arched in outer two thirds, and curved and ampliate at base; with 7–21 sharp triangular teeth distributed around the apex and along ventral margin, evenly sized and spaced, basal part of ampliate margin usually without teeth, dorsal margin entire; teeth two to four cells broad at base, cells oblong, capped by an oblong-triangular cell with obtuse apex; secondary shoot leaves asymmetrically triangular-ovate, 800–1550 µm long × 650–1300 µm wide, with 6–21 teeth; tertiary shoot leaves smaller again; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to oblong, 10–18 µm long × 7–14 µm wide, long axis parallel to leaf margin, walls with cordate to bulging trigones, trigones sometimes confluent, walls with or without continuously thickened; medial leaf cells isodiametric to ovoid, 14–19 µm long × 10–15 µm wide, walls yellow-brown pigmented, with cordate to bulging trigones, medial thickenings rare; cells in leaf base polyhedral to long and slightly sinuous oblong, 21–41 µm long × 12–20 µm wide walls with bulging trigones, medial thickening present or absent, some walls continuously thickened, trigones sometimes confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction by leaf-borne cladia produced from the ventral surface of leaf cells.

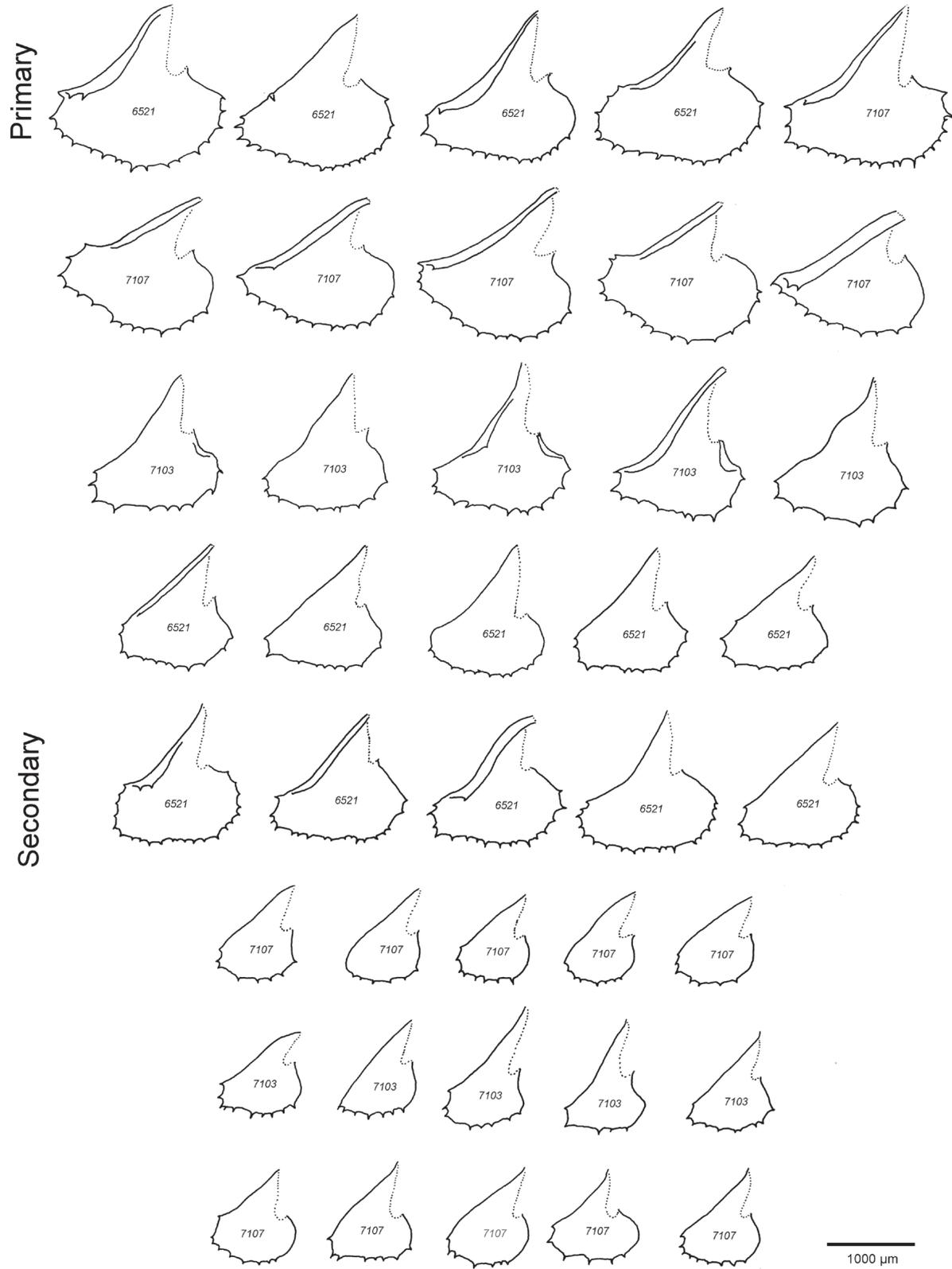
Diocious. Androecia intercalary on secondary, tertiary, or quaternary shoots that continue vegetative growth, usually in opposing pairs produced by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 4–8 pairs, imbricate, closely packed, bract-lobe spreading, reduced and much smaller than adjacent leaves, rounded, entire, epistatic, bract margin broadly rounded, weakly ampliate, entire; stem among bracts smooth. Gynoecia at apices of shoots; bracts triangular-ovate to ovate, 2000–2500 µm long and 1400–2200 µm wide; dorsal margin straight to shallowly curved, inrolled, apex rounded, ventral margin straight in outer half and ampliate at base; dorsal margin, apex and ventral margins all with short triangular teeth, evenly sized and spaced; bract cells as for leaf cells; cell surfaces smooth; female bracteole present. Subfloral innovations present, one or two produced by lateral-intercalary branching from between the female bracts. Perianth transversely obtriangular, to 2000–2200 µm long and 2500–3000 µm wide at mouth, dorsal keel with a wing along its whole length, but presence of this wing is variable, and it may be present or absent on different perianths of same individual, e.g. CANB 8407255; with a few triangular teeth around the apex, ventral keel not winged; laterally compressed but with an inflated base, lateral walls plane; labia curved, each with around 25 to 35 triangular-acuminate teeth. Fig. 60.

**Recognition:** *Plagiochila queenslandica* can be recognized by the combination of bronze-green colour, pseudodichotomous vegetative branching, the imbricate and transversely orientated ovate-triangular leaves with a broad ampliate base and have 7–21 triangular teeth evenly distributed around the apex and along the ventral margin, and the broadly obtriangular perianth whose labia bear numerous triangular-acuminate teeth.

The characteristic growth habit, wherein plants form intricately branched dense wefts from twigs and branches is fairly distinctive and this in combination with the transversely inserted and oriented, densely imbricate leaves, that roll and become strongly ventrally secund when dry impart *P. queenslandica* a distinctive field aspect.

*Plagiochila queenslandica* could be confused with any number of other *Plagiochila* species but the leaf shape and dentition are sufficient basis for identification, so long as leaves are dissected from primary shoots, and examined on slides after they have been hydrated and flattened under a cover-slip.

*Plagiochila queenslandica*



**Fig 60.** *Plagiochila queenslandica* leaves, from M.A.M. Renner 6521, E.A. Brown & V.C. Linis (NSW 898761), M.A.M. Renner 7107 & T.C. Wilson (NSW 852980), and M.A.M. Renner 7103 & T.C. Wilson (NSW 858831).

**Distribution and Ecology:** *Plagiochila queenslandica* is known from north-east Queensland, where it is an epiphyte, or occasionally a lithophyte, mostly in tropical montane forest above 600 m elevation from the Big Tableland and Mt Finnegan in the north to the Paluma Range in the south. *Plagiochila queenslandica* occupies a range of rainforest types including mesophyll and notophyll rainforest, and microphyll-vine thickets, on both ridges and in gullies. It grows anywhere on trees so long as exposed to high light levels. In tall closed rainforests *P. queenslandica* is typically an epiphyte within the canopy on upper branches and twigs. In riparian forests alongside streams *P. queenslandica* may grow on low branches and trunks of trees, shrubs and palms. On the edge of other openings in the rainforest canopy, such as roadsides, *P. queenslandica* may grow on low-hanging branches and shrubs. *Plagiochila queenslandica* has been reported from Papua New Guinea, but all records are based on misidentifications of other species.

**Representative specimens examined: Australia: Queensland:** Cook: Big Tableland, 26 km S of Cooktown, 15°43'S 145°16'E, 580 m, 11 Dec 1990, J.A. Curnow 3936 (CANB 9500720); Big Tableland, 26 km S of Cooktown, 15°43'S 145°16'E, 610 m, 4 Jul 1984, H. Streimann 30797 (CANB 781986); Cedar Bay National Park, 39 km S of Cooktown, Mt Finnegan, track to Mt Finnegan, 15°49'S 145°16'E, 880 m, 20 Oct 1995, H. Streimann 57100 (CANB 9519243); *ibid.*, H. Streimann 57101 (CANB 9519244); Daintree National Park, Mount Sorrow, vicinity of summit, 16°04'36"S 145°26'25"E, 718 m, 21 May 2014, M.A.M. Renner 6990 & T.C. Wilson (NSW 858978); Daintree National Park, between Thornton Beach and Noah Creek, 16°09'04"S 145°26'28"E, 5 m, 25 Mar 2012, M.A.M. Renner 6330, V.C. Linis & E.A. Brown (NSW 896728); Mount Lewis National Park, Mount Lewis, Leichhardt Creek, Mount Lewis Road bridge, 16°35'30"S 145°16'26"E, 950 m, 27 Mar 2012, M.A.M. Renner 6334, V.C. Linis, & E.A. Brown (NSW 896736); Lamb Range, 21 km NE of Atherton, 17°07'S 145°35'E, 1180 m, 27 Jun 1984, H. Streimann 29793 (CANB 8407964); North Kennedy: Barron State Forest, Herberton Range, 13 km S of Atherton, 17°23'S 145°37'E, 1000 m, 2 Mar 1983, H. Streimann 27203 (CANB 8303004); Mount Hypipamee National Park, Dinner Creek Falls, 17°24'53"S 145°30'19"E, 1130 m, 31 May 2014, M.A.M. Renner 7068 & T.C. Wilson (NSW 858979); Boonjie State Forest, 22 km SE of Yungaburra, 17°24'S 145°45'E, 600 m, 4 Mar 1983, H. Streimann 27608 (CANB 8305650); North Kennedy, Tully Falls National Park, Tully Falls Road, Charmillan Creek, 17°42'03"S 145°31'26"E, 1000 m, 31 May 2014, M.A.M. Renner 7102 & T.C. Wilson (NSW 858930); Wooroonooran National Park, South Johnston River catchment, Maple Creek, Maple Creek Road, 17°42'18"S 145°41'42"E, 750 m, 5 Apr 2012, M.A.M. Renner 6521, E.A. Brown & V.C. Linis (NSW 898761); Tully Falls Road, 18 km SE of Ravenshoe, 17°46'E 145°33'E, 760 m, 23 Jun 1984, H. Streimann 29127 (CANB 8407225); Tully Falls National Park, Tully Falls Road, track to Rhyolite Pinnacle from Charmillan Creek, 17°42'40"S 145°33'12"E, 1085 m, 1 Jun 2014, M.A.M. Renner 7107 & T.C. Wilson (NSW 852980); Tully Falls National Park, Tully Falls Road, track to Rhyolite Pinnacle from Charmillan Creek, 17°42'20"S 145°32'48"E, 1005 m, 1 Jun 2014, M.A.M. Renner 7115 & T.C. Wilson (NSW 858953); North Kennedy, Tully Falls National Park, Tully Falls Road, Charmillan Creek, 17°42'03"S 145°31'26"E, 1000 m, 31 May 2014, M.A.M. Renner 7103 & T.C. Wilson (NSW 858831); Tully Falls, 18 km SE of Ravenshoe, 17°47'S 145°34'E, 720 m, 1 Mar 1983, H. Streimann 27089 (CANB 8302843); Echo and Davidson Creeks divide, Cardwell Range, 46 km SE of Ravenshoe, 17°59'S 145°40'E, 780 m, 23 Jun 1984, H. Streimann 29080 (CANB 8407208); Blue Water Creek, Old Mill Road, 39 km WSW of Ingham, 18°45'S 145°48'E, 600 m, 19 Jun 1984, H. Streimann 28417 (CANB 8406227).

Representative misidentified specimens

*Plagiochila* sect. *Vagae* sp. indet.

Papua New Guinea, Simbu Province, Dirima Mission, 2km NW of Gumine, 1800 m, 6°11'S 144°55'E, Dec 1983, M. Tola 168 (CANB 8901013); *ibid.*, M. Tola 214, (CANB 8901051); *ibid.*, M. Tola 230 (CANB 8901067); *ibid.*, M. Tola 231, (CANB 8901068); *ibid.*, M. Tola 237 (CANB 8901074); Southern Highlands, Lai River, Mendi-Tari Road, 15 m SSE of Mendi, 1500 m, 6°19'S 143°38'E, 3 July 1982, H. Streimann 22164 (CANB 8403054).

***Plagiochila teysmannii*** Sande Lac., Synopsis Hepaticarum Javanicarum: 12 (1857)

Type citation: *n.v.*

Type: Java, *Teymann*, in herb. Dozy & Molck., isotype (So & Grolle 1999): ex herb. Sande Lacoste (G 00260068!) = *Plagiochila aberrans* Schiffn., Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien. Mathematisch-Naturwissenschaftliche Klasse 70: 168 (1900)

Type citation: Sumatra occid.: In monte Singalang; in silvis primaevae ad latus austro-orient. ad arbores. Regio nubium, alt. 2090 m, s. m. – 25. 7. 1894 (c. per.) (No. 880).

Type: Sumatra occid.: In monte Singalang; in silvis primaevae ad latus austro-orient. ad arbores. Regio nubium, alt. 2090 m, 25. 7. 1894, V Schiffner, *Iter Indicum 1893/94 No 880* (holotype: FH 00458026!)

=*Plagiochila fraseri* Steph., Bulletin de l'Herbier Boissier, sér. 2 3: 886 (1903) = Species Hepaticarum 2: 371 (1903)

Type citation: Birma superior (Fraser).

Type: Myanmar. Upper Burma, Jan 1896, Fraser, comm. Brotherus (G 00661401!)

=*Plagiochila latiflora* Schiffn., Die Hepaticae der Flora von Buitenzorg: 119 (1900)

Type citation: n.v.

Type: Sumatra occid., in monte Singalang, in region inferior in silva primaeva ad arbores, 1400-1500 m, 26 Jul 1894, V. Schiffner Iter Indicum 1893/94 No. 842 (syntype: G 00260066!)

=*Plagiochila multifurcata* Steph., Bulletin de l'Herbier Boissier, sér. 2 4: 600. 1904 = Species Hepaticarum 2: 451 (1904)

Type citation: Australia, Queensland (Bailey)

Type: Australia, Queensland, Bellenden ker District, 1889, F.M. Bailey 659, (lectotype designated by Inoue (1986): G 0061484!)

=*Plagiochila riddleana* Steph., Journal and Proceedings of the Royal Society of New South Wales 48: 129 (1914)

Type citation: Novae Hebridae (Epi): Riddle legit (Watts, 21).

Type: New Hebrides, Epi, 2000 ft, 21 Jan 1911, T.E. Riddle ex herb. Watts 21 (G 00061485!)

=*Plagiochila vagans* Steph., Species Hepaticarum 6: 237 (1921)

Type citation: Nova Caledonia (Franc legit)

Type: New Caledonia, Mt Kohgis, 1 Nov 1909, Franc (G 00061486!)

**Notes:** The isotype of *Plagiochila teysmannii* in G is a single shoot sector between mica sheets. The leaves bear close-set teeth around the postical margin and apex, but not on the antical margin in all but one leaf, which bears four teeth on the outer half of the antical margin. The leaf shape seems to differ from the Australian plants, in that the apex is broadly rounded because the antical and postical margins are nearly parallel. In the Australian plants the apex is narrowly rounded because the antical and postical margins are inclined at between 30 and 45°.

The type of *Plagiochila fraseri* in G consists of two shoot systems, one of which is ramified by pseudodichotomous *Frullania*-type branches into a shoot system comprising three orders of shoots, with androecia intercalary within the third order. The other is an unbranched portion of primary shoot. These both differ from Australian individuals in the production of orbicular, nearly entire leaves near the base of primary shoots, and in the size and dentition of normal leaves in mid-sectors of primary shoots. The leaves on all shoot orders bear something like half as many teeth, and the dorsal leaf margin, though inrolled, is entire or nearly so. The relationship between plants represented by the type of *P. fraseri* and other members of the *P. teysmannii* complex warrants further investigation.

The syntype of *P. latiflora* seen is not a good match with the type of *P. teysmannii* in its larger size, sparser teeth on the postical leaf margin and longer teeth around the apex, particularly on leaves from secondary shoots. The relationship between the plants represented in these types requires further investigation.

The type of *P. multifurcata* exhibits all of the distinctive vegetative features of Queensland plants, the leaves have antical and postical margins inclined and the dorsal margin is inrolled and bears teeth along its entire length.

The type of *P. riddleana* is a reasonable match with the Australian plant and the type of *P. teysmannii* in that the leaves are rectangular-ovate with a broadly truncate apex, the postical leaf margin is plane and entire, not reflexed and toothed. Branching within the type of *P. riddleana* approaches pseudodichotomous; while the parent shoot is offset slightly, it retains dominance and size differentiation.

The type of *Plagiochila vagans* comprises several shoot systems where unbranched leafy axes arise from a basal creeping stolon arising by lateral-intercalary branches. The leaves are oblong, with a broadly obtuse apex and ciliate teeth around the apex and postical margin, but not on the antical margin. The plants are a reasonable match with the type of *P. teysmannii*. The plants do not appear to bear propagules.

