

Bucklandiella seppeltii, a new species of Grimmiaceae from Australasia, and its phylogenetic position based on molecular data

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Abstract: A new species, *Bucklandiella seppeltii* Bednarek-Ochyra, Ochyra, Sawicki & Szczecińska, is delimited by its distinct morphology and biogeography. The geographical range of the new species is restricted to the southern-temperate and southern-cool-temperate zones of Tasmania and New Zealand, with maximum occurrence on the South Island of the latter insular country. The species is described and illustrated and its distribution is mapped. The systematic position of *B. seppeltii* is revealed to be a sister to New Zealand *B. allanfifei* Bednarek-Ochyra & Ochyra by molecular evidence based on parsimony analysis of nuclear sequences. In some morphological and anatomical traits, *B. seppeltii* is similar to southern South American cool-temperate *B. heterostichoides* (Cardot) Bednarek-Ochyra & Ochyra but is distinct by its smooth laminal cells, strict hyaline leaf hair points, erect growth form, and very broadly recurved leaf margin in the distal portion.

Key words: Auckland Islands, Bryophyta, Campbell Islands, distribution, molecular phylogeny, New Zealand, South America, Tasmania, taxonomy

1. Introduction

The genus *Bucklandiella* Roiv. is well represented in Australasia, both in terms of frequency and cover. The real number of species in this region is still unknown because monographic studies on this genus are in progress and constantly yield additional new species or result in the resurrection of some species from obscurity. Fife (1995) recognized only 5 species in the moss flora of New Zealand that are currently positioned in *Bucklandiella*, the largest segregate of the traditionally understood *Racomitrium* Brid. (Bednarek-Ochyra et al., 2001; Ochyra et al., 2003).

No fewer than 8 species of *Bucklandiella* have been described from Australia and given names under *Grimmia* Hedw. (Streimann and Curnow, 1989). Of these, only 2 are now accepted as good species: *B. emersa* (Müll.Hal.) Bednarek-Ochyra & Ochyra and *B. pycnotricha* (Müll.Hal.) Bednarek-Ochyra, Ochyra & Seppelt (Bednarek-Ochyra and Ochyra, 2010, 2011). Two others, *Grimmia amoena* Broth. and *G. procumbens* Mitt., are considered to be identical to *B. sudetica* (Funck) Bednarek-Ochyra & Ochyra (Bednarek-Ochyra and Ochyra, 2013a), while *Grimmia sullivanii* Müll.Hal. [= *Racomitrium sullivanii*

(Müll.Hal.) Broth.] was merged with *R. crispulum* (Hook.f. & Wilson) Hook.f. & Wilson (Clifford, 1955) and its taxonomic status needs a careful reassessment. The remaining 3 species, including *Grimmia compactula* Müll.Hal., *G. cylindropyxis* Müll.Hal., and *G. pseudopatens* Müll.Hal., have never been taxonomically assessed.

Bucklandiella crispula (Hook.f. & Wilson) Bednarek-Ochyra & Ochyra is the most often reported species in Australasia but it is a collective and heterogeneous species because many species described from different parts of the austral regions were merged with it. Studies of various authors (e.g., Bell, 1974; Bednarek-Ochyra and Ochyra, 1998, 2012a, 2012b, 2012c, 2013a, 2013b; Bednarek-Ochyra et al., 1999; Blockeel et al., 2007, 2009a, 2009b; Ochyra et al., 2008a, 2008b; Ellis et al., 2011a, 2011b, 2012a, 2012b, 2013; Ochyra and van Rooy, 2013) revealed that in fact most of them are distinct and well-defined taxa having little in common with *B. crispula*.

As a result of critical taxonomic studies in the last 2 decades, no fewer than 3 new species of *Bucklandiella* have been described from New Zealand (Bednarek-Ochyra and Ochyra, 2010, 2011), 3 reported as new records (Blockeel et al., 2008; Ellis et al., 2011b) and 1 reinstated as

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a good species (Ellis et al., 2011b). Accordingly, the genus *Bucklandiella* consists at present of 12 species in New Zealand and 8 in Australia and Tasmania. Herein, the next species of the genus is described as new to science from Tasmania and New Zealand.

2. Material and methods

The present study is based upon a revision of all available herbarium specimens deposited in New Zealand and Australia, as well as other world herbaria, including AK, ALTA, BM, CHR, H, HO, KRAM, L, MO, NY, PC, and WELT. In addition, the first 2 authors carried out field work in Tasmania and New Zealand during which fresh material was collected for molecular studies.