**Etymology:** After Johannes Elias Teijsmann (1809-1882), Dutch botanist who collected the type.

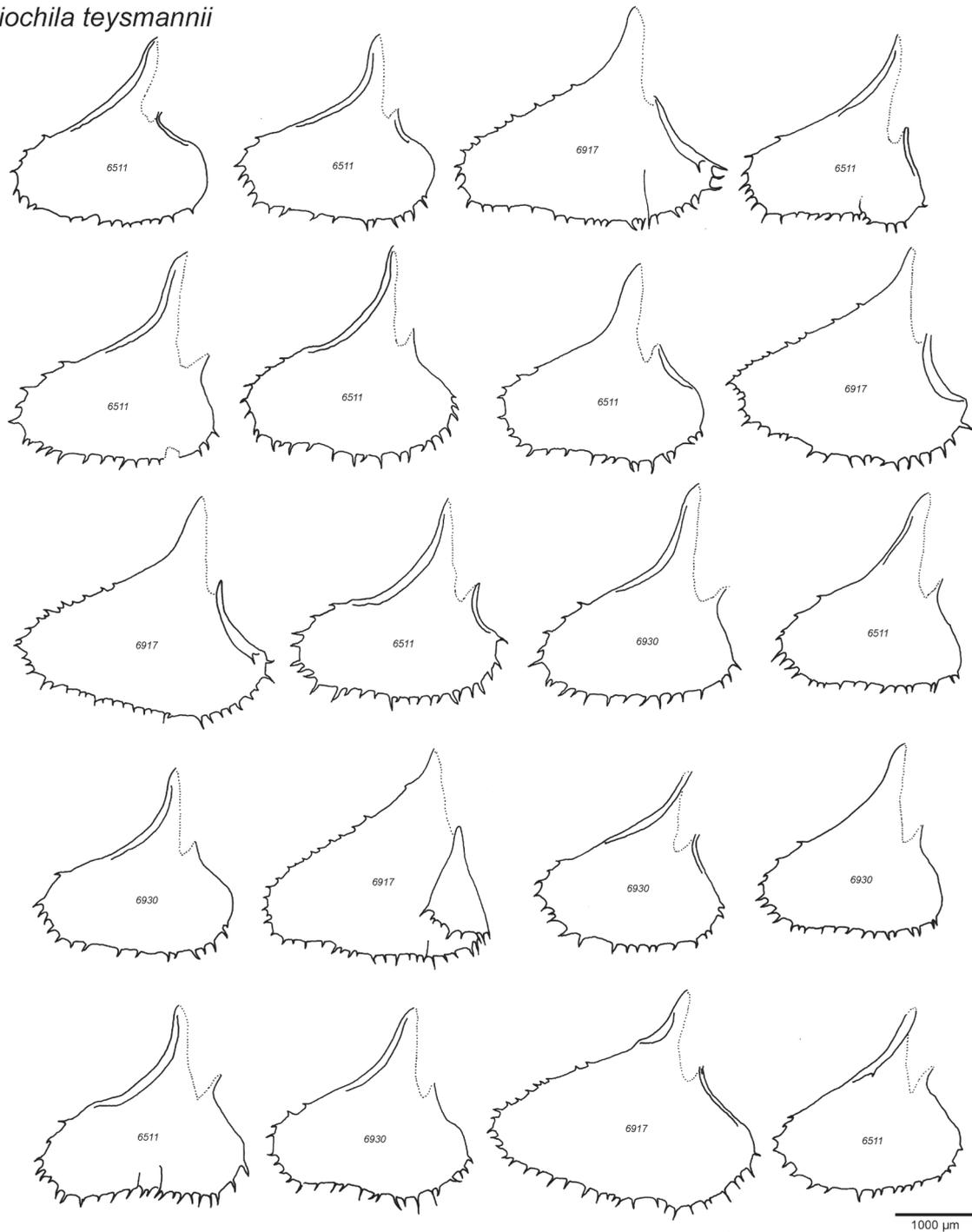
**Description:** Plants with pseudodichotomously branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 90 mm long and 50 mm wide, trimorphic; primary shoots 4.5–5.5 mm wide, secondary shoots smaller; branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 700 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 to 7 layers, fewer layers laterally, cortical cell walls strongly and continuously thickened, all walls including free external wall thickened to same degree, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, walls with triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves oblong-triangular, 2160–2810 µm long × 1730–1930 µm wide, dorsal margin straight or arched, often undulate at base, apex rounded, ventral margin straight to arched in outer two thirds, and curved and ampliate at base; with 15–40 sharp triangular teeth distributed around the apex and along ventral margin, sometimes along the dorsal margin as well, regularly spaced, teeth around the leaf ampliate margin often slightly larger and prominent, dorsal margin entire, teeth two to four cells broad at base, cells oblong, capped by an oblong-triangular cell with obtuse to rounded apex; secondary shoot leaves smaller; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells rectangular, 16–31 µm long × 9–17 µm wide, long axis parallel to leaf margin, walls with bulging to nodulose trigones, some walls continuously thickened; medial leaf cells isodiametric to ovoid, 17–39 µm long × 17–28 µm wide, walls yellow-pigmented, with bulging trigones, medial thickenings rare, cells in leaf base polyhedral to oblong, 28–72 µm long × 16–27 µm wide walls with bulging to nodulose trigones, medial thickening present or absent, some walls continuously thickened, trigones sometimes confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction by leaf-borne cladia produced from the ventral surface of leaf cells, but not present in all shoots or individuals.

Diocious. Androecia not seen. Gynoecia at apices of shoots; bracts oblong-ovate, 3500–4100 µm long and 1800–2200 µm wide; dorsal margin arched, revolute, apex narrowly rounded, ventral margin shallowly curved in outer two thirds, broadly and conspicuously ampliate at base, margins with a few long undulations; dorsal margin, apex and ventral margins with around a total of 50 spinose-ciliate teeth, evenly distributed and more or less evenly sized, slightly longer around ampliate base; bract cells as for leaf cells; cell surfaces smooth; female bracteole present, small, with ciliate lobes. Subfloral innovations present, or one or two produced by lateral-intercalary branching from between the female bracts and the perianth, or between the female bract and the preceding leaf. Perianth campanulate, to at least 2000 µm long and 2000 µm wide at mouth (only immature perianths seen), dorsal keel with a broad wing along its whole length, with a few lacinate teeth around the wing apex, ventral keel unwinged; laterally compressed but with an inflated base, lateral walls plane; labia curved, each with around 25–30 lacinate teeth. Fig. 61.

**Recognition:** *Plagiochila teysmannii* can be recognized by the pseudodichotomously branched shoots with *Frullania*-type vegetative branching -- characters that place the species within sect. *Vagae* -- and by the large shoot stature with primary shoots 4.5–5.5 mm wide, and the oblong-triangular leaves bearing 15–40 sharp triangular teeth distributed around the apex and along ventral margin. In stature, only *P. minax* approaches *P. teysmannii* among Australian species of sect. *Vagae*. For characters differentiating these two species see the recognition section of *P. minax*, below.

**Distribution and Ecology:** *Plagiochila teysmannii* has been recorded from Java, Papua New Guinea, Vanuatu, Fiji, Tahiti, New Caledonia and Australia (So 2000). In Australia *P. teysmannii* is known from a few localities within in the Wet Tropics Bioregion of north-east Queensland, in rainforests at low to moderate elevation, up to around 650 m. *Plagiochila teysmannii* has been collected as a twig and branch epiphyte in riparian vegetation alongside permanent streams, where scattered individuals form conspicuous, large pendants among luxuriant bryophyte wefts dominated by a range of species including *Frullania* and other *Plagiochila* species, particularly on hosts adjacent to waterfalls.

**Representative specimens examined:** Australia, Queensland, 1889, *F.M. Bailey* ?660 ex herb. Stephani (BM 00671204); Bellenden Ker Range, 1889, *F.M. Bailey* ex herb. Pearson as *P. teysmannii* (BM); Wooroonooran National Park, South Johnston River catchment, Maple Creek, 17°40'59"S 145°42'10"E, 590 m, 5 Apr 2012, *M.A.M. Renner* 6511, *E.A. Brown* & *V.C. Linis* (NSW 898713); *ibid.*, *M.A.M. Renner* 6512, *E.A. Brown* & *V.C. Linis* (NSW 898722); North Kennedy, Tully Gorge National Park, Cochable Creek catchment, Cannabullen creek walking track, Whispy Falls, 17°43'34"S 145°37'22"E, 234 m, 11 May 2014, *M.A.M. Renner* 6917 & *T.C. Wilson* (NSW 855511); *M.A.M. Renner* 6930 & *T.C. Wilson*.

*Plagiochila teysmannii*

**Fig 61.** *Plagiochila teysmannii* leaves, from M.A.M. Renner 6917 & T.C. Wilson (NSW 855511) and M.A.M. Renner 6511, E.A. Brown & V.C. Linis (NSW 898713), and M.A.M. Renner 6930 & T.C. Wilson (NSW).

## Misidentified specimens

*Plagiochila fasciculata*

Australia: New South Wales, Rutherford Creek 11 km SE of Nimmitable, 36°34'S 149°36'E, 850 m, 19 Feb 1982, H. Streimann 16711 (CANB 8212670).

**Excluded from synonymy of *P. teysmannii*:**

***Plagiochila semialata*** Sande Lac., Nederlandsch Kruidkundig Archief. Verslagen en Mededelingen der Nederlandsche Botanische Vereeniging 4: 93 (1856)

*Type citation:* Habitat insulam *Javae*, Jungh.

*Type:* Java. leg. Junghuhn, ex herb. Sande Lacoste (G 00265228!)

This plant has lacinate-dentate teeth on the upper part of the ampliate base and on the postical leaf margin. The antical margin is straight and untoothed. The type is however, a single shoot fragment, fairly damaged, so leaves from it have not been drawn. In its leaf shape and dentition the individual preserved in the type specimen is unlikely to belong to the same species as *P. teysmannii* and further investigation to clarify the identity and relationships of *P. semialata* is warranted.

***Plagiochila truncatula*** Sande Lac., Annales Musei Botanici Lugduno-Batavi 1: 290 (1864)

*Type citation:* Sumatra et Borneo. Korthals.

*Type:* Sumatra, *Korthals*, Sande misit 1880/82 (isosyntype: G 00128798!) Borneo, *Korthals*, Sande misit 1880/82 (isosyntype: G 00128797!)

=*Plagiochila oblongata* Sande Lac., Annales Musei Botanici Lugduno-Batavi 1: 291 (1864)

*Type citation:* Java, in m. Simpai: Korthals.

*Type:* Java, *Korthals* (isosyntype: G 00282164!)

**Notes:** The plants comprising the types of *Plagiochila truncatula* and *P. oblongata* are the same morphological entity. The Bornean isosyntype of *P. truncatula* has oblong leaves with no ampliate interior that runs onto a low decurrent wing on the ventral stem surface. The leaves separate either side of the ventral stem surface, which is thereby visible in ventral view. Teeth on the leaf margins are restricted to the apex and the ventral margin, there are none on the dorsal margin and none on the interior margin. The dorsal margin is weakly recurved, the others are plane. The shoot system is repeatedly ramified, branches are weakly pseudodichotomous and four orders of shoot are present. The Sumatran syntype is the same plant, if anything the leaves are more truncate at their apex.

These plants differ from the type of *P. teysmannii* in leaf shape and dentition, notably in the absence of an ampliate base to the leaf, and in the narrow ovate-oblong leaves that may have a truncate apex. These morphological differences suggest the plants represented in the respective types do not belong to the same species and further investigation to clarify their relationships is warranted.

***Plagiochila acutifolia*** Steph., Species Hepaticarum 6: 119 (1917)

*Type citation:* Australia. Norfolk Island. (Robinson legit)

*Type:* Australia orientalis, insula Norfolk, 1889, *Robinson*, ex herb. Melbourne and ex herb. Jack (lectotype designated by Bonner (1962): G 00064072!)

=*Plagiochila wattsiana* J.J.Engel & G.L.Merr., Nova Hedwigia 92: 511 (2010) *syn. nov.*

Replaced synonym: *Plagiochila watsii* Steph. Species Hepaticarum 6: 240 (1921) *non Plagiochila watsii* Steph. ex Rodway, Papers and Proceedings of the Royal Society of Tasmania 1917: 105 (1918)

*Type citation:* Australia. New South Wales. (Watts legit).

*Type:* Australia: New South Wales, Richmond River, Pearces Creek, 19 Apr 1900, *W.W. Watts 19* (lectotype designated by Bonner (1962): G! isolectotype: NSW 445574!)

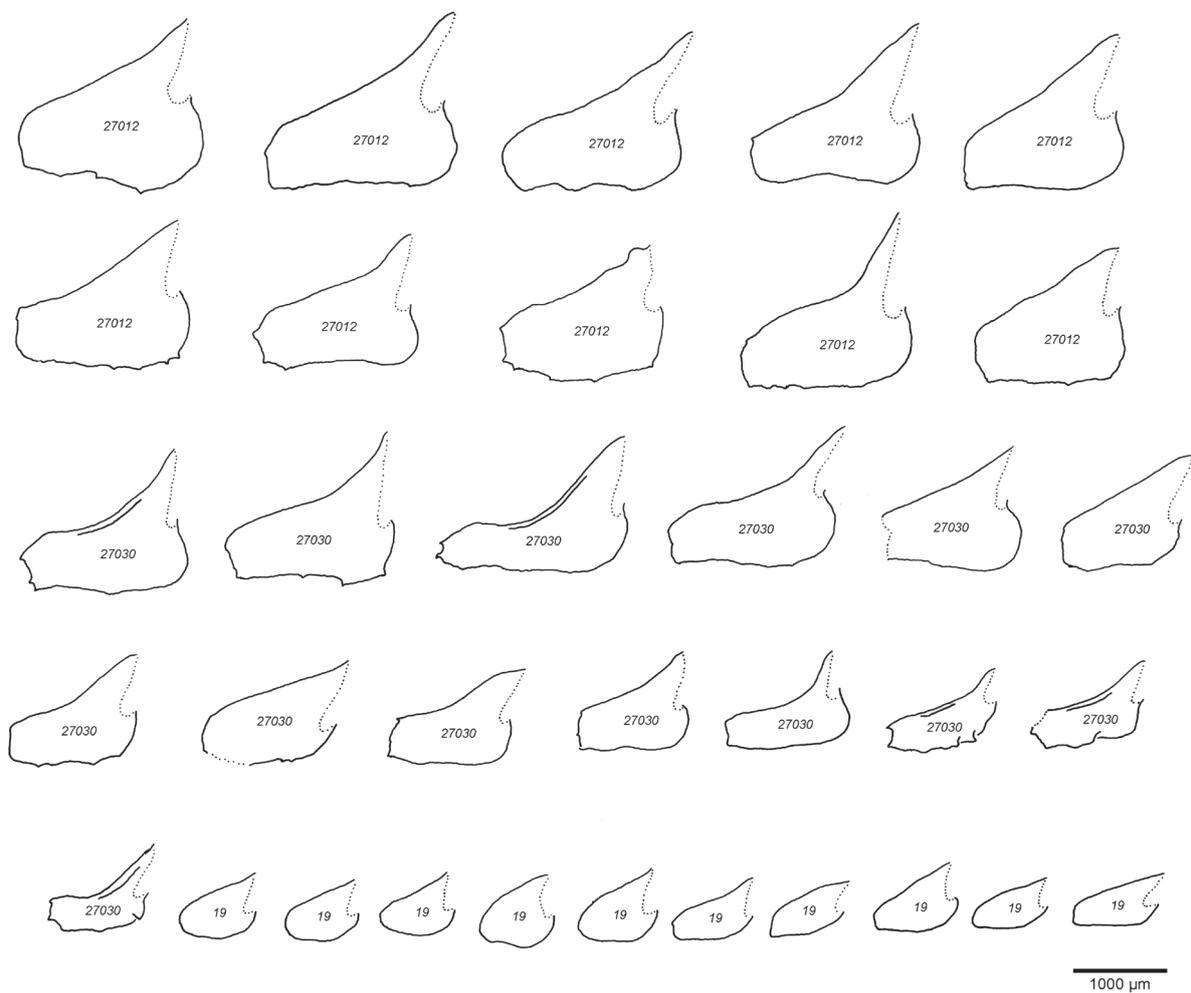
**Notes:** Engel and Merrill (2010a) independently proposed *Watts 19* in G as the lectotype of *P. watsii* Steph.

**Etymology:** acute-leaved, reference unclear.

**Description:** Plants with pseudodichotomously branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 40 mm long and 15 mm wide, dimorphic, usually short and closely branched; primary shoots 2.8–3.5 mm wide, secondary shoots smaller; branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 300 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 2 to 3 layers dorsally, and 3 or 4 layers ventrally, continuously and heavily thickened and red-brown pigmented, thickening even, free external wall not as thickened as internal walls, cortical cells smaller than medulla cells; medulla cell walls unpigmented, unthickened except for small triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector similar to leaves on erect shoots, entire, contiguous, soon fragmenting and disarticulating, leaving stolon bear. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves oblong-triangular, 950–2300 µm long × 570–1500 µm wide, dorsal margin straight or arched, apex

truncate, ventral margin straight in outer two thirds, and curved and ampliate at base; margin sometimes slightly irregular, otherwise entire, without teeth, or in some individuals with two small triangular teeth at the apex only; secondary shoot leaves smaller; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to oblong, 9–17  $\mu\text{m}$  long  $\times$  7–10  $\mu\text{m}$  wide, long axis parallel to leaf margin, cell walls thin with concave trigones, medial thickenings absent; medial leaf cells isodiametric to ovoid, 12–20  $\mu\text{m}$  long  $\times$  10–16  $\mu\text{m}$  wide, cell walls thin with concave trigones, medial thickenings absent; basal cells ovoid to oblong, 16–26  $\mu\text{m}$  long  $\times$  8–17  $\mu\text{m}$  wide, cell walls thin with concave trigones, medial thickenings absent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction by leaf-borne cladia produced from the ventral surface of leaf cells.

Dioicous. Androecia intercalary on secondary shoots that continue vegetative growth, singly or in pairs by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 3–5 pairs, imbricate, closely packed, bract-lobe spreading, smaller than adjacent leaves, entire, epistatic, bract margin broadly rounded, weakly ampliate, entire; stem among bracts smooth. Gynoecea not seen. Fig. 62.



**Fig 62.** *Plagiochila acutifolia* leaves, from *H. Streimann* 27012 (CANB 8302763), *H. Streimann* 27030 (CANB8302781), and *W.W. Watts* 19 (NSW 445574).

**Recognition:** *Plagiochila acutifolia* can be recognized by the yellow-green, pseudodichotomous shoots with *Frullania*-type vegetative branching, the production in some individuals of leaf-borne cladia, the oblong-triangular leaves with a truncate apex, ampliate base, and straight ventral margin with no or few small and obscure triangular teeth. The pseudodichotomous *Frullania*-type vegetative branching are characteristic of *Plagiochila* sect. *Vagae*, from whose species *P. acutifolia* is distinct in the near or complete absence of dentition on the leaf margins. Among Australian species *Plagiochila acutifolia* is similar to *P. paucidens* and is likely to be

confused with this species. However, *P. paucidens* differs from *P. acutifolia* in that the margins of many teeth bear small triangular teeth, though many leaves have entire margins. As entire and toothed-margin leaves may co-occur within individuals it is necessary to examine a range of leaves from several shoots to confirm the presence of marginal teeth on the leaves. These leaves should be dissected from the stem and slide-mounted, to facilitate an assessment of their shape, which also differs from *P. acutifolia*. Whereas in *P. acutifolia* the leaves are oblong-triangular and have a truncate apex and ampliate base, and a straight to shallowly arched dorsal margin, the leaves of *P. paucidens* are oblong-elliptic with a broader apex relative to their length, do not have an ampliate base, and have a shallowly arched to shallowly curved dorsal margin. The significance of these differences requires critical assessment.

**Distribution and ecology:** *Plagiochila acutifolia* is sparsely distributed over a broad range up the eastern coast of Australia from the Atherton Tableland in north-east Queensland, to north-eastern New South Wales, and on Norfolk Island. In Queensland *P. acutifolia* has been collected in rainforests on the Atherton Tableland, and at Kalpower. *Plagiochila acutifolia* is a trunk epiphyte, and forms loose wefts, but does not seem to occur anywhere in great abundance based on the available herbarium specimens.

**Specimens examined: Queensland:** Cook, Curtain Tree Fig, 10 km ESE of Atherton, 17°17'S 145°34'E, 720 m, 1 Mar 1983, *H. Streimann* 27030 (CANB8302781); Scrubby Creek, Wongabel State Forest 5 km SSE of Atherton, 17°18'S 145°30'E, 800 m, 28 Feb 1983, *H. Streimann* 27012 (CANB 8302763); Gadgarra State Forest, 15 km NE of Malanda, 17°18'S 145°47'E, 680 m, 15 Dec 1990, *J.A. Curnow* 4044 (CANB 9500828); North Kennedy, Mt Spec State Forest, Paluma Range, 6 km W of Paluma, 19°01'S 146°09'E, 920 m, 18 June 1986, *J.A. Curnow* 908 (CANB 00781967); Scrub Creek, Kalpower, 30 km NE of Monto, 24°31'S 151°17'E, 400 m, 17 Jan 1980, *H. Streimann* 9919 (CANB 8002462); *ibid.*, *H. Streimann* 9925 (CANB 8002468); **Norfolk Island:** Mt Pitt Road, Norfolk Island National Park, 29°01'04"S 167°56'14"E, 200 m, 27 Apr 1994, *R. Ward* 94-6 (CANB 9507859); Track to Hollow Pine, Mount Pitt Reserve, 29°01'30"S 167°56'15"E, 220 m, 2 Dec 1984, *H. Streimann* 31976 (CANB 00781997); Mt Pitt Road, Mount Pitt Reserve, 29°01'30"S 167°56'15"E, 230 m, 2 Dec 1984, *H. Streimann* 31892 (CANB 00781995); Botanic Gardens, 29°01'35"S 167°56'08"E, 110 m, 20 Apr 1995, *J.A. Curnow* 4872 & *H. Lepp* (CANB 9513841).

***Plagiochila paucidens* Steph.**, Bulletin de l'Herbier Boissier, sér. 2 3: 117 (1903) = Species Hepaticarum 2: 297 (1903)

*Type citation:* Tahiti (Vesco)

*Type:* Tahiti, 1847, *Vesco* (lectotype designated by Bonner 1962: G 00061457!)

= *Plagiochila metcalfii* Steph., Bulletin de l'Herbier Boissier, sér. 2 3: 533 (1903) = Species Hepaticarum 2: 337 (1903)

*Type citation:* Norfolk Insula (*Metcalf*)

*Type:* Australia: Norfolk Island, 1884, *P.M. Metcalfe* 56 (lectotype designated by Bonner 1962: G 00112896!)

= *Plagiochila erectifolia* Steph., Species Hepaticarum 6: 151 (1918)

*Type citation:* New Caledonia (Lerat legit)

*Type:* New Caledonia Montague de Cresnon, ?*Dr L. Le Rat* 411 ex herb. ?Giulrat Paris (lectotype designated by Bonner (1962): G 00064214! [=G-14223])

= *Plagiochila camarae* Steph. ex Dugas, Contribution à l'Étude du Genre *Plagiochila* Dum.: 130 (1928)

*Type citation:* *n.v.*

*Type:* Australia. New South Wales, Tweed River, 1882, *Camara*, hb. Melbourne 61 as *P. paucidens* Steph. (holotype: PC, isotype: M [c. per.] ??ex herb. Stephani BM [c and.])

= *Plagiochila subgedena* Steph., Species Hepaticarum 6: 214 (1921)

*Type citation:* Nova Caledonia (Franc legit)

*Type:* New Caledonia, 1909, *Franc*, ex herb. Thériot 175 (lectotype designated by Bonner 1962: G 00064211!)

= *Plagiochila trigona* Steph. Revue Bryologique 35: 32 (1908)

*Type citation:* none provided, but 'Elles ont été récoltés par M. Le Rat...' in introduction.

*Type:* New Caledonia, Mt. Table, Feb 1907, *Le Rat* 206 ex herb. E.C. Paris (G 00064212!)

**Notes:** *Plagiochila paucidens* was published in February of 1903, *Plagiochila metcalfii* was published in June 1903. The type of *P. metcalfii* is relatively large plant with pseudodichotomous branching, subentire leaves, with few small teeth, as described by Stephani, and manifest in the CANB vouchers, together with copious propagules from the ventral surface of leaves on all shoot orders. The possible type of *P. camarae* agrees in these details, has more teeth and an obtuse leaf apex. *Plagiochila camarae* and *P. erectifolia* are in good agreement.

The type plant of *Plagiochila paucidens* is similar in respects to the type of *P. metcalfii* but differs in its remote leaves that bear around 6 small triangular teeth around the apex and onto the ventral margin.

*Plagiochila subgedena* was synonymized with *P. metcalfii* by Inoue (1970) and So (2000). In *P. subgedena* the leaves are rectangular-ovate and bear numerous small serrate teeth on their postical margin and around their apex. On the apex two teeth may be more prominent than the others. On leaves from secondary shoots there are often two prominent teeth at the apex. Scattered teeth may occur on the antical margin, which is weakly inrolled. No propagules were observed in the type. *Plagiochila trigona* was also synonymized with *P. metcalfii* by So (2000).

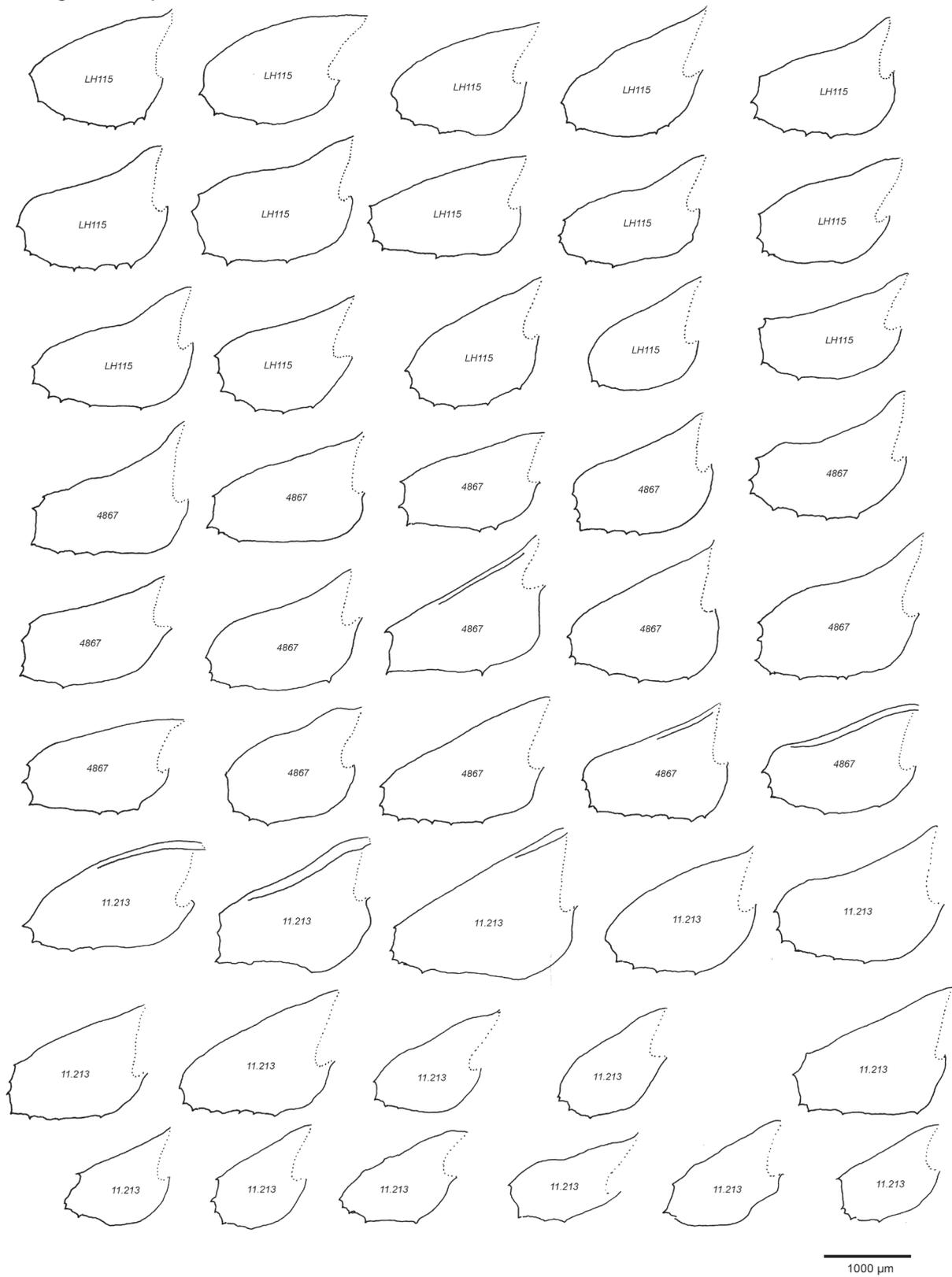
**Etymology:** *paucidens* with few teeth, in reference to the leaves.

**Description:** Plants with pseudodichotomously branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 70 mm long and 60 mm wide, but usually much less than this, trimorphic, shoot systems often slender and openly branched; primary shoots 3.5–4.0 mm wide, secondary shoots c. 2.0–2.7 mm wide; branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; reddish-brown, in primary shoots to 300 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 or 5 layers, continuously and heavily thickened and red-brown pigmented, fading to yellow-brown in innermost layer, thickening even, free external wall not as thickened as internal walls, cortical cells smaller than medulla cells; medulla cell walls unpigmented, unthickened except for small triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves contiguous to imbricate on primary shoots, remote to contiguous on secondary and tertiary shoots, succubously inserted and orientated, on primary shoot leaves oblong-elliptic to oblong ovate, 1450–2000 µm long × 1000–1400 µm wide, dorsal margin straight or arched, apex broadly rounded to truncate, ventral margin straight to curved in outer two thirds, and curved at base but not ampliate; with 2–8 small triangular teeth distributed around the apex and along the outer part of the ventral margin, teeth two to four cells broad at base, cells oblong, capped by a triangular cell with obtuse to rounded apex; secondary shoot leaves oblong-ovate, 1200–1800 µm long × 750–900 µm wide, with 2–5 teeth; tertiary shoot leaves smaller again; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells quadrate to oblong, 8–17 µm long × 6–9 µm wide, long axis parallel to leaf margin, walls with triangular to convex trigones, walls not continuously thickened; medial leaf cells isodiametric to ovoid, 11–23 µm long × 9–15 µm wide, walls unpigmented, with triangular to convex trigones, medial thickenings rare, cells in leaf base oblong, 13–25 µm long × 11–15 µm wide walls with bulging trigones, medial thickening present or absent, some walls continuously thickened, trigones sometimes confluent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction by leaf-borne cladia produced from the ventral surface of leaf cells.

Dioicous. Androecia intercalary on secondary or tertiary shoots that continue vegetative growth, usually singly but also in opposing pairs produced by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 3–5 pairs, imbricate, closely packed, bract-lobe spreading, slightly smaller than adjacent leaves, with around 10 short triangular teeth on the ventral margin and apex, apex rounded to truncate, epistatic, bract dorsal margin broadly rounded, entire; stem among bracts smooth. Gynoecia not seen. Fig. 63.

**Recognition:** *Plagiochila paucidens* can be recognized by the ovate leaves that do not have a pronounced ampliate base, and bear 2–8 small triangular teeth around the leaf apex and on the outer half of the ventral margin. Like all species of *Plagiochila* sect. *Vagae* *P. paucidens* exhibits size-correlated variation in leaf shape and dentition resulting in hierarchical structure in shoot systems. This can complicate identification when primary shoots in some individuals are smaller than those in others. For example, plants from Norfolk Island have primary shoots with leaves smaller and bearing fewer teeth than plants from Lord Howe or Tahiti.

*Plagiochila paucidens*



**Fig 63.** *Plagiochila paucidens* leaves, from Meagher LH-115 (NSW), J.A. Curnow 4867 & H. Lepp (CANB 9513836) and R.D. Hoogland 11.213 (CANB 172808). The lowest row of leaves and middle two leaves of the second lowest row are from secondary shoots.

*Plagiochila paucidens* could be confused with *P. acutifolia* but *P. acutifolia* has a relatively narrower truncate leaf apex, and oblong-triangular leaves with an ampliate base, not elliptic oblong, leaves without an ampliate base. For more detail on how to differentiate these two quite similar, and broadly sympatric, species see the recognition section of *P. acutifolia*, above. Leaves of *P. paucidens* tend to roll inward along both margins when dry, whereas leaves of *P. acutifolia* tend to dry flat.

*Plagiochila paucidens* could be confused with *P. meridionalis* but *P. meridionalis* has primary shoot leaves with 8–20 marginal teeth, not 2–8, and the leaves have an ampliate base. *Plagiochila meridionalis* is also a larger plant, with primary shoot leaves averaging  $2.3 \times 1.6$  mm whereas in *P. paucidens* primary shoot leaves average  $1.7 \times 1.2$  mm.

**Distribution and Ecology:** The distribution of *Plagiochila paucidens* includes Tahiti in the east, New Caledonia, Norfolk Island, and the east coast of Australia in the west. *Plagiochila paucidens* probably occurs on other islands in the western Pacific. *Plagiochila paucidens* was reported for the Wet Tropics Bioregion of north-east Queensland by So (2000) when she placed *P. bellenderiensis* in synonymy with *P. metcalfii*. However, the type of *P. bellenderiensis* is *P. daviesiana* and no collections of *P. paucidens* from the Wet Tropics are known. In Australia *P. paucidens* is confined to the North Coast of New South Wales where it inhabits subtropical rainforest, and Norfolk Island and Lord Howe Island. *Plagiochila paucidens* has been collected on rocks within dry watercourses, shaded basalt outcrops on ridges, and as an epiphyte on trees and shrubs in low forest.

**Representative specimens examined: Australia: Norfolk Island:** Bridle Track from Captain Cook Monument to Red Road, Norfolk Island National Park, 29°00'20"S 167°56'35"E, 110 m, 28 Apr 1994, R. Ward 94-1A, CANB9507854; Norfolk Island Botanic Gardens, 29°01'35"S 167°56'08"E, 100 m, 20 Apr 1995, J.A. Curnow 4878 & H. Lepp, CANB9513847; Above Duncombe Bay Road, 29°00'32"S 167°56'05"E, 200 m, 19 Apr 1995, J.A. Curnow 4867 & H. Lepp, CANB9513836; NE slopes of Mt Bates, along Bridle Track (Duncombe Road) between Bird Rock and Captain Cook Monument, 29°00'20"S 167°56'40"E, 120 m, 24 Oct 1967, R.D. Hoogland 11.173 (CANB172814.1); N. slopes of Mt Bates, 29°00'30"S 167°56'10"E, 150 m, 27 Oct 1967, R.D. Hoogland 11.213 (CANB172808); Marshs Road (abandoned track), Norfolk Island National Park, 29°00'36"S 167°56'31"E, 230 m, 15 Apr 1994, H. Streimann 53755 (CANB 9406271); Mt Bates, Norfolk Island National Park, 29°00'40"S 167°56'10"E, 290 m, 15 Jun 1992, H. Streimann 49651 (CANB 9216672); Filmy Fern Trail, off Selwyn Pine Road, Mount Pitt Reserve, 29°01'S 167°57'E, 130 m, 3 Dec 1984, H. Streimann 32099 (CANB 00781999); Filmy Fern Trail, off Selwyn Pine Road, Mount Pitt Reserve, 29°01'S 167°57'E, 140 m, 3 Dec 1984, H. Streimann 32132 (CANB 00782000); *ibid.*, H. Streimann 32154 (CANB 00783101); King Fern Valley, Mt Pitt Reserve, 29°01'S 167°56'E, 260 m, 7 Dec 1984, H. Streimann 34521 (CANB 00783108); **Lord Howe Island:** Northern Hills, just east of the junction of Max Nicholls Memorial Track with the track to Kims Lookout, on shady side of large boulder, 31°31'00"S 151°03'02"E, 115 m, 5 Nov 2009, D. Meagher LH115 (NSW); ridge to Malabar Hill above Catalina monument, 31°31'01"S 159°03'36"E, 110 m, 23 Jun 1992, H. Streimann 50049 (CANB 9218951); Junction of Kims Lookout and Max Nicholls Tracks, 31°31'08"S 159°03'01"E, 100 m, 6 Feb 1995, H. Streimann 55767 (CANB 9514094); Max Nicholls Track, 31°31'06"S 159°03'02"E, 110 m, 20 Jun 1992, H. Streimann 49885 (CANB 9218786); **New South Wales:** North Coast, Dalwood, Richmond River, 32°37'S 151°25'E, 15 Aug 1900, W.W. Watts 154, (NSW 444136); Marshall's Falls, 28°51'S 153°25'E, Jul 1900, W.W. Watts 101 (NSW 444138); near Ballina, back of Websters Slaughter House, 30 Jun 1902, W.W. Watts 507 (NSW 763536); Lismore, Rous Road, 2 Jun 1901, W.W. Watts 289 (NSW 763504); Park Grays Island, 6 May 1900 W.W. Watts 45 (NSW 763503); Wingham-Comboyne Road, 24 km NNW of Taree, 31°40'S 152°25'E, 390 m, 17 Apr 1998, H. Streimann 60478 (CANB 9906508); **Tahiti:** 1847, Vesco (G 00061456).

***Plagiochila norfolkiensis* Steph.**, Bulletin de l'Herbier Boissier, sér. 2, 3: 877 (1903) = Species Hepaticarum 2: 362 (1903)

Type citation: Australia, Norfolk Island (Robinson)

Type: Australia: Norfolk Island, 1884, I. Robinson, ex herb. Melbourne (G 00069848!)

**Notes:** The type of *P. norfolkiensis* comprises one shoot fragment mounted between mica sheets and two branches terminated by male branches, from which nearly all leaves have been fragmented and damaged to some extent. Stephani (1903) states that the plant has large bifid underleaves with angulate or shortly spinose margins, and lacinate-lanceolate lobes. The only other lineage within *Plagiochila* whose species produce comparable underleaves is sect. *Cucullatae*, from whose species *P. norfolkiensis* differs in the *Frullania*-type pseudodichotomous branching and production of leaf-borne cladia. Duplicates and additional material should be sought in other herbaria, and the morphology of other poorly known species such as *P. acutifolia* better circumscribed by additional collections – especially of male plants – before an informed appraisal of how this name should be applied can be made. The male bracts are leaf like and entire except for the apex which is acute, and the margins are undulate. There are lacinate underleaves and paraphyllia on the ventral

stem surface between the bracts. These are manifest on vegetative shoot sectors as well, where they are large, with lacinate and deeply bifid lobes. Branching is *Frullania*-type and pseudodichotomous.

**Description** (from So and Grolle 2001): Plants in herbaria grey brown, not glossy, shoot systems pseudodichotomously branched, vegetative branching *Frullania*-type; shoots 4–6 cm long, 1.9–2.6 mm wide, stem 200–220  $\mu\text{m}$  in diameter; both stem surfaces almost completely hidden by leaves; paraphyllia absent. Leaves imbricate, oblong-ovate, 1200–1400  $\mu\text{m}$  long  $\times$  830–1000  $\mu\text{m}$  wide, ventral margins undulate, small teeth distributed on all leaf margins, teeth 1–4 cells long, 1–3(–4) cells wide at base, terminal cell not elongated, 14  $\times$  15  $\mu\text{m}$ ; dorsal leaf base long decurrent, apex subacute, ventral leaf base ampliate, ventral insertion line moderately decurrent and bearing a low wing; subapical cells 13–15  $\times$  19–25  $\mu\text{m}$ , median cells 18–20  $\times$  20–25  $\mu\text{m}$ , basal cells 18–20  $\times$  58–78  $\mu\text{m}$ , trigones small, walls thin throughout, cuticle smooth. Underleaves large, divided into 4 ciliate lobes. Leaf-borne propagules in the form of short leafy cladia arising from the ventral leaf surface. Male and female plants similar in size. Androecia terminal, intercalary, male shoots continuing vegetative growth after production of 3 or 4 pairs of imbricate male bracts, ventral margin of bract lobe undulate, apex acute, antheridia one per bract; male branch subtended by one *Frullania*-type innovation. Gynoecia terminal on short branches, usually with one lateral-intercalary innovation, that may itself produce a gynoecium, bracts broadly spatulate, much larger than stem leaves, 2.2 mm long, 1.3 mm wide; perianth obovoid, 2.6–2.8 mm long  $\times$  1.0–1.3 mm wide, both keels unwinged, mouth slightly arched, dentate; sporophytes unknown.

**Etymology:** of Norfolk Island, in reference to the origin of the type gathering.

**Recognition:** *Plagiochila norfolkiensis* can be recognized by the combination of undulate ventral margins of leaves and male bract lobes, presence of filiform underleaves on sterile shoot sectors and among the male bracts, the production of leaf-borne cladia, and pseudodichotomously branched shoot systems. This combination of characters is unique among Australasian species, meaning *P. norfolkiensis* is unlikely to be confused with any other regional species. Even on the basis of the scrap that the type specimen in Geneva has been reduced to, it is evident that this species is distinct.

The leaves on tertiary shoots in the syntype of *P. watsiana* Steph. from Norfolk Island are not undulate and although underleaf remnants may occur on some shoot sectors they are not prominent, and deeply bilobed as in the type of *P. norfolkiensis*.