2.1. DNA extraction

Total genomic DNA was extracted from herbarium material. Single stems were ground with silica beads in a Mini-BeadBeater-1 tissue disruptor for 50 s and subsequently processed using the Plant MiniSpin DNA kit (A&A Biotechnology) or Zymo Plant/Seed kit (Zymo) following the manufacturers' protocols. Extracted DNA samples were quantified using a Qubit fluorometer with dsDNABR kit (Invitrogen) and stored at -20°C .

2.2. ITS amplification and sequencing

For amplification and sequencing of the internal transcribed spacer (ITS) we used the primers of Fiedorow et al. (1998), which were successfully applied in previous studies on mosses (Sawicki et al., 2009). The ITS sequences were amplified in a volume of 25 μL containing 20 mM $(\text{NH}_4)\text{SO}_4$; 50 mM Tris-HCl (pH 9.0 at 25°C); 1.5 mM MgCl_2 ; 1 μL BSA; 200 μM each dATP, dGTP, dCTP, and dTTP; 1.0 μM of each primer, 1 U of Tfl polymerase (Epicentre), and 60 ng of the DNA. The reaction was processed at 94°C for 4 min followed by 30 cycles at 94°C for 1 min, 59°C for 1 min, and 72°C for 1.5 min, with a final extension step of 72°C for 5 min. Finally, 5 μL of the amplification product was visualized on 1.5% agarose gel with GelView staining (Novazym). Purified PCR products were sequenced in both directions using the ABI BigDye 3.1 Terminator Cycle Kit (Applied Biosystems) and then visualized using an ABI Prism 3130 Automated DNA Sequencer (Applied Biosystems).

2.3. Chloroplast *trnH-psbA* region amplification and sequencing

For amplification and sequencing of *trnH-psbA* we used the primers of Sang et al. (1997). The spacers were amplified in a volume of 25 μL containing 20 mM $(\text{NH}_4)\text{SO}_4$; 50 mM Tris-HCl (pH 9.0 at 25°C); 1.5 mM MgCl_2 ; 1 μL BSA; 200 μM each dATP, dGTP, dCTP, and dTTP; 1.0 μM of each primer; 1 U of Tfl polymerase (Eux); and 60 ng of the DNA. The reaction was processed at 94°C for 4 min followed by 35 cycles at 94°C for 1 min, 55°C for 1 min, and 72°C for 1 min, with a final extension step of 72°C

for 5 min. Subsequent stages were carried out as with the ITS sequences.

2.4. Molecular data analysis

Electropherograms were edited and assembled using Geneious R6 (Biomatters, USA). The assembled sequences were aligned using Muscle 3.6 (Edgar, 2004) and manually adjusted with Geneious R6. The gaps were excluded from all phylogenetic analyses because the alignment of ITS with the outgroup taxa resulted in many indels. Phylogenetic analyses were based exclusively on the ITS data set and were carried out using maximum parsimony (MP) with MEGA5 software (Tamura et al., 2007). The pairwise distances were estimated with the maximum composite likelihood method and initial trees were generated using the neighbor-joining method. The MP trees were obtained using the close-neighbor-interchange algorithm with search level 1 in which the initial trees were obtained with the random addition of sequences (10 replicates) as implemented in MEGA5. The strict consensus tree was created using MEGA5. Statistical significance of clades within inferred trees was evaluated using the bootstrap method (Felsenstein, 1985) with 2000 replicates.

Molecular delimitation of the closely related *Bucklandiella allanfifei* Bednarek-Ochyra & Ochyra, *B. heterostichoides* (Cardot) Bednarek-Ochyra & Ochyra, *B. seppeltii* sp. nov., and *B. striatipila* (Cardot) Bednarek-Ochyra & Ochyra was tested using the Species Delimitation plugin (Masters et al., 2011) available in the Geneious R6 software (Biomatters). This plugin implements the method of Rosenberg (2007) for calculating the probability of reciprocal monophyly under the null model of random coalescence. The Species Delimitation plugin also shows the probability that a member of a putative species could be identified correctly given the current alignment as the reference data set, based on findings of Hebert et al. (2003) and Ross et al. (2008). Both the ITS and the *trnH-psbA* data sets were used in this analysis.

3. Results

3.1. Molecular analysis

The ITS alignment has a total length of 529 bases. The data set contains 171 variable sites, of which 142 are parsimony-informative. The MP analysis resulted in 369 most-parsimonious trees with a consistency index of 0.810924 and a retention index of 0.871060.