**Distribution and Ecology:** *Plagiochila norfolkiensis* is known from a handful of collections from New Caledonia and Norfolk Island, all made during the 19<sup>th</sup> Century (So & Grolle 2001). No recent collections of *P. norfolkiensis* have been made in Australia, suggesting the species may be extinct at its type locality. Nothing is known of its ecology.

**Additional specimens examined:** none.

### *Plagiochila meridionalis* M.A.M. Renner *sp. nov.*

**Diagnosis:** *Plagiochila meridionalis* is distinguished by the combination of pseudodichotomous, *Frullania*-type vegetative branching, primary shoots 3.4–5.0 mm wide, with imbricate asymmetrically ovate leaves with a rounded to truncate apex, shallowly curved ventral margin and ampliate base, with apex and ventral margins bearing 8–20 irregularly spaced triangular teeth, cells of the teeth not elongated; the absence of underleaves; the male bract lobule margin entire; the perianth with dorsal and ventral keels unwinged, and with 20–30 spinose to spinose-ciliate teeth on each labium.

**Type:** Australia, Queensland, Morton National Park, Macpherson Range, west of Toolona Lookout, 28°15'37"S 153°10'19"E, 1176 m, 6 Mar 2014, M.A.M. Renner 6826 & A.E. Orme (holotype: NSW 858805; isotypes: BRI, CANB, G, MEL)

**Etymology:** *meridionalis* – southern in reference to the geographic distribution of this species in Australia's south-eastern mesothermic archipelago.

**Description:** Plants with pseudodichotomously branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 70 mm long and 40 mm wide, trimorphic or quadrimorphic; primary shoots 3.4–5.0 mm wide, secondary shoots c. 2.0–3.5 mm wide, tertiary branches 2.2 mm wide, quaternary branches c. 1.7 mm; branches arising by *Frullania*-type branching, lateral- and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; reddish-brown, in primary shoots to 500  $\mu\text{m}$  diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 or 5 layers, cortical cell walls strongly and continuously thickened, all walls including free external wall thickened to same degree, all cortical cells smaller than medulla cells; medulla cell walls yellow-pigmented, walls with triangular trigones. Rhizoids scattered,

on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves asymmetrically ovate, 1920–2550  $\mu\text{m}$  long  $\times$  1250–1900  $\mu\text{m}$  wide, dorsal margin straight or slightly arched, apex rounded to truncate, ventral margin shallowly curved and ampliate at base; with 8–20 triangular teeth distributed around the apex and along ventral margin, fairly regularly spaced and evenly sized, ampliate margin with one or two teeth, dorsal margin entire, teeth three to six cells broad at base, cells long rectangular, capped by a triangular cell with an acute apex; secondary shoot leaves asymmetrically ovate, 1250–1950  $\mu\text{m}$  long  $\times$  860–1380  $\mu\text{m}$  wide, smaller than primary shoot leaves and with 8–16 teeth, tertiary shoot leaves smaller again, 1050–1450  $\mu\text{m}$  long  $\times$  700–890  $\mu\text{m}$  wide with 4–14 teeth; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells oblong, 12–18  $\mu\text{m}$  long  $\times$  5–12  $\mu\text{m}$  wide, long axis parallel to leaf margin, walls with bulging trigones and weak continuous thickening; medial leaf cells isodiametric to ovoid, 14–25  $\mu\text{m}$  long  $\times$  11–19  $\mu\text{m}$  wide, walls unpigmented, with bulging trigones, medial thickenings absent, cells in leaf base polyhedral to long and slightly sinuous oblong, 23–41  $\mu\text{m}$  long  $\times$  10–19  $\mu\text{m}$  wide walls with bulging to nodulose trigones, medial thickening absent. Cell surfaces smooth. Oil-bodies 4–8(9) per cell, fusiform, granular, greyish. Underleaves present or absent, vestigial, persistent, triangular. Asexual reproduction by leaf-borne cladia produced from the ventral surface of leaf cells.

Dioicous. Androecia intercalary on secondary, tertiary, or quaternary shoots that continue vegetative growth, usually in opposing pairs produced by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 4–9 pairs, imbricate, closely packed, bract-lobe reduced and smaller than adjacent leaves, with four to seven triangular teeth, epistatic, bract interior margin broadly rounded to weakly ampliate, entire; stem among bracts smooth. Gynoecia at apices of shoots; bracts ovate to triangular-ovate, 2600–3100  $\mu\text{m}$  long  $\times$  1400–2400  $\mu\text{m}$  wide; dorsal margin curved to arched, inrolled, apex rounded to weakly truncate, ventral margin straight in outer half and ampliate at base, all margins with 30–45 triangular teeth, unequal in size, dorsal margin sometimes entire on basal half; bract cells as for leaf cells; cell surfaces smooth; female bracteole present. Subfloral innovations absent, or one or two produced by lateral-intercalary branching from between the female bracts. Perianth triangular to campanulate, 2300–2700  $\mu\text{m}$  long  $\times$  1700–2600  $\mu\text{m}$  wide at mouth, dorsal and ventral keels unwinged; laterally compressed but with an inflated base, lateral walls plane; labia curved, each with 20–30 spinose to spinose-ciliate teeth. Figs 64–66.

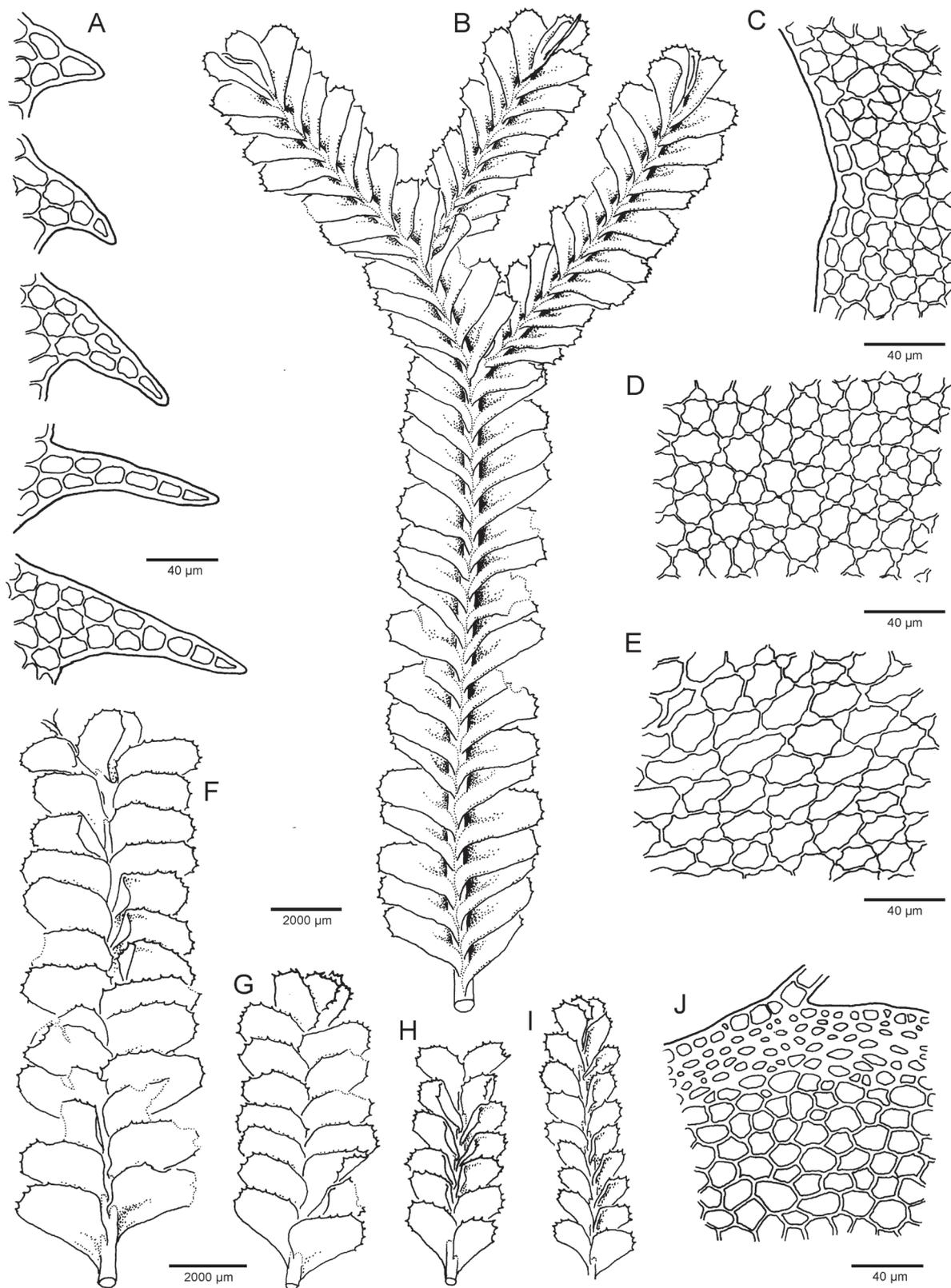
**Recognition:** *Plagiochila meridionalis* can be recognized by the combination of pseudodichotomously branched shoots with *Frullania*-type vegetative branching, the imbricate asymmetrically ovate leaves with 8–20 evenly sized and spaced small triangular teeth around the apex and on the ventral margin. Female plants have perianths without a wing on the dorsal keel.

*Plagiochila meridionalis* could be confused with *P. apatila*, but *P. apatila* has fewer, larger triangular to spinose teeth on the ventral leaf margin and elongate leaf apical cells, female plants have perianths with a wing on the dorsal perianth keel; and male plants of *P. apatila* have the interior bract margin obscurely crenate to toothed, while in *P. meridionalis* the interior bract margin is ampliate but entire, without crenulations or teeth.

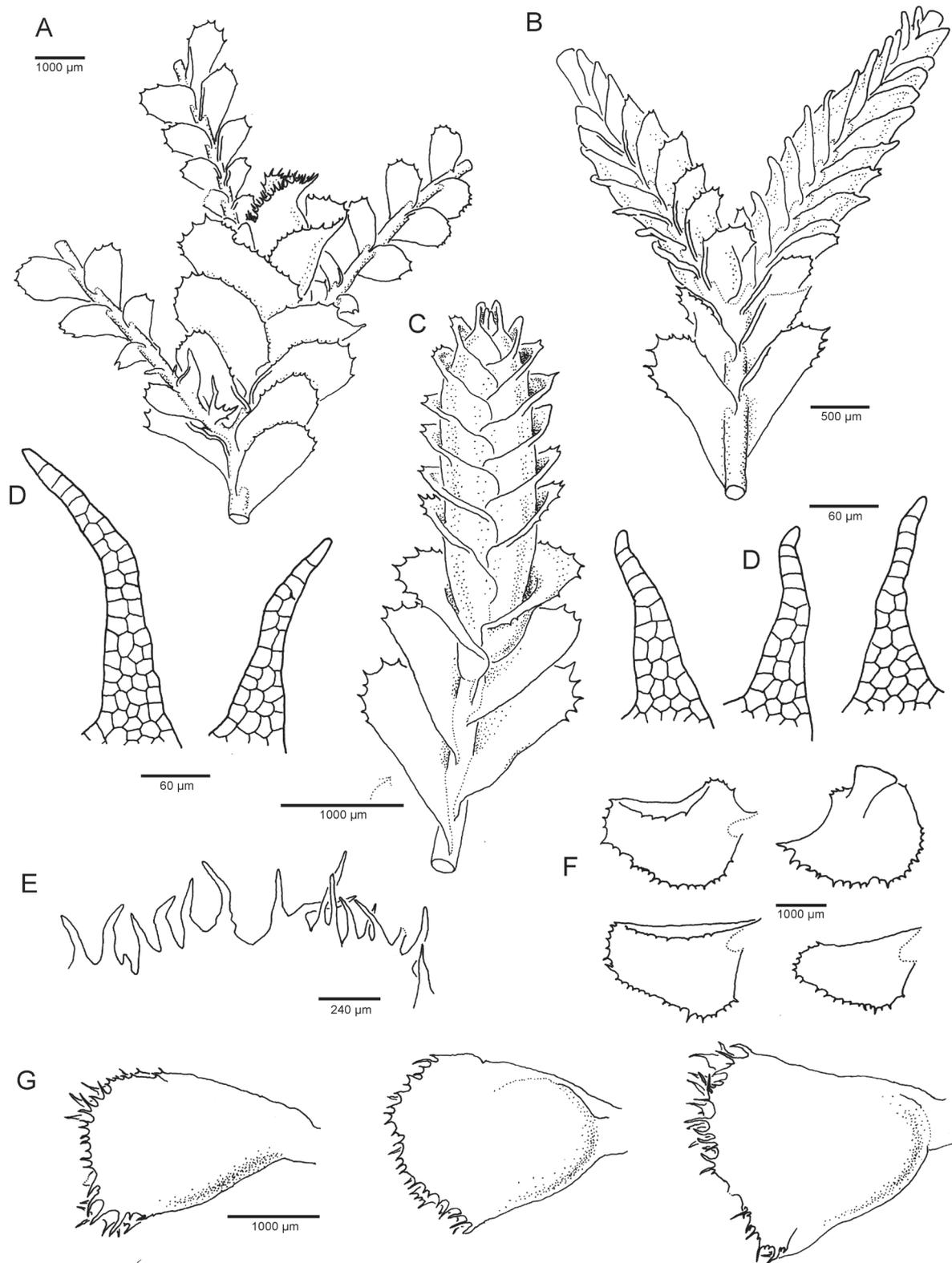
*Plagiochila meridionalis* could be confused with *P. nebulosa*, but *P. nebulosa* has longer spinose teeth on the leaves, elongate leaf marginal cells and teeth cells, particularly the apical cell which is elongate; female plants have perianths with a wing on the dorsal perianth keel; male plants have bracts whose lobes have an acute apex, and margins without teeth, while in *P. meridionalis* the male bract lobes are rounded and bear small triangular teeth.

In New South Wales this species has been referred to *Plagiochila fasciculata* when it has been identified to species level. It differs in many details, starting with the pseudodichotomous branching, such that the two species shouldn't really have been confused.

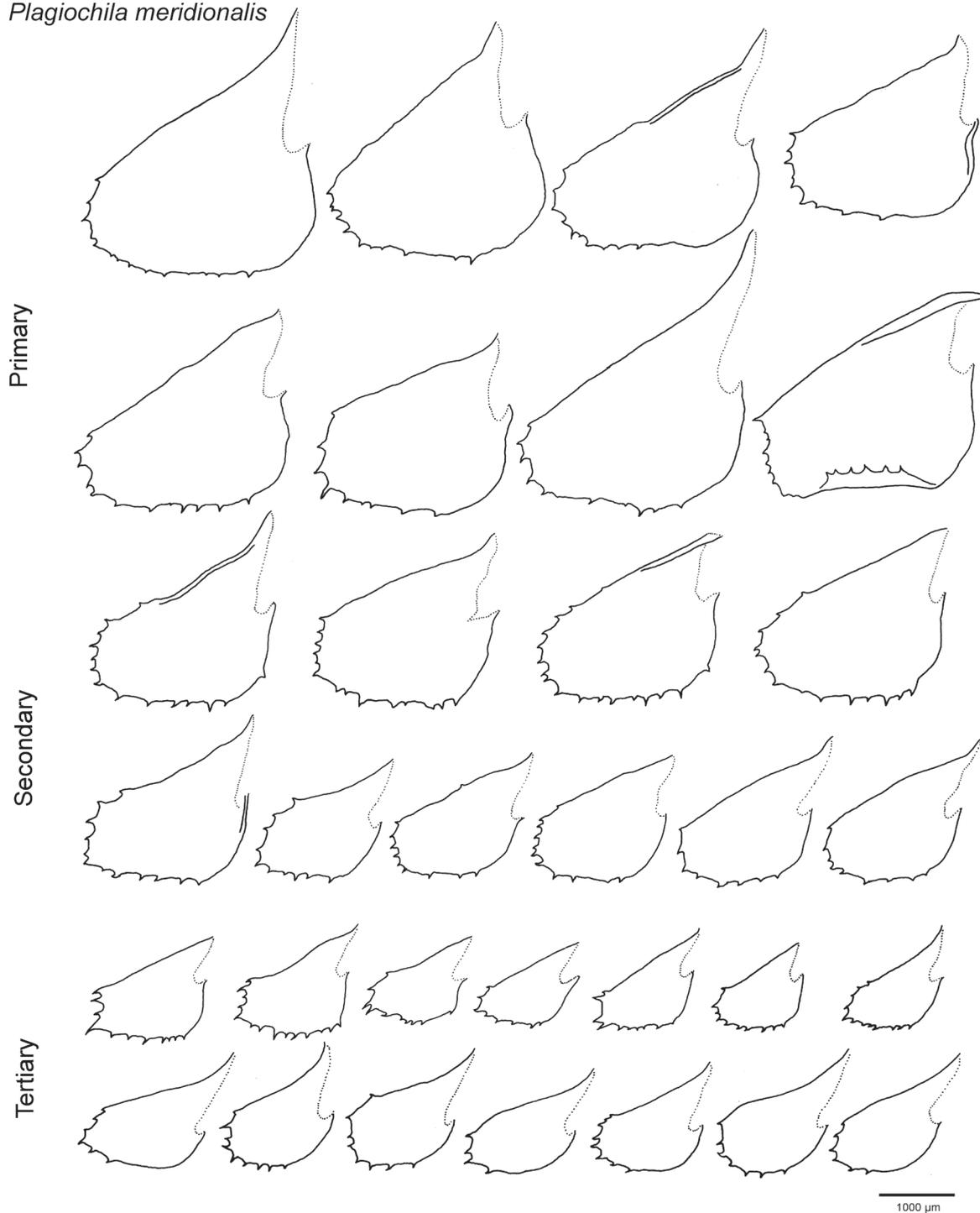
**Distribution and Ecology:** *Plagiochila meridionalis* is endemic to the south-east coast of Australia, from the Border Ranges in southern eastern Queensland in the north to the Shoalhaven River in the south, and between 300 and 1100 m elevation. *Plagiochila meridionalis* grows in cool to warm temperate rainforest on summits, ridges, faces, and gullies wherever prolonged water stress does not occur, and occupies a range of microsites, including branches and trunks of trees, liana stems, saplings, rotting wood, boulders on the forest floor or within waterways, and the faces of bluffs. *Plagiochila meridionalis* may be locally dominant within epiphytic bryophyte communities, as in the Nightcap Range, where cloud forests along the summit ridge are festooned with copious wefts formed by this species.



**Fig 64.** *Plagiochila meridionalis*. A: five teeth from leaf margin. B: dorsal view of primary and secondary shoot system. C: marginal leaf cells. D: medial leaf cells. E: basal leaf cells. F: ventral view of primary shoot. G: ventral view of secondary shoot. H: ventral view of tertiary shoot. I: ventral view of quaternary shoot. J: dorsal sector or transverse section through stem from primary leafy shoot. All from *M.A.M. Renner 6826 & A.E. Orme (NSW 858805)*.



**Fig 65.** *Plagiochila meridionalis*. A: ventral view of perianth bearing shoot. B: ventral view of male branches. C: dorsal view of male branch. D: five teeth from perianth mouth. E: perianth mouth. F: four female bracts. G: three perianths in lateral view. All from M.A.M. Renner 6826 & A.E. Orme (NSW 858805).

*Plagiochila meridionalis*

**Fig 66.** *Plagiochila meridionalis* leaves, all from *M.A.M. Renner 6839 & A.E. Orme* (NSW 870815).

**Representative specimens examined:** **Australia: Queensland:** South Queensland, *H. Schneider* ex herb. Kidz 20 (BM as *P. fasciculata*); ex Australia, 1883 misit Bailey ex herb. Kidz 216 (BM); Wide Bay, Kondalilla Falls, SE of Nambour, 26°40'S 152°53'E, 7 Jul 1983, *W.B. Schofield 80558 & M.I. Schofield* (NSW 738492); Purling Brook Falls, Springbrook, 23 km SSW of Nerang, 28°11'S 153°16'E, 480 m, 8 Jan 1990, *H. Streimann 43493* (CANB 9007395); Moreton: Lamington National Park, Macpherson Range, Border Track, 28°14'38"S 153°08'53"E, 962 m, 6 Mar 2014, *M.A.M. Renner 6840 & A.E. Orme*, (NSW 858815); Moreton: Lamington National Park, Macpherson Range, Border Track, 28°15'35"S 153°9'53"E, 1130 m, *M.A.M. Renner 6839 & A.E. Orme* (NSW 870815); **New South Wales:** Brindle Creek, Wiangaree State Forest, 27 km NNE of Kyogle, 28°07'S 153°06'E, 750 m, 3 Sep 1978, *H. Streimann 6030* (CANB 7900277); Mt Lindesay State Forest, north-western side of Mount Glennie, 28°21'57"S 152°45'38"S, 850 m, 3 Mar 2014, *M.A.M. Renner 6805 & A.E. Orme*

(NSW 850847); Mt Lindesay State Forest, Richmond River catchment, north-western side of Mount Glennie, 28°21'56"S 152°45'37"E, 836 m, *M.A.M. Renner 6806* & *A.E. Orme* (NSW 850848); *ibid*, *M.A.M. Renner 6807* & *A.E. Orme* (NSW 850849); Brindle Creek, Rainforest Walk, Wiangaree Forest Drive, McPherson Range, 28°22'S 153°03'E, 10 Jul 1983, *W.B. Schofield 80654*, *H.P. Ramsay* & *M.I. Schofield* (CANB 793712.1); Border Ranges National Park, Brindle Creek, 27 km NNE of Kyogle, 28°22'S 153°04'E, 750 m, 24 Apr 1998, *H. Streimann 61065* (CANB 9910469.1); Border Ranges National Park, Brindle Creek Road, 28 km NE of Kyogle, 28°23'S 153°07'E, 870 m, 24 Apr 1998, *H. Streimann 61146* (CANB 9910554.1); North Coast, Border Ranges National Park, Tweed Range, Brindle Creek, Red Cedar loop track, 28°22'40"S 153°04'00"E, 750 m, 3 Sep 2013, *M.A.M. Renner 6769* (NSW 978728); Border Ranges National Park, Forest Tops, 26 km NNE of Kyogle, 28°23'S 153°04'E, 700 m, 24 Apr 1998, *H. Streimann 61048A* (CANB 9910399.1); Border Ranges National Park, The Pinnacle Lookout Track, 28°24'12"S 153°07'24"E, 22 Feb 2000, *R.G. Coveny 18446*, *E.A. Brown* & *T. Pócs* (CANB 867057.1, NSW 793302); Pinnacle Hill, Border Ranges National Park, 22 km NE of Kyogle, 28°25'E 153°07'E, 910 m, 24 Apr 1998, *H. Streimann 61232* (CANB 9910849.1); Border Ranges National Park, Tweed Range, Bar Mountain Loop track, 28°27'38"S 153°07'35"E, 1110 m, 2 Sep 2013, *M.A.M. Renner 6755* (NSW 978714); Tooloom National Park, 23 km WSW of Woodenbong, 28°29'S 152°23'E, 630 m, 23 Apr 1998, *H. Streimann 60912* (CANB 9910246.1); *ibid*, *H. Streimann 60915* (CANB 9910249.1); Tooloom Nature Reserve, Plantation Road, 24 km NNE of Kyogle, 28°30'S 152°23'E, 660 m, 23 Apr 1998, *H. Streimann 60997* (CANB 9910339.1); Toonumbar Forest Way, Toonumbar State Forest, above Eden Creek, 26 km NW of Kyogle, 28°30'S 152°45'E, 450 m, 18 Oct 1978, *H. Streimann 7004* (CANB 7905896); North Coast, Nightcap National Park, Mount Nardi, summit between radio masts, 28°32'37"S 153°17'23"E, 785 m, *M.A.M. Renner 6753* (NSW 978711); Dorrigo, Feb 1916, *J.L. Boorman* (NSW 763495); North Coast, Booyong, Richmond River, 28°45'S 153°27'E, 31 Jul 1902, *W.W. Watts 584* (NSW 444140); Waihou Forest Reserve, near trig, 20 km NW of Coffs Harbour, 30°06'S 153°01'E, 300 m, 19 Apr 1998, *H. Streimann 60593* (CANB 9906629); Escarpment below Waihou Trig Station, 25 km NW of Coffs Harbour, 30°06'S 153°02'E, 340 m, 12 Oct 1978, *H. Streimann 6571* (CANB 7905078); 'Botanical Walk', Wilson River Primitive Reserve, Boss State Forest, 49 km NW of Port Macquarie, 30°12'30"S 152°58'30"E, 245 m, 17 Jun 1999, *H. Streimann 63783* (CANB 604776.1); North Coast, Tysons track near Darkwood, Bellingen River, 30°25'00"S 152°39'46"E, 120 m, 28 Apr 1989, *E.A. Brown 89/114c* (NSW 436409); Cockerawombeeba Creek, Mt Boss State Forest, 46 km NW of Wauchope, 31°15'S 152°20'E, 700 m, 21 Oct 1978, *H. Streimann 7256* (CANB 7906277); The Scrub Road, Broken Bago State Forest near Educational Trail, 9 km SW of Wauchope, 31°31'S 152°40'E, 60 m, 31 Aug 1987, *H. Streimann 38561* (CANB 781973); *ibid*, *H. Streimann 38576* (CANB 00781974); Rawson Falls, 31 km NNW of Taree, 31°37'S 152°25'E, 460 m, 27 Apr 1998, *H. Streimann 61540* (CANB 9911176.1); Camden Haven State Forest, 28 m SW of Port Macquarie, 31°39'S 152°46'E, 480 m, 29 Aug 1987, *H. Streimann 38441* (CANB 781970); *ibid*, *H. Streimann 38444* (CANB 781971); Dingo Tops Forest Park, Bulga State Forest, 31 km NW of Wingham, 31°40'S 152°09'E, 700 m, 1 Sep 1987, *H. Streimann 38694* (CANB 9201354); *ibid*, *H. Streimann 38697* (CANB 781976); Camden Haven State Forest, 28 km SW of Port Macquarie, 31°39'S 152°46'E, 480 m, 29 Aug 1987, *H. Streimann 38444* (CANB 781971); Middle Brother, Middle Brother State Forest, 31 km NE of Taree, 31°43'S 152°40'E, 550 m, 4 Jan 1990, *H. Streimann 43362* (CANB 9007262); *ibid*, *H. Streimann 43366* (CANB 9007266); Nowra, along Shoalhaven River, inside the 'animal park', 34°52'S 150°34'E, 13 May 1986, *D. Vitt 27428* & *H.P. Ramsay* (CANB 00781858).

### Excluded from the Australasian flora

*Plagiochila inflata* Steph., Bulletin de l'Herbier Boissier, sér. 2, 3: 961 (1903) = Species Hepaticarum 2: 376 (1903)

Type citation: *Nova Guinea orientalis* (Micholitz).

Type: Papua New Guinea, Micholitz (holotype *vide* So and Grolle (1999): G-12270, lectotype designated here: separate subpacket within G 00061435!).

**Notes:** *Plagiochila acutifolia* Steph. was listed as a synonym of *P. inflata* Steph. by So (2001). The lectotype of *P. inflata* differs from *P. acutifolia* in that the leaf has a pronounced inflated cnemis formed by lamina dorsally assurgent above the stem and decurrent along the stem with the leaf insertion line, the presence of lateral-intercalary vegetative branches and absence of *Frullania*-type vegetative branching, the presence of four to six small denticulate teeth on the leaf margin at its extreme dorsal base, the broad ampliate interior lobule margin which is often imbricate and completely obscuring the stem in ventral view, and the strong fuscous pigmentation.

The holotype of *P. inflata* is a mixture of two *Plagiochila* species, and lectotypification within the holotype is required. The protologue of *P. inflata* (Stephani 1903) provides a number of characters that serve to differentiate between the two elements in the type, and unambiguously associate the name with the larger of the two. The protologue is quoted below and pertinent characters are italicized.

‘Dioica, magna, gracilis robusta, rigida, brunneola, dense caespitosa, corticola. Caulis ad 12 cm. longus, simplex superne vage longeque ramosus ramis parum divergentibus, validus, fuscus et rigidus. Folia pro planta parva 3 mm. longa, parum imbricate, oblique patula, angulo 58° in sicco arcte decurva, utrinque decurrentia, ala antica falde inflata, postice applicata alteque cristata, subsymmetrica *in plano oblong-trigona, basi amplissima*, apice fere 5plo antusiora, *marginē antice stricto nudo, ipsa basi 4-5 denticulato, sub apice breviter 3 dentato, dentibus remotis, marginē postico e basi semicirculari stricto nudo sub apice remote bidentulo, apice ipso rotundato 4 spinuloso*. Cellulae apicales 18 μ, basales 18 × 36 μ, trigonis magnis acutis.’

This lectotypification maintains *P. inflata* in its current usage. The residual element may be an ally of *P. trapezoidea*, in its possession of scattered paraphyllia on the dorsal stem surface, and complete absence of *Frullania*-type branching. This latter plant is interesting for its occasional production of rhizoids from the dorsal stem surface.

Misidentified specimens examined:

*Plagiochila meridionalis*

Australia: Queensland, unknown 111 (MEL 1039224).

***Plagiochila furcata*** Steph., Bulletin de la Société Royale de Botanique de Belgique 31: 120 (1892) [1893]

Type citation: Madagascar. Antsianaka. leg. Perrot.

Type: Madagascar, Antsianaka, Perrot 250 (holotype *vide* Grolle: G 00045475!)

**Notes:** The type of *Plagiochila furcata* is a small plant with pseudodichotomous branching and untoothed, obovate, concave leaves that are both orientated toward the shoot apex and postically secund with down-rolled interior and exterior margins. The leaves lay alongside, rather than across, the stem in ventral view. The leaves are usually entire, but occasionally one to four small triangular teeth, comprising two or three cells at most are present around the leaf apex. The female bracts bear lacinate dentate teeth.

The only Australian species to which *P. furcata* bears any similarity is *P. metcalfii*, and then only in size and its nearly entire leaves. However, the type of *P. furcata* differs from *P. metcalfii*, and indeed all other Australasian species in leaf dentition and leaf shape. I can only assume that *P. furcata* was listed in McCarthy (2006) on the basis of speculatively identified specimens, perhaps of one of the two Australian species mentioned above. No specimens from Australia examined for this study correspond with plant in the type of *P. furcata*, and I did not locate any Australian specimens so identified. This Madagascan species is accordingly excluded from the Australian flora.

***Plagiochila* sect. *Cucullatae* Schiffn.**, Hep. Fl. Buitenzorg: 107 (1900)

Type: *Plagiochila sandei* Sande Lac. (lectotype designated by Grolle 1976)

= *Plagiochila* subg. *Metaplagiochila* Inoue., The genus *Plagiochila* in South East Asia: 27 (1984)

Type: *Plagiochila sandei* Sande Lac.

Section *Cucullatae* is distinguished by the ventral merophyte 5-10 cell rows broad on the stem, the pouch at the ventral base of the leaf, and the capsule epidermal cells are hyaline and thin-walled. Male branches tend to be long and bear 20 or more pairs of hypostatic male bracts, whose lobe and lobule margins are often entire. In some species the leaves bear moniliform spinose-ciliate teeth, and shoots bear conspicuous underleaves. Partly due to its distinctive appearance, section *Cucullatae* was recognized as subg. *Metaplagiochila* by Inoue (1984). Around 20 species are currently accepted in this section (Söderström *et al.* 2016), most species occur in Malesia and Oceania. One New Zealand species, *P. reischeckiana* Steph. was attributed to this section (Engel and Merrill 2013), based on its inrolled leaf base but this species belongs in synonymy of *P. subfasciculata* (see above).

***Plagiochila vitiensis*** Mitt., Bonplandia 9: 367 (1861)

Type citation: Seemann, No. 862

Type: Fiji, Viti-Levu Isl., leg. Seemann no 862 (NY)

= *Plagiochila brotheri* Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 775 (1904) = Species Hepaticarum 2: 453 (1904)

Type citation: Queensland (Bailey).

*Type:* Australia, Queensland, Bellenden Ker District, 1889, *F.M. Bailey 599* (either a Bailey collecting number or a Brotherus herbarium number (lectotype designated by Bonner (1962): G00061556! isolectotype: BM!)

**Notes:** Inoue (1981) reported *P. vitiensis* for New South Wales on the basis of the type specimen of *Plagiochila serrifolia* Steph., which however is *Acrobolbus epiphytum*, see below.

**Etymology:** from Viti, in reference to the source of the type specimen on Viti Levu.

**Description:** Plants with sparingly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; leafy shoots horizontally spreading or pendulous, to 40 mm long, monomorphic; primary shoots 2.5–5.5 mm wide, branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; reddish-brown, to 280 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells 3 or 4 layers dorsally and ventrally, narrowing to one layer laterally, cells unequally sized, largest twice the diameter of the smallest, cortical cell walls continuously but not heavily thickened, red-brown pigmented; medulla cells larger than cortical cells, walls are yellow-pigmented with weak continuous thickening and small triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves remote to contiguous to slightly imbricate, succubously inserted and orientated, on primary shoot leaves asymmetrically ovate to ovate-oblong 1250–2600 µm long × 850–1550 µm wide, dorsal margin straight or shallowly curved, revolute immediately above stem insertion otherwise plane, apex truncate to rounded, ventral margin curved, base not ampliate, often revolute immediately above stem insertion, not forming a pouch; dorsal margin usually entire, rarely with one or two triangular teeth, apex and ventral margin with 6–15 sharp triangular to spinose teeth fairly regularly sized and spaced, absent from the ventral base margins, teeth two or three cells broad at base, uniseriate above, cells rectangular, capped by a more or less rectangular cell that narrows toward its rounded apex; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving four or more cortical cell rows leaf-free. Marginal leaf cells oblong, 24–35 µm long × 12–16 µm wide, long axis parallel to leaf margin, walls with triangular trigones and weak continuous thickening on the free external wall, medial thickenings absent; medial leaf cells isodiametric or ovoid, 22–38 µm long × 19–32 µm wide, walls unpigmented, with triangular trigones, medial thickenings absent, cells in leaf base ovoid, 24–44 µm long × 19–28 µm wide walls with triangular trigones, medial thickening absent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction rare, by caducous leaf fragments from the outer half of the leaf, inner half of the leaf usually remaining intact on older shoot sectors.

Dioicous. Androecia not seen. Gynoecia terminal on shoots, female bracts larger than subtending vegetative leaves and with longer cilia. Perianth labia long-ciliate. Fig. 67.

**Recognition:** *Plagiochila vitiensis* can be recognized by the remote to contiguous, asymmetrically ovate to ovate-oblong leaves that bear 6–15 sharp triangular to spinose teeth around their apex and on the outer half of the ventral margin. *Plagiochila vitiensis* has the characteristic large leptodermous leaf cells of sect. *Cucullatae*, and may produce caducous leaf fragments, but unlike other species in this section in Australia *P. vitiensis* does not bear leaf pouches, even on the largest leaves, and has no underleaves.

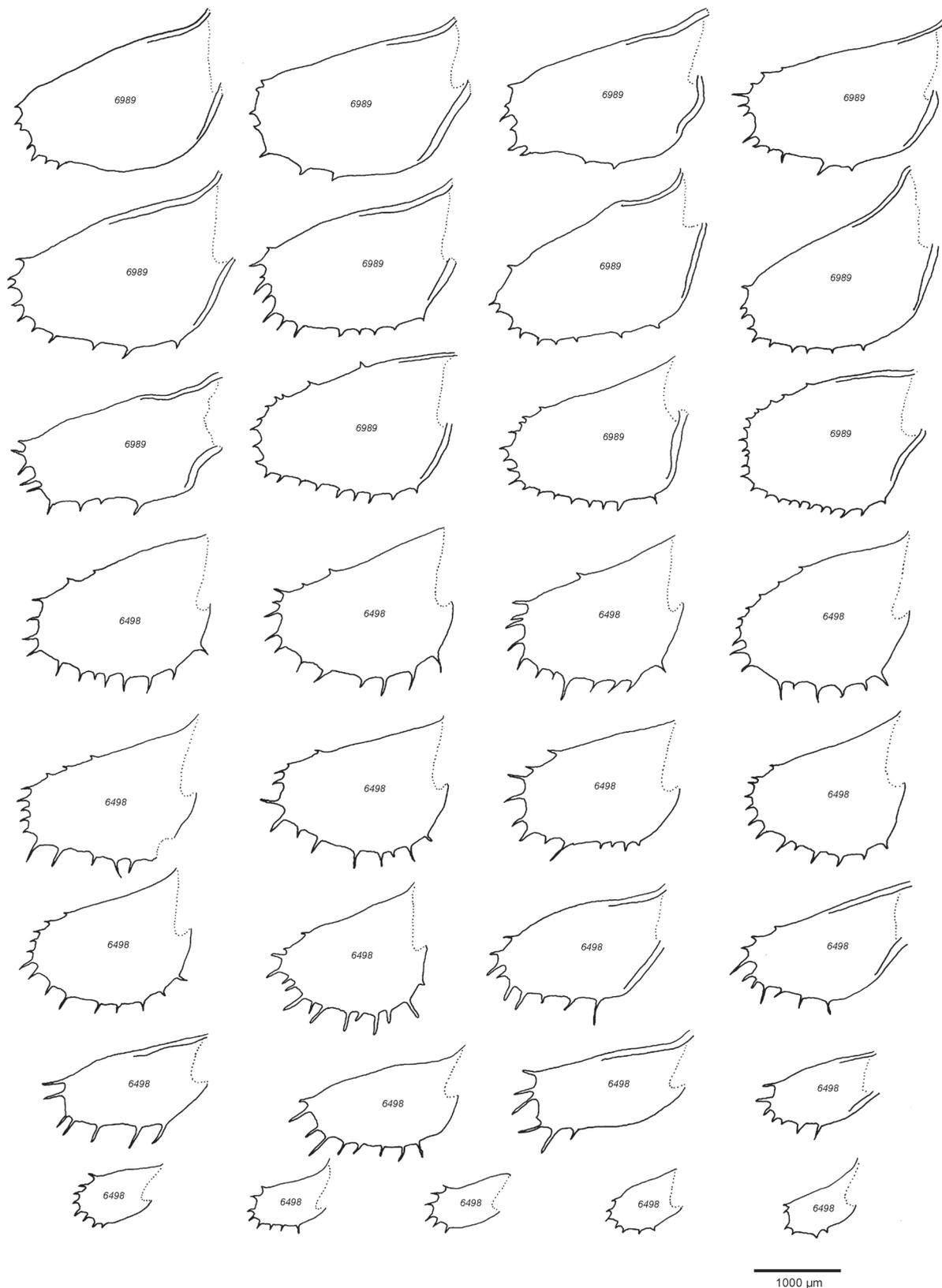
*Plagiochila vitiensis* is similar to *P. blepharophora* but *P. blepharophora* has more numerous and longer teeth on the leaf margins, 5–29 spinose ciliate teeth, and the leaves are triangular-ovate in shape. These differences are best ascertained when leaves have been dissected from shoots and slide mounted.

*Plagiochila vitiensis* is similar to some phases of *P. sydneyensis* in the absence of a leaf pouch, but *P. sydneyensis* tends to bear small sharp triangular teeth on the dorsal leaf margin, whereas the dorsal leaf margin in *P. vitiensis* is entire.

*Plagiochila vitiensis* could be confused with *P. sciophila* but lacks conspicuous teeth on the dorsal leaf margin and, unlike *P. sciophila*, does not bear conspicuous bifid underleaves.