Species of the genus *Bucklandiella* formed a monophyletic, well-supported clade (99% bootstrap support [BS]) (Figure 1). The main subjects of this study, *B. heterostichoides* and *B. seppeltii*, together with *B. striatipila* and *B. allanfifei*, joined in a moderately supported clade (69% BS). Within this clade, *B. seppeltii* and *B. striatipila* formed 2 separated, well-supported monophyletic clades (99% BS, respectively). Relatively good bootstrap

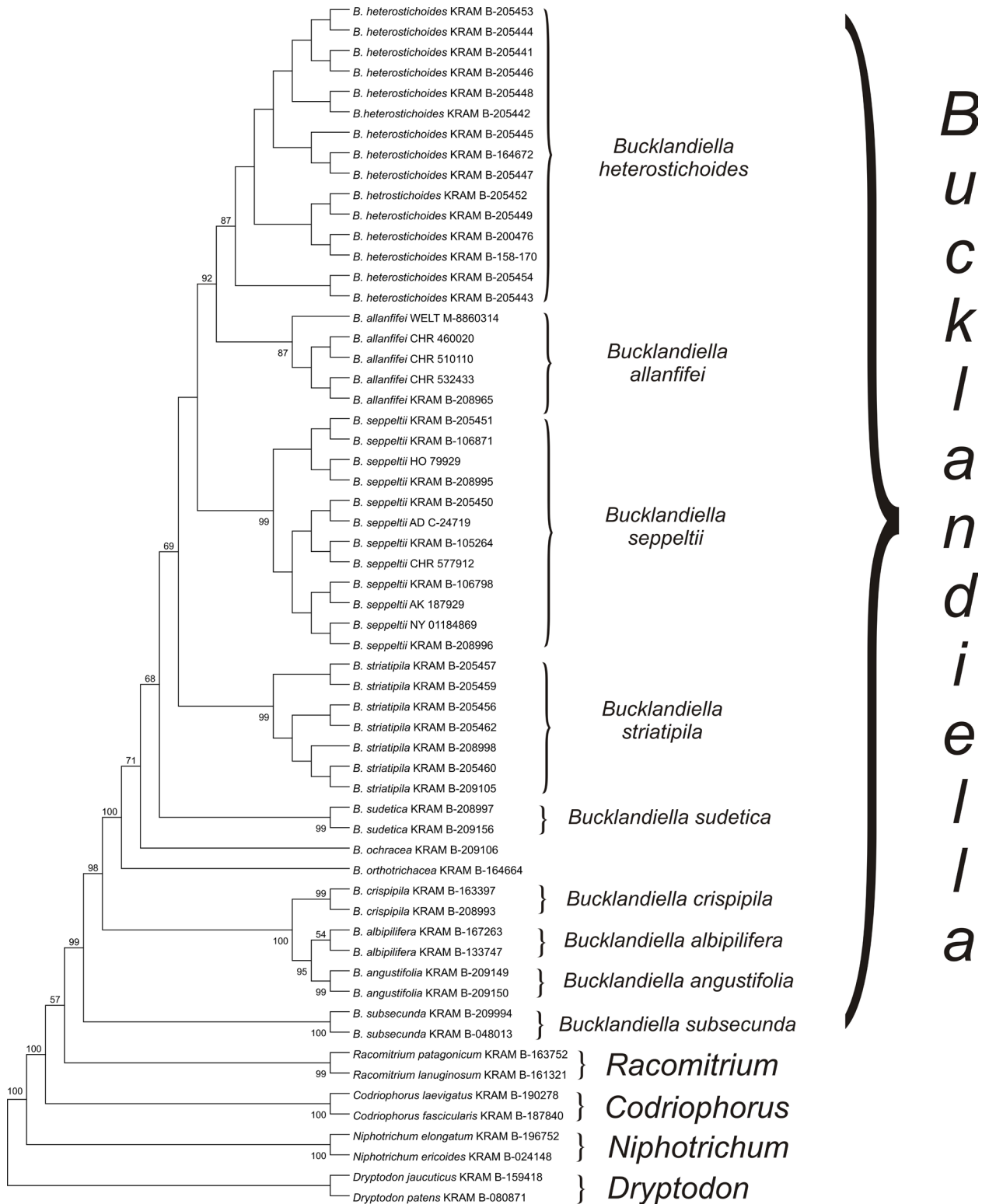


Figure 1. Strict consensus tree of *Bucklandiella* and other close taxa reconstructed by maximum parsimony using ITS data. Bootstrap values exceeding 50% are indicated above the branches.

support (87% BS) was obtained for respective clades of *B. heterostichoides* and *B. allanfifei*, whereas the sister relationship of these 2 taxa was well supported (92% BS). Phylogenetic relationships among these 4 taxa remain partially unresolved. *Bucklandiella seppeltii* shared a common ancestor with *B. allanfifei* and *B. heterostichoides*, though this clade showed very poor support (33% BS).