*Plagiochila vitiensis* is superficially similar to *P. conturbata* in colour, size, and the leaf spacing, but *P. conturbata* has ovate-triangular leaves with fewer triangular teeth, and smaller leaf cells whose walls bear bulging trigones. *Plagiochila conturbata* also produces *Frullania*-type vegetative branching, which never occurs in *P. vitiensis*.

**Distribution and Ecology:** *Plagiochila vitiensis* occurs in Fiji, New Caledonia, Samoa, Tahiti and Australia (Inoue 1981). In Australia all records are from the Wet Tropics Bioregion of north-east Queensland, where *Plagiochila vitiensis* has been collected between Mount Sorrow in the north and Babinda Stream in the south, at a range of elevations between 75 m and 800 m above sea level, within a variety of rainforest types but often near permanent water courses. *Plagiochila vitiensis* has been collected on tree trunk bases, tree roots, and buttress roots of living and dead trees.



**Fig 67.** *Plagiochila vitiensis* leaves, from *M.A.M. Renner 6989* & *T.C. Wilson* (NSW 870755), *M.A.M. Renner 6498*, *V.C. Linis* & *E.A. Brown* (NSW 909775).

**Representative specimens examined:** Australia: Queensland: Cook, Daintree National Park, Mount Sorrow, vicinity of summit, 16°04'36"S 145°26'25"E, 718 m, 21 May 2014, *M.A.M. Renner 6989* & *T.C. Wilson* (NSW 870755); Barron Gorge, Kuranda, 16°50'S 145°38'E, 3 Jul 1936, *S. Egan* (CANB 360611); Kauri Creek, Mt Haig Road, Lamb Range, 2 km NE of Atherton, 17°08'S 145°36'E, 800 m, 27 Jun 1984, *H. Streimann 29868*,

(CANB 8408223); Mulgrave River Forestry Road, 18 km S of Gordonvale, 17°16'S 145°47'E, 80 m, 15 Dec 1990, *H. Streimann* 46525 (CANB 9015006); Wooroonooran National Park, Babinda Stream, Goldfields track, 17°19'54"S 145°51'52"E, 75 m, 3 Apr 2012, *M.A.M. Renner* 6498, *V.C. Linis & E.A. Brown* (NSW 909775).

***Plagiochila sydneyensis*** Beauverd, *Species Hepaticarum* 6: 572 (1924) *nom. nov. pro Plagiochila remyana* Steph. 1921

Replaced synonym: *Plagiochila remyana* Steph., *Species Hepaticarum* 6: 203 (1921) *nom. illeg.*

*Type citation:* Australia prope Sydney (Remy legit).

*Type:* Australia, New South Wales, Wallarah prope Sydney, *Jules Remy*, ex herb. Douin No. 4 (holotype: G 00061569!)

**Notes:** Inoue's (1986) illustration of the leaves of *P. sydneyensis* show only part of the range of variation expressed by this species, on the specimen illustrated the leaf pouches are also complete, and pyriform in shape as well as fusiform as illustrated.

**Etymology:** from Sydney, invoking a fairly generous interpretation of *prope*.

**Description:** Plants with sparingly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; leafy shoots horizontally spreading or pendulous, to 30 mm long, monomorphic; primary shoots 5.5–6.3 mm wide, branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; reddish-brown, to 400 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells 2 or 3 layers dorsally and ventrally, narrowing to one layer laterally, cells unequally sized, largest twice the diameter of the smallest, cortical cell walls continuously but not heavily thickened, pale brown pigmented; medulla cells larger than cortical cells, walls are yellow-pigmented with weak continuous thickening and small triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, obliquely spreading, asymmetrically ovate, oblong, triangular-oblong to ovate-oblong 1850–2600 µm long × 950–1550 µm wide, dorsal margin straight or shallowly curved or arched, revolute immediately above stem insertion otherwise plane, apex broadly rounded, ventral margin straight to shallowly curved, base weakly ampliate, usually with a pouch formed by invagination of abaxial leaf surface, pouch fusiform when small to pyriform when fully expressed, with (0–)2–4(–5) spinose-ciliate teeth on the free margin; dorsal margin usually entire or with several widely spaced sharp triangular teeth, apex and ventral margin with 11–30 spinose to spinose-ciliate teeth, fairly regularly spaced, teeth two or three cells broad at base, uniseriate above, cells rectangular, capped by a more or less rectangular cell that narrows toward its rounded apex; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving four or more cortical cell rows leaf-free. Marginal leaf cells oblong, 19–26 µm long × 10–13 µm wide, long axis parallel to leaf margin, walls with triangular trigones and weak continuous thickening on the free external wall, medial thickenings absent; medial leaf cells isodiametric, pentagonal, hexagonal, or ovoid, 17–27 µm long × 14–23 µm wide, walls unpigmented, with triangular trigones, medial thickenings absent, cells in leaf base ovoid, 19–30 µm long × 14–23 µm wide walls with triangular trigones, medial thickening absent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction rare, by caducous leaf fragments from the outer half of the leaf, inner half of the leaf usually remaining intact on older shoot sectors.

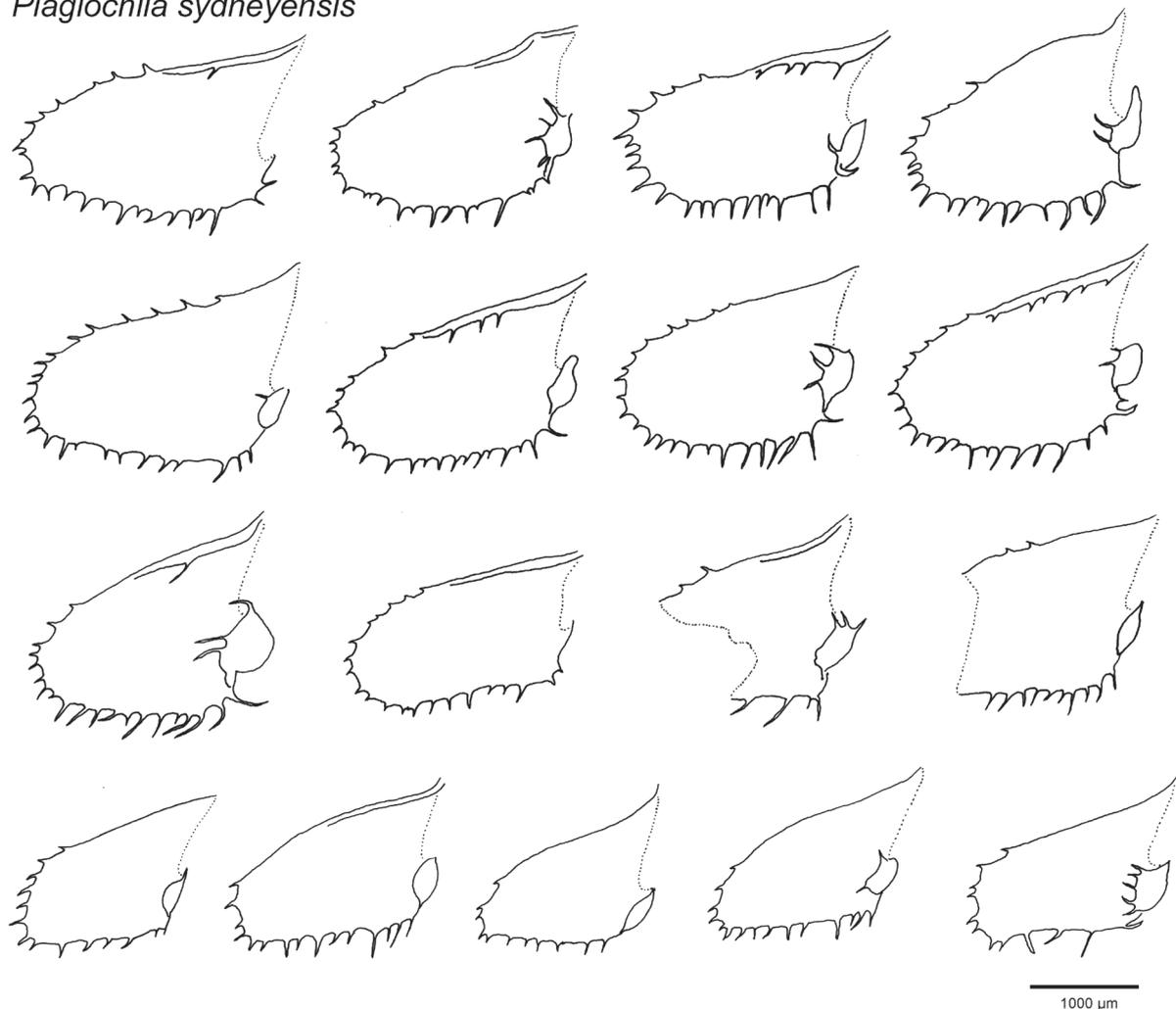
Fertile material not seen. Fig. 68.

**Recognition:** *Plagiochila sydneyensis* can be recognized by the imbricate, obliquely spreading leaves with a revolute base of the dorsal margin, which may also bear small sharp triangular teeth, the margins with 11–30 spinose to spinose-ciliate teeth that are longer toward the ventral base, and the presence, especially in larger leaves, of a leaf pouch that varies from fusiform to pyriform and may have as many as four or five teeth on the free margin.

*Plagiochila sydneyensis* could be confused with *P. bantamensis*, but *P. bantamensis* bears conspicuous bifid and often heavily ciliate underleaves whereas *P. sydneyensis* has none.

*Plagiochila sydneyensis* could be confused with *P. vitiensis* but *P. vitiensis* never bears a leaf pouch, not even on the largest leaves, and the teeth are fewer in number (6–15) and concentrated around the leaf apex, the dorsal margin is entire.

*Plagiochila sydneyensis* could be confused with *P. blepharophora* but *P. blepharophora* has longer ciliate teeth, and no leaf pouch on leaves with a slightly ampliate base.

*Plagiochila sydneyensis*

**Fig 68.** *Plagiochila sydneyensis* leaves, all from *M.A.M. Renner 6541 E.A. Brown & V.C. Linis* (NSW 899754).

**Distribution and Ecology:** *Plagiochila sydneyensis* is so far known only from Australia, where it is confined to the Wet Tropics Bioregion of north-east Queensland, from Mount Sorrow in the north to Dalrymple Creek, Cardwell, in the south (Inoue 1986), at elevations from 75 to 720 m above sea level. This distribution is similar to that reported above for *P. vitiensis*, and probably reflects more the geographical coverage and location, of collections examined for this study than the true northern and southern limits for both species within Australia. *Plagiochila sydneyensis* has been collected as a lithophyte on granite boulders close to the summit of Mt Sorrow in simple windswept notophyll forest, and on tree roots exposed by a stream over an eroded streambank, and on rotting but corticated log on the forest floor, where it formed a mixed turf with *P. bantamensis* in cyclone-damaged complex mesophyll vine forest at Babinda Stream.

**Representative specimens examined:** Australia: Queensland: Cook, Daintree National Park, Mount Sorrow, vicinity of summit, 16°04'36"S 145°26'25"E, 718 m, 21 May 2014, *M.A.M. Renner 6992 & T.C. Wilson* (NSW 870786); Cook, Wooroonooran National Park, South Johnston River catchment, Maple Creek Road, 17°42'06"S 145°40'22"E, 600 m, 5 Apr 2012, *M.A.M. Renner 6541 E.A. Brown & V.C. Linis* (NSW 899754); Wooroonooran National Park, Babinda Stream, Goldfields track, 17°19'54"S 145°51'52"E, 75 m, 3 Apr 2012, *M.A.M. Renner 6492, V.C. Linis & E.A. Brown* (NSW 909521 p.p.).

***Plagiochila blepharophora* (Nees) Lindenb.,** *Species Hepaticarum* 2-4: 102 (1840)

Basionym: *Jungermannia blepharophora* Nees, *Enumeratio plantarum cryptogamicarum Javae*: 71 (1830)

Type citation: n.v.

Type: Java: in tumulis sanctis Baduorum Java, Buitenzorg ex herb. Lindenberg (G 00115176!)

=*Chiloscyphus defectistipulus* (Steph.) J.J.Engel et R.M.Schust., *Nova Hedwigia* 39: 414 (1984) [1985]

*Lophocolea defectistipula* Steph., Bulletin de l'Herbier Boissier, sér. 2, 6: 950 (1906) = Species Hepaticarum 3: 130 (1906)

Type citation: *Insulae Carolinae* (Parkinson)

Type: Iles Caroline, Aug 1908, R. Parkinson (G 00061183)

=*Plagiochila blepharophora* var. *exilis* Schiffn., Die Hepaticae der Flora von Buitenzorg: 162 (1900)

Type citation: *n.v.*

Type: Java, Prov. Batavia, in monte Pantjar, in arbores in siva primaeva, Regio calida, 350 m, 28 Dec 1893, V. Schiffner Iter Indicum 1893/94 No 700 (FH 00458028!); Prov. Batavia, ad pedem Montis Salak ad viarum curvaturam latera, Regio pluvialis, 610 m, 4 July 1893, V. Schiffner Iter Indicum 1893/94 No 701 (FH 00458029!); Prov. Batavia, In monte Salak; in silvis primaevae ad latus septentr. ad arbores, Regio pluvialis, 1000 m, 5 Dec 1893, V. Schiffner Iter Indicum 1893/94 No 702 (FH 00458030!); Prov. Batavia, Ad decliv septentr. montis Salk in faucibus torrentis Tjiapus, ad saxa, Regio pluvialis 800 m, 28 Jan 1894, V. Schiffner Iter Indicum 1893/94 No 703 (FH 00458031!);

=*Plagiochila blepharophora* var. *multiciliata* Schiffn., Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien. Mathematisch-Naturwissenschaftliche Klasse 70: 189 (1900)

Type citation: *n.v.*

Type: Sumatra "Sumatra occid.: in monte Singalang, ... (n.707)", 24 Jul. 1894

=*Plagiochila elegantissima* Herzog, Transactions of the British Bryological Society 1: 289 (1950)

Type citation: *n.v.*

Type: Sarawak

*Plagiochila estipulata* Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 29 (1904) = Species Hepaticarum 2: 401 (1904)

Type citation: *Nova Guinea* (Exped. d. Gazelle)

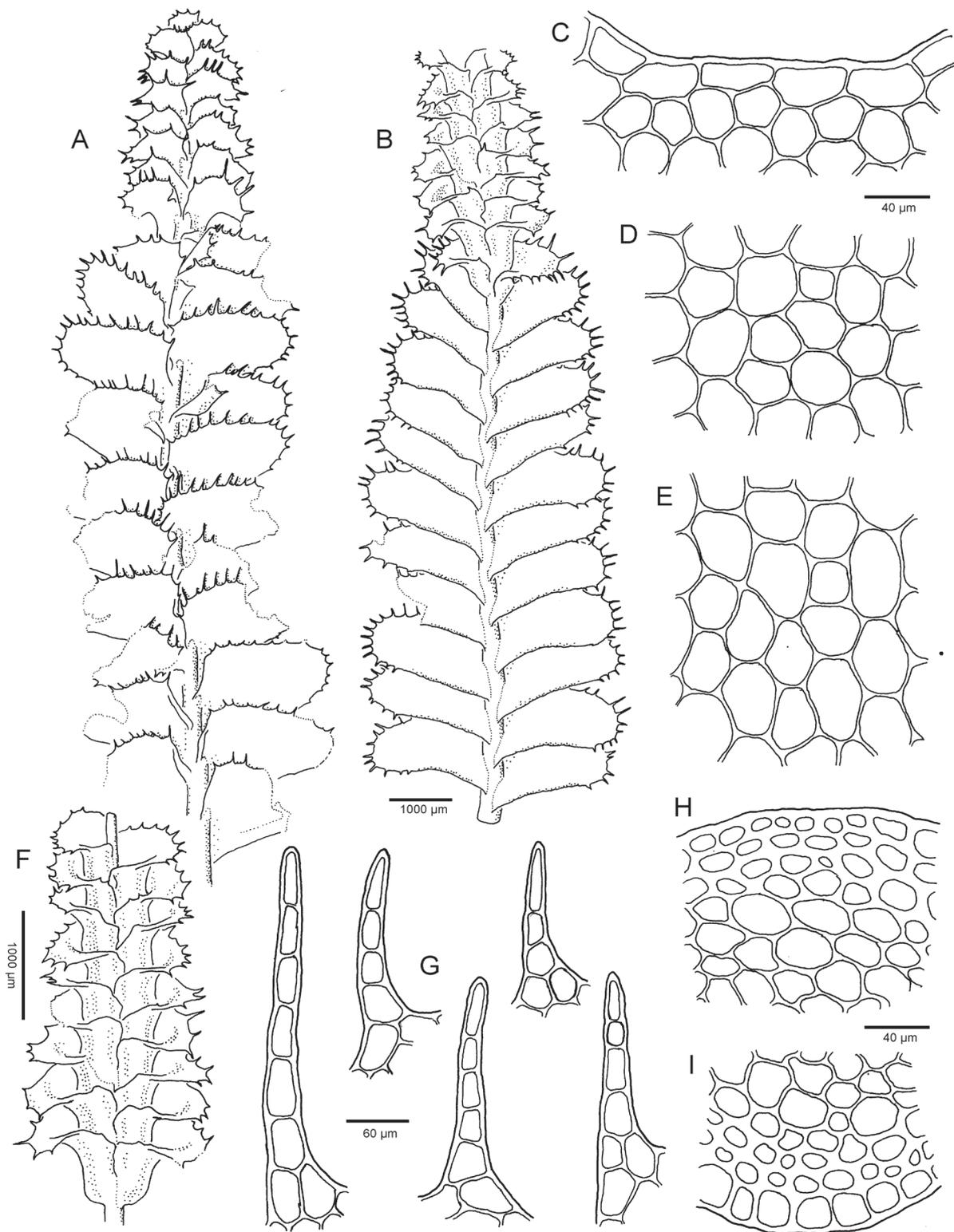
Type: New Guinea, Gazelle Expedition (G 00064119!)

**Notes:** The plant in the type of *P. estipulata* is consistent in its entire antical leaf margins, and small, triangular teeth around apex and on the postical leaf margin. No long ciliate or spinose dentate teeth are present. The sac is consistently small, inclined with respect to the stem, and the ventral stem surface is visible between the leaves. The male bracts are more or less entire. The relationships between the plants represented in the types of *P. estipulata* and *P. blepharophora* require further investigation.