The phylogenetic analysis of ITS sequences enabled us to distinguish other major groups (Figure 1). All outgroup genera, *Codriophorus* P.Beauv., *Niphotrichum* Bednarek-Ochyra & Ochyra, and *Racomitrium*, formed well-supported clades with bootstrap support varying from 99% (*Racomitrium*) to 100% (*Codriophorus*, *Niphotrichum*). The phylogenetics analysis based on plastid *trnH-psbA* spacer was congruent with ITS, but resolved only clades at the species level (results not shown).

The molecular distinctiveness of the studied species was also confirmed by the Species Delimitation plugin software (Table). *Bucklandiella allanfifei*, *B. heterostichoides*, *B. seppeltii*, and *B. striatipila* are monophyletic and characterized by good clade support varying from 52% (ITS2 region for *B. allanfifei* and *B. heterostichoides*) to 100% in the case of the remaining species pairs. The usefulness of applied molecular markers was also confirmed by high values of P ID, the probability of correct identification based on tree (strict) or barcoding (liberal) approaches.

3.2. Taxonomic treatment

Bucklandiella seppeltii Bednarek-Ochyra, Ochyra, Sawicki & Szczecińska **sp. nov.** (Figures 2 and 3)

Diagnosis: *Species haec* *Bucklandiellae heterostichoidis similis sed cellulis laminae laevibus, pilis hyalinis foliorum strictis, marginibus foliorum uno latere latissime recurvatis,*

altero planis in parte superiori, caulibus erectis vel ascendentibus et ITS sequentiae DNA facillime recedit.

Type: Tasmania, Cradle Mountain National Park, along trail from Wombat Tarn to Waldheim Carpark, alt. 931 m, 41°38'47.0"S, 145°57'19.0"E, on quartzite outcrops near edge of *Nothofagus* forest associated with *Rhacocarpus purpurascens* and *Andreaea* sp., 14 February 2013, *Seppelt s.n.* (Holotype: KRAM!; isotypes: CHR!, CBG!, HO!).

Description: *Plants* small- to medium-sized, mostly gracile or sometimes moderately coarse, stiff and rigid, often rather fragile and easily broken off in upper part on drying, sometimes somewhat hoary, especially in green or dark olive-green plants; forming loose or most often compact wefts, tufts, turves, or extensive mats or patches, sometimes hemispheric cushions; slightly lustrous, bright, golden or olive-yellow throughout or golden, golden-brown, yellow-, golden-, or olive-green above, brown or sometimes blackish-brown below, occasionally dark green above and blackish-brown to blackish below. *Stems* erect or ascending, occasionally prostrate, especially at edges of mats or patches, straight, usually 1.5–3.5 cm tall, rarely as short as 0.5–1.0 cm or, sometimes, to 7 cm high, thin but rigid, yellow- or orange-brown, usually sparsely irregularly or dichotomously branched to simple, on prostrate stems with more numerous short, erect-ascending lateral, cuspidate branchlets in distal portion giving plants a cristate aspect, with sparse reddish-brown, glossy, smooth, and almost unbranched rhizoids near base or scattered in clusters along prostrate stems, in transverse section rounded, lacking a central strand and consisting of 1–2-layered cortex of small cells with strongly thickened, orange- or yellow-brown walls and small lumina and central medulla of 5–6 rows of large, yellowish-hyaline

Table. Parameters used in the molecular delimitation of the 4 closely related *Bucklandiella* species.