**Etymology:** eyelash bearing, in reference to the long spinose-ciliate teeth around the leaf margin.

**Description:** Plants with irregularly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 40 mm long, monomorphic; primary shoots 2.8–3.7 mm wide; branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, in primary shoots to 400 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 3 layers, cortical cells on the dorsal side of the stem have walls continuously thickened, are evenly sized and smaller than medulla cells; on the ventral side of the stem the inner two cortical cell layers have continuously thickened, yellow-brown pigmented cell walls, while the outer layer comprises larger cells quadrate in cross-section with longitudinal radial walls not as thickened as inner layer walls, this layer forms a weak hyalodermis on the ventral side of the stem; medulla cell walls are yellow-pigmented with weak continuous thickening and small triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves triangular-ovate, 1250–2450 µm long × 1070–1950 µm wide, dorsal margin straight or curved, apex rounded, ventral margin straight to shallowly curved in outer two thirds and curved at base; with 5–29 spinose ciliate teeth distributed around the apex and along ventral margin, evenly sized and spaced, dorsal margin entire or with a few teeth at outer end, teeth two cells broad at base, uniseriate above, cells long rectangular, capped by an elongated triangular cell with a rounded to acute apex; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving two or more cortical cell rows leaf-free. Marginal leaf cells oblong, 36–51 µm long × 17–27 µm wide, long axis parallel to leaf margin, walls with triangular trigones, free external wall with thin continuous thickening; medial leaf

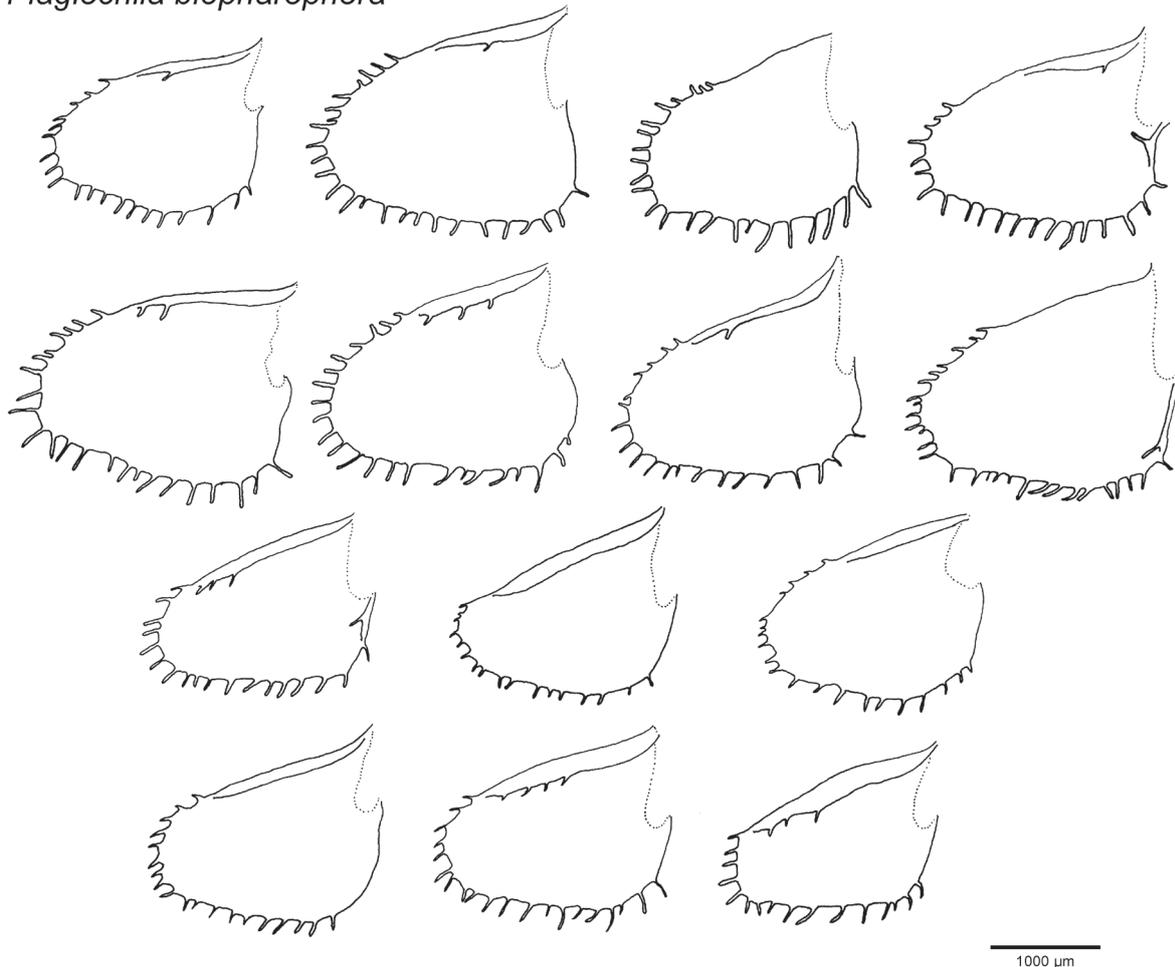
cells isodiametric to ovoid, 24–49  $\mu\text{m}$  long  $\times$  21–39  $\mu\text{m}$  wide, walls unpigmented, with triangular trigones, medial thickenings absent, cells in leaf base isodiametric to oblong, 27–60  $\mu\text{m}$  long  $\times$  29–41  $\mu\text{m}$  wide walls with triangular trigones, medial thickening absent. Cell surfaces smooth. Oil-bodies not known. Underleaves absent. Asexual reproduction by caducous leaf fragments.



**Fig 69.** *Plagiochila blepharophora*. A: ventral view of primary shoot terminated by male branch. B: dorsal view of primary shoot with male branch. C: marginal leaf cells. D: medial leaf cells. E: basal leaf cells. F: dorsal view of male bracts. G: five teeth from the leaf margin. H: dorsal sector of transverse section of stem from primary leafy shoot. I: ventral sector of transverse section of stem from primary leafy shoot. All from *M.A.M. Renner 6549 et al.* (NSW 880463).

Dioicous. Androecia intercalary on secondary or tertiary shoots that continue vegetative growth, singly or in pairs, the second produced by *Frullania*-type branching at the base of the leading male branch; lateral-intercalary and ventral-intercalary branches not associated with male branches; bracts in 5–20 pairs, contiguous to imbricate, but not closely packed, bract-lobe reduced and smaller than adjacent leaves, spinose-dentate with 3–8 teeth, apex rounded, epistatic, bract interior margin entire or with one tooth, not amplate; stem among bracts smooth. Gynoecia not seen. Figs 69, 70.

*Plagiochila blepharophora*



**Fig 70.** *Plagiochila blepharophora* leaves, all from M.A.M. Renner 6549 *et al.* (NSW 880463).

**Recognition:** *Plagiochila blepharophora* can be recognized by the combination of patent, imbricate, ovate-triangular leaves bearing spinose-ciliate teeth around the apex and on the ventral margin, the ventral leaf base being revolute but not forming a leaf pouch, the absence of conspicuous ciliate underleaves, and the male bract lobes bearing up to eight teeth. *Plagiochila blepharophora* could be confused with any of the other sect. *Cucullatae* species in Australia, with which it shares the ciliate leaf teeth, and patent leaves with revolute basal margins. In particular small phases of *P. blepharophora* are similar to *P. vitiensis*, and small plants of *P. bantamensis* are similar to *P. blepharophora* in their absence of a conspicuous leaf pouch and ciliate leaf margins.

However, *Plagiochila blepharophora* can be distinguished from *P. bantamensis* in that the leaves of *P. bantamensis* are triangular-oblong or triangular-falcate and have teeth on all margins, rather than triangular ovate with an entire dorsal margin, and conspicuous underleaves are present on all shoots of *P. bantamensis* regardless of size. In addition the male bracts of *P. bantamensis* are usually entire, while those of *P. blepharophora* are conspicuously and consistently dentate.

*Plagiochila blepharophora* can be distinguished from *Plagiochila vitiensis* by the more numerous teeth, up to 29, on the margins of ovate triangular leaves, versus fewer teeth, up to 15, on the margins of oblong ovate leaves in *P. vitiensis*.

*Plagiochila blepharophora* can be distinguished from *P. sydneyensis* but the longer ciliate teeth on the ventral leaf margin, the entire dorsal margin, and the absence of a fusiform or pyriform leaf pouch from all leaves, including the largest.

*Plagiochila blepharophora* can be distinguished from *P. sandei* by the entire dorsal leaf margin and smaller plant size, with shoots up to 4 mm wide, as opposed to the shoots up to 13 mm wide in *P. sandei*.

**Distribution and Ecology:** *Plagiochila blepharophora* is distributed from southern Japan, through Thailand, Malaysia, Indonesia, the Philippines, east to the Caroline Islands (Inoue 1984) and south to Australia. In Australia *P. blepharophora* is known from a few locations in the Wet Tropics Bioregion of north-east Queensland in rainforests between 100 and 1000 m elevation, where it grows as an epiphyte on tree trunk bases or a lithophyte on the sides of granite boulders.

**Variation:** Australian plants have ovate leaves, and conspicuously toothed male bracts, which is discordant with patterns of variation in overseas specimens. Further investigation into relationships between Australian, Malesian and Oceanian plants is required.

**Representative specimens examined:** Australia, Queensland, Cook, Palmerston National Park, track to Cedar Falls and Tchupala Falls, c. 100 m from Crawford Lookout, 17°36'43"S 145°47'32"E, 11 Jul 1994, *E.A. Brown 94/439, R.G. Coveny & B. Tan* (NSW 297001); Cook, Wooroonooran National Park, South Johnston River, Maple Creek, at Maple Creek Road crossing, 17°41'19"S 145°41'55"E, 590 m, 5 April 2012, *M.A.M. Renner 6549, V.C. Linis & E.A. Brown* (NSW 880463); Tully Falls Road, Charmill Creek, Tully Falls National Park, 17°42'03"S 145°31'26"E, 1000 m, 31 May 2014, *M.A.M. Renner 7086 & T.C. Wilson* (NSW 870335).

***Plagiochila bantamensis*** (Reinw., Blume & Nees) Mont., Voyage dans l'Amérique Méridionale... Botanique 7(2): 82 (1839)

Basionym: *Jungermannia bantamensis* Reinw., Blume & Nees, Nova Acta Physico-Medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosorum Exhibentia Ephemerides sive Observationes Historias et Experimenta 12: 235 (1824) [1825]

*Type citation:* Habitat in montibus altis Provinciae *Bantam* Iavae insulae ad terram. *Blume*. V. c. fr.

*Type:* Indonesia. Java. Bantam, Blume (c. per.) (holotype: STR, isotype: FH)

=*Plagiochila aequitexta* Steph., Bulletin de l'Herbier Boissier, sér. 2, 3: 531 (1903) = Species Hepaticarum 2: 335 (1903)

*Type citation:* *N. Guinea*, ad Flum. Gogol (Kärnbach), *Borneo*, Baram, (Everett)

*Type:* Borneo, Baram, 1892, *A. Everett 17* (lectotype designated by Bonner (1962): G 00064096!)

=*Plagiochila auriculata* Mitt., Seemann, Flora Vitiensis: 408 (1871) [1873]

*Type citation:* Samoa (Powell! n.6)

*Type:* Samoa, *Powell 6* (holotype: NY; isotype: G 00121816!)

=*Plagiochila bantamensis* var. *minor* Lindenb., Species Hepaticarum 2-4: 105 (1840)

*Type citation:* *n.v.*

*Type:* Philippines: in Manila insula, *Meyen* (holotype: STR)

=*Plagiochila didrichsenii* Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 26 (1904) = Species Hepaticarum 2: 398 (1904)

*Type citation:* *Insulae Nicobarae* (F. Didrichsen).

*Type:* Nicobar Islands: *Insulae Nicobarae*, *F. Didrichsen*, ex herb. Jack ex herb. Gottsche sub *Plag. Didericiana* G. ms. (G 00064095!)

=*Plagiochila elmeri* Steph., Leaflets of Philippine Botany 2: 385 (1908)

*Type citation:* Type specimen 9343 *A.D.E. Elmer*, Lueban, Province of Tayabas, Luzon, May, 1906.

*Type:* Philippines: Lucban, Province of Tayabas, Luzon, May 1906, *Elmer*, n.9343

=*Plagiochila everettiana* Steph., Bulletin de l'Herbier Boissier, sér. 2, 3: 969 (1903) = Species Hepaticarum 2: 384 (1903)

*Type citation:* *Borneo*, Sarawak (Everett)

*Type*: Borneo, Sarawak, Peninsula Theis, 1892, *A. Everett* (lectotype designated by Bonner (1962): G 00064094!)  
 = *Plagiochila goethartiana* Schiffn., Die Hepaticae der Flora von Buitenzorg: 170 (1900)

*Type citation*: n.v.

*Type*: Borneo: ... in herbario Lugduno-Batavo (ex herb. Sande Lacoste) leg. Korthals, n.v.

= *Plagiochila grandistipula* Inoue, Bulletin of the National Science Museum, Tokyo. Series B, Botany 1: 89 (1975)

*Type citation*: New Caledonia: Poindimié, Povila, forêt humid, cur crête schisteuse, 400 m alt., leg. McKee no. 28-769 (TNS; duplicate in PC)

*Type*: n.v.

= *Plagiochila meyeniana* Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 23 (1904) = Species Hepaticarum 2: 394 (1904)

*Type citation*: Manila (Meyen)

*Type*: Philippines: Manila, *Meyen* ex herb. Nees (G 00112895!)

= *Plagiochila parvisacculata* Steph., Bulletin de l'Herbier Boissier, sér. 2, 3: 973 (1903) = Species Hepaticarum 2: 388 (1903)

*Type citation*: Nova Guinea orientalis (Lauterbach)

*Type*: Papua New Guinea: Morobe Prov., River Gogol, *Lauterbach 873d* (lectotype designated by Piippo (1989): G 00113127!) Residual syntype: *Lauterbach 988d* (G 00113126! JE)

**Notes**: The type of *P. aequitexta* contains a couple of well-developed shoots, and they equate well with *P. meyeniana*.

The type of *P. auriculata* is similar to the type of *P. meyeniana*, including the underleaves.

The type of *Plagiochila didrichsenii* has leaves with a basal sac whose margin is obscured from below, but ciliate such that the cilia spread onto the ventral surface of the leaf. The leaves are falcate, and sparsely ciliate on margins, but not on the dorsal margin. The leaves are caducous.

The plant in the type of *P. everettiana* has long narrow leaves with long cilia around their postical margin and apex, but not the antical margin, the leaf base has flap within which is embedded a nearly spherical sac. Plants are relatively large.

The plant in the type of *P. meyeniana* has large underleaves with a prominent disc that covers the bases of adjacent leaves, including their sacs. It is also a large plant.

The leaves bear numerous close-set cilia toward the base of the postical margin, and smaller spinose teeth around the apex. There are numerous one or two celled triangular teeth on the antical margin. The auricle bears numerous hooked cilia, and is quite intricate; there is a weakly inflated sac. The underleaf margins are covered by dense, sometimes branched, cilia, and are deeply bifid to near the base, the underleaf disc is ventrally pinched at the sinus apex. This plant possesses a number of unusual features associated with the ornamentation of leaves and underleaves, and the stature of the underleaves suggesting that relationships between it and plants represented in types of other names currently synonymized with *P. bantamensis* may warrant further investigation.

The plant in the type of *P. parvisacculata* has leaves with small triangular teeth around the apex, which increase in length along the postical margin toward the stem insertion becoming long cilia toward the small sac with its densely ciliate auricle whose margin is visible in ventral view. Small bifid underleaves are present on the stem.

**Etymology**: from the Bantam Province, Java.

**Description**: Plants with sparingly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; leafy shoots horizontally spreading or pendulous, to 40 mm long, monomorphic; primary shoots 2.5–4.2 mm wide, branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown, to 350 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 4 layers dorsally and ventrally, narrowing to two layers laterally, cortical cells have walls continuously thickened, red-brown pigmented, the cells of the outermost tier are smaller than the internal cortical cells, which are similar in size to the medullar cells; medulla cell walls are yellow-pigmented with weak continuous thickening and small triangular trigones. Rhizoids scattered, on stolons arising from the lateral merophytes at

the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves imbricate, succubously inserted and orientated, on primary shoot leaves triangular-oblong to oblong-falcate, 2400–3550  $\mu\text{m}$  long  $\times$  1300–1700  $\mu\text{m}$  wide, dorsal margin straight or shallowly curved in outer half and shallowly arched in inner half, inrolled, apex truncate, ventral margin straight to continuously shallowly arched, base moderately ampliate, often with a pouch formed by invagination of abaxial leaf surface, pouch nearly spherical when fully expressed; dorsal margin, apex and ventral margin with 35–57 ciliate teeth fairly regularly spaced, somewhat closer at base of dorsal and ventral margins, longer on ventral margin and especially on the ampliate base, teeth two or three cells broad at base, uniseriate above, cells long rectangular, capped by an elongated triangular cell with an acute apex; leaf insertion J-shaped, recurved at ventral end, decurrent dorsally, attaining dorsal stem midline, not attaining the ventral stem midline, leaving four or more cortical cell rows leaf-free. Marginal leaf cells oblong, 23–35  $\mu\text{m}$  long  $\times$  10–19  $\mu\text{m}$  wide, long axis parallel to leaf margin, walls with triangular trigones and weak continuous thickening on the free external wall, medial thickenings absent; medial leaf cells isodiametric, pentagonal, hexagonal, or ovoid, 20–31  $\mu\text{m}$  long  $\times$  15–26  $\mu\text{m}$  wide, walls unpigmented, with triangular trigones, medial thickenings absent, cells in leaf base ovoid, 29–47  $\mu\text{m}$  long  $\times$  20–27  $\mu\text{m}$  wide walls with triangular trigones, medial thickening absent, walls sometimes with thin continuous thickening. Cell surfaces smooth. Oil-bodies not known. Underleaves present, well-developed, bifid, armed with numerous ciliate teeth on margins of lobes and disc. Asexual reproduction by caducous leaf fragments from the outer half of the leaf, inner half of the leaf usually remaining intact on older shoot sectors.

Diocious. Androecia intercalary shoots that continue vegetative growth, singly or rarely in pairs, the second produced by *Frullania*-type or lateral-intercalary branching at the base of the leading male branch; ventral-intercalary branches not associated with male branches; bracts in up anything from 5 to 35 or more pairs, male branches often characteristically long, bracts imbricate, but not closely packed, bract-lobe reduced and smaller than adjacent leaves, spreading, transversely orientated, rounded to ovate, entire or with bidentate apex, epistatic, bract interior margin entire, not ampliate; stem among bracts smooth, underleaves present among bracts. Gynoecia at apices of shoots; bracts triangular-oblong, 3000–3800  $\mu\text{m}$  long  $\times$  1800–2400  $\mu\text{m}$  wide; dorsal margin arched, inrolled, apex truncate, ventral margin straight in outer half and ampliate at base; dorsal margin, apex, and ventral margins with around 50 lacinate teeth, curved, sometimes branched, coarser than teeth on leaves, longer on the ampliate base; bract cells as for leaf cells; cell surfaces smooth; female bracteole present. Subfloral innovations present, one or two produced by lateral-intercalary branching from between the female bracts and the perianth, or between the female bracts and the preceding vegetative leaves. Mature perianth not seen, immature perianth campanulate, dorsal and ventral keels without wings; laterally compressed but with an inflated base, lateral walls plane; labia curved, each with spinose-ciliate teeth. Fig. 71.

**Recognition:** *Plagiochila bantamensis* is a fairly distinctive species, despite exhibiting considerable variation among individuals. The leaves are oblong-falcate, to oblong-triangular and have long ciliate teeth on the margins, particularly around the ventral base. Larger leaves have the saccate pouch at the ventral leaf base so characteristic of sect. *Cucullatae*, in *P. bantamensis* this pouch bears ciliate teeth on its free margin, and also occasionally on its surface. *Plagiochila bantamensis* shoots bear conspicuous bifid underleaves whose margins are similarly armed with long ciliate teeth, underleaves are present regardless of shoot stature though their size is positively correlated with shoot stature and the largest most conspicuous underleaves are borne on the largest shoots, which also tend to have the largest leaf pouches.

*Plagiochila bantamensis* shares with *P. chauviniana* the ciliate teeth and leaf pouch, but *P. chauviniana* differs from *P. bantamensis* in that the margin of the leaf pouch flares onto the ventral leaf surface, forming a distinct auricle, whereas in *P. bantamensis* the pouch margin is not flared, and is obscured by the pouch itself; the teeth on leaf margins in *P. chauviniana* are long triangular rather and the dorsal margin is entire, rather than the ciliate teeth and toothed dorsal margin as found in *P. bantamensis*; and the leaves are broadly elliptic oblong, rather than oblong-falcate or triangular-oblong as in *P. bantamensis*.

Small plants of *Plagiochila bantamensis* are superficially similar to *P. vitiensis* but *P. vitiensis* has fewer shorter teeth on the leaf margins, and the leaves are elliptic-ovate, rather than oblong-falcate to oblong-triangular, and no underleaves. Even the largest plants of *P. vitiensis* do not develop a leaf pouch, at most they express revolute dorsal and ventral leaf margins immediately above the stem insertion.