Sequence	Species	Closest species	Monophyletic	Clade support	Rosenberg P(AB)	P ID Strict/Liberal
ITS1	<i>B. allanfifei</i>	<i>B. heterostichoides</i>	Yes	0.99	0.02	0.79 / 1.00
	<i>B. seppeltii</i>	<i>B. striatipila</i>	Yes	1	0.01	0.79 / 1.00
	<i>B. heterostichoides</i>	<i>B. allanfifei</i>	Yes	0.66	0.02	0.79 / 1.00
	<i>B. striatipila</i>	<i>B. seppeltii</i>	Yes	0.87	0.01	0.87 / 0.98
ITS2	<i>B. allanfifei</i>	<i>B. heterostichoides</i>	Yes	0.64	9.5E-7	0.87 / 0.97
	<i>B. seppeltii</i>	<i>B. striatipila</i>	Yes	0.96	1.3E-11	0.99 / 1.00
	<i>B. heterostichoides</i>	<i>B. allanfifei</i>	Yes	0.52	4.4E-9	0.99 / 1.00
	<i>B. striatipila</i>	<i>B. heterostichoides</i>	Yes	1	8.6E-8	0.95 / 1.00
<i>trnH-psbA</i>	<i>B. allanfifei</i>	<i>B. heterostichoides</i>	Yes	0.97	0.01	0.87 / 0.98
	<i>B. seppeltii</i>	<i>B. striatipila</i>	Yes	1	8.2E-4	0.79 / 1.00
	<i>B. heterostichoides</i>	<i>B. allanfifei</i>	Yes	0.59	0.01	0.79 / 1.00
	<i>B. striatipila</i>	<i>B. allanfifei</i>	Yes	1	0.01	0.59 / 0.98

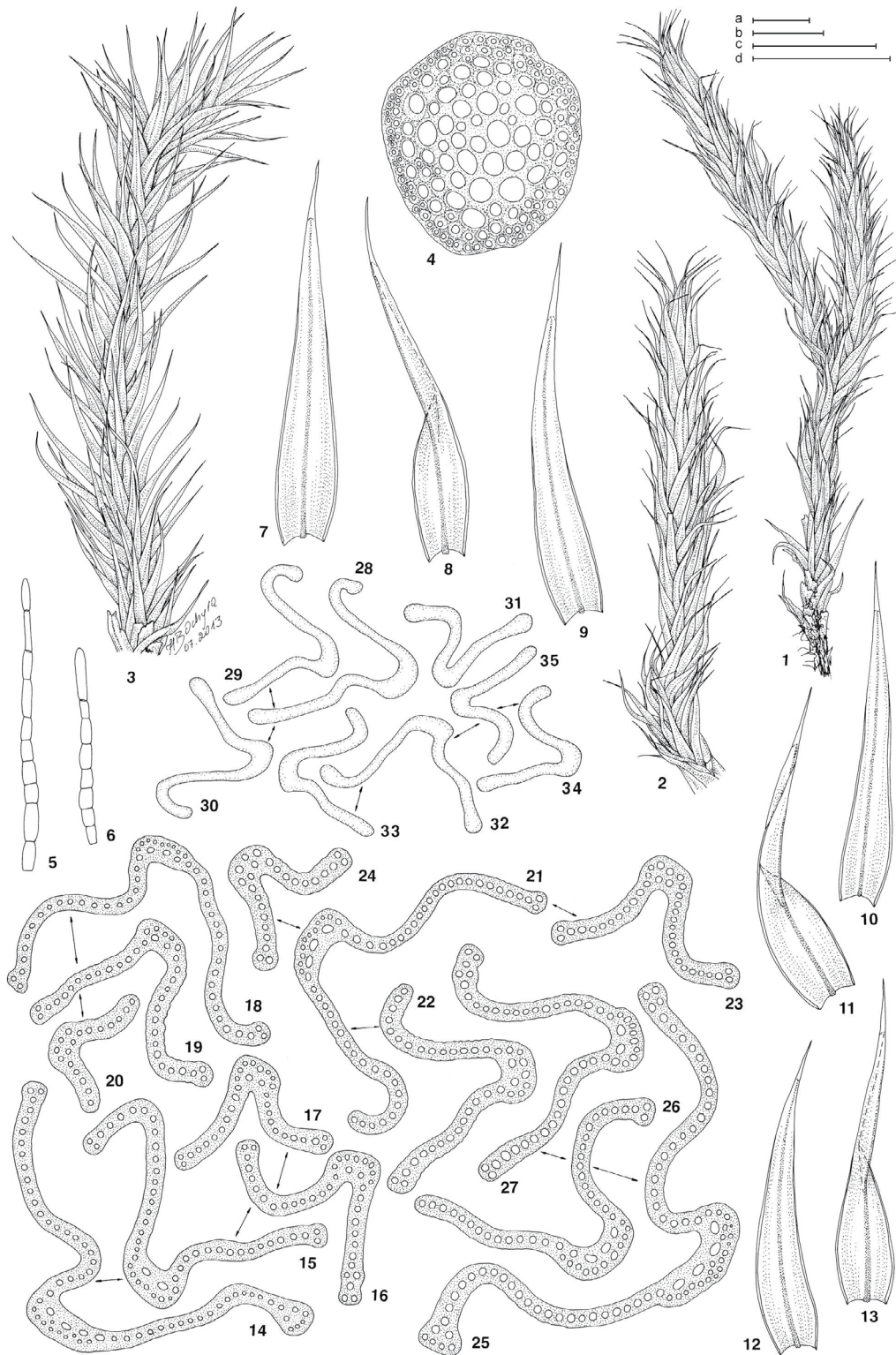


Figure 2. *Bucklandiella seppeltii*. 1. Habit. 2. Portion of branch, dry. 3. Portion of branch, wet. 4. Transverse section of stem. 5–6. Axillary hairs. 7–13. Leaves. 14–27. Transverse sections of leaves. 28–35. Outlines of transverse sections of leaves. (1–2, 18–20 from MAE-194, KRAM; 3, 5–6, 10–13, 21–24, 32–35 from *Seppelt s.n.*, 14.02.2013, holotype, KRAM; 4, 14–17, 28–30 from *Vitt 9180*, KRAM; 7–9, 25–27 from *Bednarek-Ochyra & Ochyra 2888/13*, KRAM; 31 from *Paul s.n.*, 22.04.2002, CHR.) Scale bars: a – 1 mm (1); b – 1 mm (2–3) and 100 µm (28–35); c – 100 µm (4, 14–27); d – 1 mm (7–13) and 100 µm (5–6).

cells with moderately thickened, yellow walls; *axillary hairs* uniseriate, filiform, hyaline, 8–10-celled, consisting of relatively short, barrel-shaped proximal cells and a few elongate distal cells. *Stem* and *branch leaves* similar, crowded, closely imbricate, stiff, straight to somewhat curved, not altered, erect and appressed on drying, erect-spreading on wetting, (2.0–)2.3–2.6(–3.0) mm long, (0.3–)0.4–0.6 mm wide in widest part above base, narrowly lanceolate to ovate-lanceolate, gradually long-acuminate, sharply acute, ending in a long hair point, concave, not plicate, with a single fold on 1 side of costa near base, narrowly canaliculate to keeled in distal part, broader canaliculate in proximal part, not decurrent and not auriculate; *hair point* hyaline, flat below becoming terete distally, capillaceous, erect, (0.2–)0.3–0.4(–0.7) mm long, strict, straight, erect to slightly inclined or recurved, sharply acute, with a distinct areolation of linear cells, entire, nondecurrent down margins of lamina; *margins* entire, smooth or somewhat lumpy at sides near apex, plane on one side, reflexed to broadly recurved on other side throughout leaf length, giving leaf sections characteristic appearance of an arm broken at a 90° or obtuse angle, bistratose throughout for 1(–2) rows of cells, occasionally unistratose near apex and 3–5-layered streaks in proximal portion; *costa* single, percurrent, deeply yellow to yellow-brownish, sharply demarcated from laminal cells, 60–70 µm wide near base, gradually tapering upwards, 35–40 µm wide near apex, narrowly canaliculate throughout; in transverse section moderately convex on abaxial side, semiterete to short rectangular in distal part, reniform- to crescent-shaped, asymmetric due to leaf fold, distinctly flattened and situated at bottom of a shallow furrow in proximal part; bistratose throughout, sometimes incompletely tristratose at extreme base, consisting of 2(–3) adaxial and 4–8 abaxial substereid cells of similar size and shape in distal and median parts, 3–4 enlarged adaxial guide cells and 8–14 small, substereid abaxial cells in proximal part, sometimes with incomplete median row of several substereid cells in extreme base; *laminal cells* smooth, unistratose except for margins, with strongly thickened, sinuose or nodulose longitudinal walls throughout lamina, mostly short- to long-rectangular, (10–)15–40(–45) × 5–8 µm, very seldom short and irregular in shape near apex, short-rectangular, quadrate, rounded to oblate, (5–)8–10 × 5–7 µm, becoming short-rectangular in midleaf, 10–15 × 5–7 µm, to long-rectangular, 30–35 µm below midleaf; *basal* and *suprabasal cells* long-rectangular to linear-rectangular, with strongly incrassate and nodulose walls, (35–)40–60(–65) × 3–8 µm, yellow- or orange-tinged in 1–2 rows and forming a distinct strip along leaf insertion; *alar cells* not differentiated; *basal marginal cells* strongly differentiated, forming a biseriate band of hyaline, transparent, short-rectangular to linear cells, 15–25(–35) × 3–6 µm, with