*Plagiochila bantamensis* differs from *P. sydneyensis* in the long ciliate teeth on the oblong-falcate leaves, and the spheroidal leaf pouch, in *P. sydneyensis* the teeth are triangular to spinose-ciliate, and the pouch is often fusiform or pyriform, rather than spheroidal, and the leaves are oblong-ovate.

*Plagiochila bantamensis* differs from *P. vitiensis* again in the long ciliate teeth on the oblong-falcate leaves, and spheroidal leaf pouch, in *P. vitiensis* the teeth are triangular to triangular-acuminate, the leaves are oblong and never develop a pouch—at most the dorsal and ventral margins immediately above the stem insertion are revolute.

*Plagiochila bantamensis*

**Fig 71.** *Plagiochila bantamensis* leaves, from M.A.M. Renner 6287 et al. (NSW 896671), M.A.M. Renner et al. (NSW 849176) M.A.M. Renner 6286, V.C. Linis & E.A. Brown (NSW 896670), M.A.M. Renner 6492, V.C. Linis & E.A. Brown (NSW 909521 p.p.) (NSW 870777) NSW 870748, NSW 899754.

**Distribution and Ecology:** *Plagiochila bantamensis* occurs in southern Japan on Ryukyu Islands in the north, Sri Lanka in the west, through Malaysia, Cambodia, Philippines, Borneo, Java, Papua New Guinea, New Caledonia to Samoa in the east, and Australia in the south (Inoue 1984, 1986). In Australia *Plagiochila bantamensis* is confined to the Wet Tropics Bioregion of north-east Queensland, where it grows in wide range

of tropical rainforests from close to sea level to more than 1000 m elevation, including complex mesophyll-vine forest and microphyll-vine thickets. *Plagiochila bantamensis* occupies a wide range of microsites usually close to the forest floor, including on exposed roots over boulders on the side of a stream; on the side of granite boulders, on tree trunks, and on buttress roots, on vines, on dead standing trees, and on shrubs.

**Representative specimens examined:** Australia: Queensland: Cook, Daintree National Park, Mossman Gorge, Rex Creek, 16°28'11"S 145°19'37"E, 105 m, 24 Mar 2012, *M.A.M. Renner 6286, V.C. Linis & E.A. Brown* (NSW 896670); *ibid.*, *M.A.M. Renner 6287, V.C. Linis & E.A. Brown* (NSW 896671); *ibid.*, *M.A.M. Renner 6293, E.A. Brown & V.C. Linis*, (NSW 849176); Cook, Daintree National Park, Mossman Gorge, Rex Creek, upstream from swingbridge, 16°28'13"S 145°19'42"E, 105 m, 24 Mar 2012, *M.A.M. Renner 6277, V.C. Linis & E.A. Brown* (NSW 896658); Cook, Daintree National Park, Mossman Gorge, Rex Creek, at water intake, 16°28'26"S 145°19'21"E, 160 m, 17 May 2014, *M.A.M. Renner 6947 & T.C. Wilson* (NSW 870748); Little Surprise Creek, track to Barron Falls, 2 km SE of Kuranda, 16°50'S 145°38'E, 360 m, 9 Jul 1994, *H. Streimann 54120* (CANB 9501793); Mulgrave River Forestry Road, 18 km S of Gordonvale, 17°16'S 145°47'E, 80 m, 15 Dec 1990, *H. Streimann 46525* (CANB 9015006); Wooroonooran National Park, Babinda Stream, Goldfields track, 17°19'54"S 145°51'52"E, 75 m, 3 Apr 2012, *M.A.M. Renner 6494, V.C. Linis & E.A. Brown* (NSW 909522); The Boulders, 6 km W of Babinda, 17°21'S 145°53'E, 80 m, 3 Dec 1990, *J.A. Curnow 3734* (CANB 9408831); Wooroonooran National Park, Babinda Stream, Goldfields track, 17°19'54"S 145°51'52"E, 75 m, 3 Apr 2012, *M.A.M. Renner 6492, V.C. Linis & E.A. Brown* (NSW 909521 *p.p.*); North Kennedy, Tully Falls National Park, Tully Falls Road, Charmill Creek, 17°42'03"S 145°31'26"E, 1000 m, 31 May 2014, *M.A.M. Renner 7085 & T.C. Wilson* (NSW 870787); North Kennedy, Tully Falls National Park, Tully Falls Road, track to Rhyolite Pinnacle from Charmillan Creek, 17°42'40"S 145°33'12"E, 1085 m, 1 Jun 2014, *M.A.M. Renner 7109 & T.C. Wilson* (NSW 870812); Cooroo Logging Area, 16 km WNW of Innisfail, 17°31'S 145°53'E, 100 m, 28 Jun 1984, *H. Streimann 29993* (CANB 8408348); Walter Hill Range, 25 km SE of Ravenshoe, 17°46'S 145°41'E, 780 m, 2 Jul 1984, *H. Streimann 30501* (CANB 8409006); Cardwell Range 41 km SE of Ravenshoe, Culpha Creek catchment, 17°56'S 145°40'E, 780 m, 23 Jun 1984, *H. Streimann 28988* (CANB 8407116); *ibid.*, *H. Streimann 28993* (CANB 8407121); Echo and Davidson Creeks Divide, Cardwell Range, 46 km SE of Ravenshoe, 17°59'S 145°40'E, 780 m, 23 Jun 1984, *H. Streimann 29077* (CANB 8407205); My Tyson Track, 2 km W of Tully, 17°56'S 145°55'E, 480 m, 2 Dec 1990, *J.A. Curnow 3659* (CANB 9408746); Blencoe Creek, Cardwell Range, 48 km NW of Cardwell, 18°03'S 145°39'E, 740 m, 17 Jun 1986, *J.A. Curnow 821* (CANB 781949); Kirrama State Forest, 7<sup>th</sup> bridge along road, SE slope above Kennedy, 18°11'44"S 145°52'07"E, 386 m, 15 Jun 2001, *D.C. Cargill 127* (CANB 644610.1); Yuccabine Creek, Kirrama Road, Cardwell Range, 27 km WNW of Cardwell, 18°12'S 145°45'E, 550 m, 20 Jun 1984, *H. Streimann 28679* (CANB 8406686); Blue Water Creek, Old Mill Road, 39 km WSW of Ingham, 18°45'S 145°48'E, 600 m, 19 Jun 1984, *H. Streimann 28382* (CANB 8406188); Paluma Range, Paluma Reservoir Road, Mt Spec State Forest, 35 km S of Ingham, 18°58'S 146°09'E, 880 m, 27 Oct 1995, *H. Streimann 57892* (CANB 9607376).

***Plagiochila sandei*** Dozy ex Sande Lac., Nederlandsch Kruidkundig Archief. Verslagen en Mededelingen der Nederlandsche Botanische Vereeniging 4: 92 (1856)

*Type citation:* Habitat insulam *Javae*, prope *Gadok*, Jungh.

*Type* (So & Grolle 1999): Indonesia. Java. prope *Gadok*, *F. W. Junghuhn s.n.* (L 99396)

=*Plagiochila altecristata* Steph., *Species Hepaticarum* 6: 120 (1917)

*Type citation:* Java. (Fleischer legit.)

*Type:* *n.v.*

=*Plagiochila blepharophora* var.  $\delta$  *major* Schiffn., *Forschungsreise S.M.S. "Gazelle"* 4, *Botanik*: 5 (1889) [1890]

*Type citation:* *n.v.*

*Type:* Bismarck Archipelago, Neu-Hannover, Bachscrufurt, Bergworld an adsten, 24 July 1895, *Gazellen Expedition* (FH 00458032!)

=*Plagiochila kaernbachii* Steph., *Bulletin de l'Herbier Boissier*, sér. 2, 3: 968 (1903) = *Species Hepaticarum* 2: 383 (1903)

*Type citation:* *New Guinea* (Kaernbach)

*Type:* *n.v.*

=*Plagiochila nubila* Steph., *Bulletin de l'Herbier Boissier*, sér. 2, 3: 972 (1903) = *Species Hepaticarum* 2: 387 (1903)

*Type citation:* Nova Guinea, Cloudy Mountains (Micholitz), Sattelberg (Lauterbach).

*Type:* n.v.

=*Plagiochila nymanii* Steph., Species Hepaticarum 6: 186 (1921)

*Type citation:* Nova Guinea (Nyman legit)

*Type:* n.v.

=*Plagiochila sandei* f. *remotidens* Herzog, Transactions of the British Bryological Society 1: 287 (1950)

*Type citation:* Sarawak G. Balapau, c.300m, 1932, leg. Richards n.2458.

*Type:* n.v.

=*Plagiochila seemannii* Mitt., Bonplandia 9: 367 (1861)

*Type citation:* Seemann, No. 864.

*Type:* Fiji, Seemann, n.864, (NY, ex herb. Mitten G 00265227!)

=*Plagiochila seemannii* var. *perspinosa* Herzog, Hedwigia 78: 243 (1938)

*Type citation:* Fiji, leg. A.C. Smith, n.1857

*Type:* n.v.

=*Plagiochila spinosociliata* Steph., Bulletin de l'Herbier Boissier, sér. 2, 3: 973 (1903) = Species Hepaticarum 2: 388 (1903)

*Type citation:* Nova Guinea orient. (Kärnback, Lauterbach, Weinland, Micholitz).

*Type:* n.v.

=*Plagiochila robinsonii* Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 24 (1903) = Species Hepaticarum 2: 396 (1903)

*Type citation:* Norfolk Insula (Robinson)

*Type:* Australia, Norfolk Island, Isaac Robinson comm. F. v. Muller Feb 1885, ex herb. Stephani (G 00067826! BM 000671201! MEL 1039481!)

**Notes:** The type of *P. robinsonii* is a huge plant, which is a reasonable match with the illustration of *P. sandei* in Inoue (1984).

The type of *Plagiochila seemanii* is not a good match with *Plagiochila sandei* as illustrated by Inoue (1984), or indeed with the plant represented in the type of *P. robinsonii*, *P. seemanii* has long triangular oblong leaves, an entire antical margin, and short triangular teeth on the leaf margin. *Plagiochila sandei* may be a complex and further investigation of its circumscription is probably warranted.

**Etymology:** sandei, of Sande Lacoste.

**Description:** As no Australian specimens besides the type of *Plagiochila robinsonii* have been seen, the description here is adapted from Inoue (1984) Plants with irregularly branched leafy shoots arising from a basal creeping stolon; stolons arising from other stolons by lateral-intercalary branching; horizontally spreading or pendulous; shoot systems to 120 mm long, monomorphic; primary shoots 10–13 mm wide; branches arising by lateral-intercalary branching, *Frullania*-type and ventral-intercalary vegetative branching absent. Stems without paraphyllia, lamellae or paraphyses; stem reddish-brown to blackish, in primary shoots to 800 µm diameter, transversely elliptic, surfaces apparently smooth; cortical cells in 5–8 layers, cell walls heavily and continuously thickened; medulla cell walls thin or more or less thick-walled. Rhizoids scattered, on stolons arising from the lateral merophytes at the base of leaves and from the ventral merophyte row. Leaves within stolon sector reduced, entire, remote to contiguous. Leaves closely imbricate, succubously inserted and nearly horizontally orientated, spreading, oblong-ovate, 4500–5300 µm long × 3200–4000 µm wide, dorsal margin nearly straight or shallowly arched, apex rounded, ventral margin straight to in outer two thirds and ampliate at base with a tubular sac at the stem insertion, sac oblong in outline, variable in size, free margin strongly inrolled with many irregularly sized cilia; teeth persistent, spinose, one or two cells broad at base, uniseriate above for up to 12 cells, with a sharp, acute terminal cell. Medial leaf cells ovoid, 35–42 µm long × 28–37 µm wide, cells in leaf base isodiametric to oblong, 55–75 µm long × 35–50 µm wide walls thin or slightly thickened, trigones absent or very small. Oil-bodies not known. Underleaves usually absent, or vestigial, 1 or 2 celled, filiform. Asexual reproduction by propagules on leaves.

Dioicous. Androecia intercalary on shoots that continue vegetative growth, in terminal clusters of (1–)2–6 produced by lateral-intercalary (and *Frullania*-type?) branching at the base of the leading male branch, long spicate; bracts in 5–20 pairs, contiguous to imbricate, but not closely packed, bract-lobe reduced and smaller than adjacent leaves, entire, apex rounded. Gynoecia at apices of shoots; bracts similar to leaves in size and shape, with a smaller tubular sac on the ventral base, teeth on margin more numerous and coarser than on leaves. Subfloral innovations present, one produced when unfertilized. Perianth long cylindrical, 5000–5400 µm long and around 3000 µm wide, labia curved, each with spinose-dentate teeth, dorsal and ventral keels without wings.

**Recognition:** *Plagiochila sandei* can be recognized by its large size, absence of conspicuous underleaves and well-developed leaf pouch. The combination of stature, with shoots up to 13 mm wide, and conspicuously ciliate leaves with ciliate teeth on all margins will prevent confusion with other species of sect. *Cucullatae*. However, the isotype of *P. robinsonii* in MEL had been identified as *P. intertexta*, from which *P. sandei* differs in the ciliate, rather than spinose, teeth.

**Distribution and Ecology:** Java, Sumatra, Borneo, Philippines, Papua New Guinea, Fiji,

The only Australasian record is the type of *Plagiochila robinsonii* from Norfolk Island, collected in the late 19<sup>th</sup> century by Isaac Robinson. That this large, conspicuous epiphyte and lithophyte of forest interiors has not been collected elsewhere in Australia, and has not been recollected on Norfolk Island suggests it no longer occurs there.

**Excluded from the Australian flora.**

***Plagiochila chauviniana*** Mont., Annales des Sciences Naturelles; Botanique, sér. 3, 11: 34 (1849)

Type citation: Patria ignota.

Type: New Guinea, patria ignota, ex herb. Chauvin and ex herb. Bischerelle (isotype: G 00121242!)

=*Plagiochila aurita* Schiffn., Forschungsreise S.M.S. "Gazelle". 4, Botanik: 6 (1889) [1890]

Type citation: n.v.

Type: Indonesia. West Irian. Mac-Cluer-Bay. 1875, Naumann (holotype: FH! isotype: G 00282868!)

=*Plagiochila longispica* Mitt., Seemann, Flora Vitiensis: 407 (1871) [1873]

Type citation: Samoa (Powell ! n. 58).

Type: Samoa. Powell 58 (BM, G, NY)

=*Plagiochila micholitzii* Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 21. 1903 = Species Hepaticarum 2: 393 (1903)

Type citation: *Insulae Salomonis* (Micholitz).

Type: Solomon Islands, *Micholitz* (lectotype designated by Piippo (1989): G 00067670! isolectotypes: G 00067671! G 00067672!)

=*Plagiochila miokensis* Steph., Bulletin de l'Herbier Boissier, sér. 2, 4: 24 (1903) = Species Hepaticarum 2: 396 (1903)

Type citation: *Insula Mioko*, Neulauenburg (Micholitz).

Type: New Guinea. Bismarck Archip.: Duke of York group, Mioko, Oct 1893, (?Neulauenburg) *Micholitz* (holotype: G 00064120, isotype: BM)

=*Plagiochila novae-guineae* Sande Lac., Annales Musei Botanici Lugduno-Batavi 1: 292 (1863) [1864]

Type citation: n.v.

Type: New Guinea. *Zippelius* (holotype: L, isotypes: FH, JE, L-910, S)

=*Plagiochila zippelii* Sande Lac., Annales Musei Botanici Lugduno-Batavi 1: 293 (1863) [1864]

Type citation: n.v.

Type: New Guinea. *Zippelius* (holotype: L-901.314.21, isotypes: G, FH, L-901.314.22, S)

**Notes:** The isotype of *P. chauviniana* in G comprises two shoots between mica sheets and another packet containing several shoot fragments and loose leaves. The plant has ovate leaves with an elliptical sac and exposed ciliate 'wing' appressed against the leaf. The teeth are ciliiform and continuous around the margin

from the apex to the base, increasing in length toward the base, uniseriate for most of their length and with elongate cells in the upper part.

The plant in the type of *Plagiochila aurita* has teeth short triangular, cells in teeth quadrate, sac spherical, wing large, auriculate, ciliate. Leaves narrower oblong than plant in type of *P. chauviniana*. Relationships between the plants represented in these two types requires further investigation.

Three specimens of the original material of *P. micholitzii* collected by Micholitz and held in G, may be duplicates of the same gathering, containing the same plant forming near pure turfs on the same ligniferous humic substrate in association with the same *Hymenophyllum*. One of these specimens was lectotypified by Piippo (1989), the others may then be isolectotypes. The plant within the lectotype of *P. micholitzii* exhibits considerable size based variation in sac development, but on large leaves when these are developed cilia project from behind the sac, so presumably the margin is not entire. Small underleaves of a few cells are present on the stems.

The plant in the type of *P. miokensis* bears a few widely separated cilia on its postical leaf margin, and has a sac that sits out away from the stem, the sac exhibits considerable size-based variation in development, on smaller leaves it is a simple inrolled tube, on large leaves it is a full, large, irregularly pyriform sac; in both cases the sac margins are entire, and are not visible in ventral view; there is no auricle.

***Plagiochila sciophila*** Nees ex Lindenb., Species Hepaticarum 2-4: 100 (1840)

Type citation: *n.v.*

Type: Nepal, Wallich, Herb. Neesii ab Esenbeck *n.v.*

No Australian specimens of *P. sciophila* have been seen, previous reports (Meagher 2005) may be referable to *P. vitiensis* or small phases of the widespread *P. bantamensis* within which leaves are fully caducous, and may not produce leaf-pouches in small shoots.

**Excluded from *Plagiochila***

***Acrobolbus epiphytus*** (Colenso) Briscoe, Phytotaxa 202: 59 (2015)

Basionym: *Marsupidium epiphytum* Colenso, Transactions and Proceedings of the New Zealand Institute 21: 64 (1889)

Type citation: Epiphytical on trunks of tree-ferns, low wet woods near Norsewood, County of Waipawa; 1885; W. C.

Type: *n.v.*

=*Plagiochila serrifolia* Steph., Journal and Proceedings of the Royal Society of New South Wales 48: 130 (1914) *syn. nov.*

Type citation: Australia, New South Wales (Wyong): Watts, 1100.

Type: Australia, New South Wales, Wyong, Aug 1910, W.W. Watts 1100 (holotype: G 00067820!)

**Notes:** The type of *Plagiochila serrifolia* bears striolate-papillose ornamentation, and in size, leaf shape, and dentition agrees with *Acrobolbus epiphytus*. Unfortunately the type is somewhat fragmented and basal plant parts and reproductive structures are missing, however the presence of the surface ornamentation is, in this instance, conclusive. *Plagiochila serrifolia* was placed in synonymy of *P. vitiensis* by Inoue (1986).

***Cryptoplagiochila radiculosa*** (Mitt.) S.D.F.Patzak, M.A.M.Renner & Heinrichs, Organisms, Diversity and Evolution 16: 492 (2016)

Basionym: *Plagiochila radiculosa* Mitt. in Hooker, Flora Novae-Zelandiae 2: 132 (1855).

Type citation: Northern Island: on *Weinmannia* bark, Tarawera, Colenso.

Type: New Zealand: Tarawera, Colenso 531 (lectotype designated by Inoue and Schuster (1971): NY 01020758!)

=*Plagiochila wattsii* Steph. ex Rodway, Papers and Proceedings of the Royal Society of Tasmania 1917: 105 (1918) *syn. nov.*

Type citation: On *Fagus* log, Pioneer track, Blue Tier (Weymouth). Determined by Stephani.

Type: *n.v.*

**Notes:** I have not located the type of *Plagiochila watsii* Steph. ex Rodway, but Rodway's description of dorsally secund, bifid leaves with an ampliate base is compatible only with *Cryptoplagiochila radiculosa*, a species widespread in Tasmania.

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