esinuose, moderately thickened longitudinal walls and usually thicker transverse walls, consisting of 10–20 cells in outer row. *Dioecious*. *Perigonia* bud-like, to 2.2 mm; *outer perigonial leaves* similar to vegetative leaves but smaller, to 2 mm long, with a hair point reaching 0.3–0.35 mm; *innermost perigonial leaves* broadly ovate, 0.9–1.0 × 0.4–0.5 mm, concave, broadly acute to obtuse, epilose, yellowish-hyaline, with a lax, thin-walled areolation and a costa ceasing well below apex, bearing about 10 brownish, claviform, short-stalked antheridia and lacking paraphyses. *Perichaetia* terminal on branches near apex, cylindrical, to 2 mm long; *outermost perichaetial leaves* similar in shape and areolation to vegetative leaves, lanceolate to ovate-lanceolate, 1.8–1.9 mm × 0.6–0.7 mm, epilose; *median perichaetial leaves* oblong-ovate, short-acuminate, 1.8–1.9 × 0.5–0.6 mm, with squarrose or recurved apex on wetting, percurrent costa and areolation of linear cells with nodulose walls in lower part and long-rectangular, sinuose-walled cells in upper half; *innermost perichaetial leaves* oblong, broadly acute to truncate with a short apiculus, 1.5–1.6 × 0.6–0.65 mm; with areolation of sturdy cells throughout leaves, rectangular to long-rectangular with thickened and nodulose longitudinal walls in lower half, becoming shorter and variable in shape in distal portion, mostly rectangular to irregular, with strongly incrassate walls. *Sporophytes* singly in perichaetium; *seta* fairly thin, 6–8 mm long, yellow to yellow-brownish, brown with age, twisted clockwise when dry, minutely furrowed; in transverse section with 3–4-stratose cortex of small, thick-walled cells, abruptly passing into 3–4-layered medulla of larger, hyaline, thick-walled cells and distinct, small central duct; *vaginula* cylindrical, 0.9–1.0 mm long, with elongate, thick- and sinuose-walled epidermal cells. *Capsules* erect, exerted, straight, symmetric, narrowly short-cylindrical to obloid, 2.0–2.1 × 0.5 mm, rather abruptly narrowed into seta, lacking apophysis, yellow-brown, dull to slightly glossy, leptodermous; *annulus* compound, deciduous, composed of 2(–3) rows of cells, with upper row of large, thick-walled, transparent, vesiculous cells and basal row of smaller, isodiametric, thick-walled cells; *operculum* distinctly conic-convex, with a straight, acute rostrum, to 1 mm long; *exothecial cells* variable in shape but predominantly oblong to elongate-rectangular, 40–70 × 8–15 µm, mixed with some elliptical or irregular cells, 20–35 × 15–20 µm, with strongly incrassate walls, becoming smaller, rounded, rounded-quadrate to oblate at urn rim, and forming bright, orange-brown strip of 4–5 rows of cells at orifice; *stomata* at extreme base of urn, 6–10 per urn, superficial, rounded or subrounded, bicellular, round-pored, small, 24–30 × 22–26 µm in diameter; *peristome* single, consisting of 16 narrowly lanceolate, golden- or yellow-brownish to golden teeth, 300–360 µm long, 35–40 µm wide at base, lacking basal membrane; straight, erect-

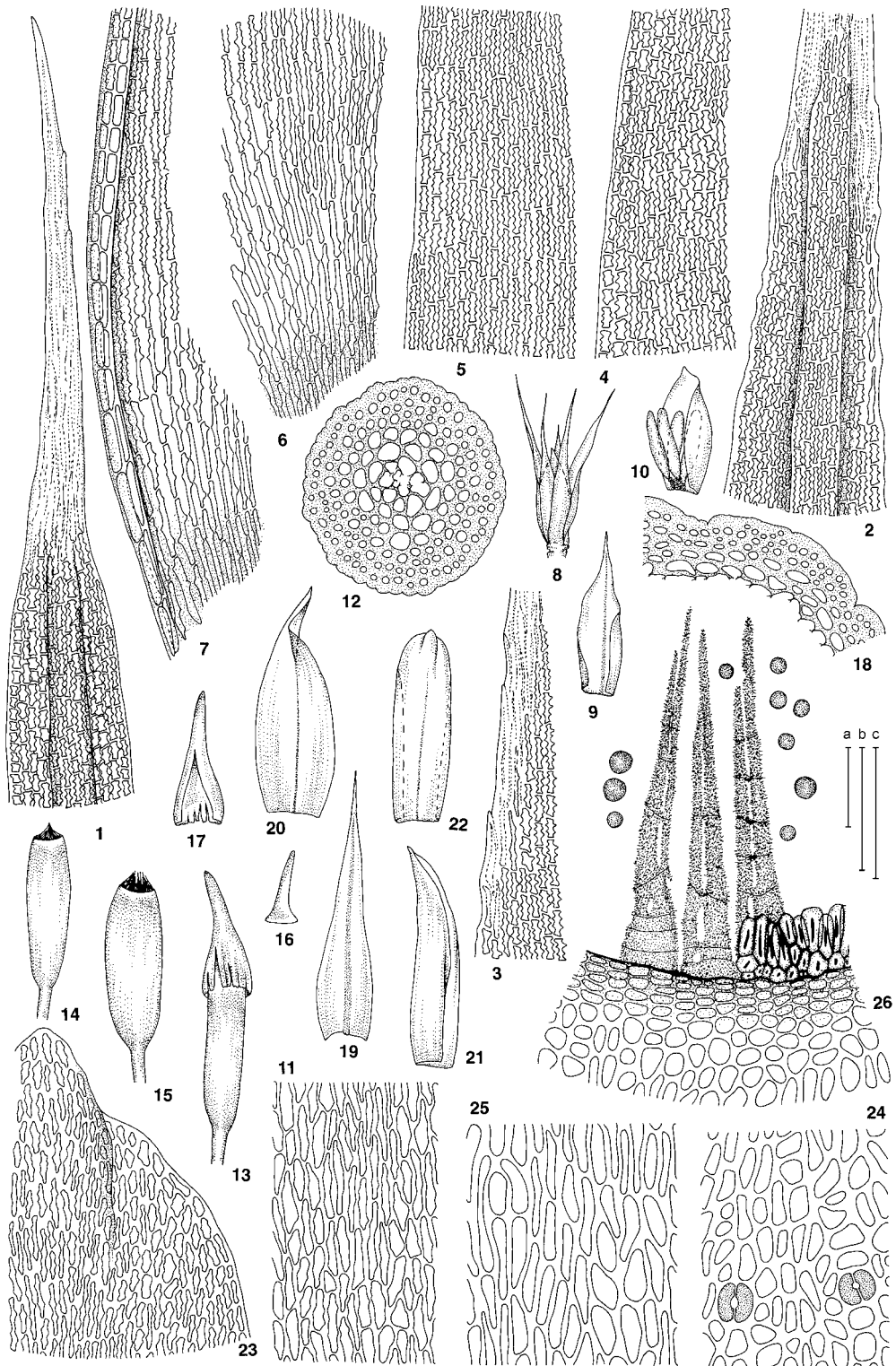


Figure 3. *Bucklandiella seppeltii*. 1. Leaf apex with hyaline hair point. 2. Leaf apex at base of hyaline hair point. 3. Decurrent part of hyaline hair point and uppermost laminal cells. 4. Upper laminal cells. 5. Midleaf cells at margin. 6. Basal juxtacostal cells. 7. Basal marginal cells. 8. Perigonium. 9. Inner perigonial bract. 10. Innermost perigonial bract with antheridia. 11. Epidermal cells of vaginula. 12. Transverse section of seta. 13. Young capsule with calyptra, wet. 14–15. Deperculate capsules, wet. 16. Operculum. 17. Calyptra. 18. Transverse section of calyptra. 19–22. Perichaetial leaves, sequentially from outermost to innermost. 23. Areolation of innermost perichaetial leaf at apex. 24. Exothecial cells at base of urn and stomata. 25. Mid-urn exothecial cells. 26. Portion of peristome, exothecial cells at capsule mouth, annulus, and spores. (1, 4–6 from MAE-194, KRAM; 2–3, 7 from Seppelt s.n., 14.02.2013, holotype, KRAM; 8–10 from Bednarek-Ochyra & Ochyra 2056/13, KRAM; 11–26 from Paul s.n., 22.04.2002, CHR). Scale bars: a – 1 mm (8, 13–17); b – 1 mm (9); c – 100 μ m (1–7, 11–12, 18–26).

spreading when dry, deeply cleft into 2 unequal, terete prongs to middle or below, sometimes only perforate, spiculose-papillose throughout on both surfaces. *Spores* globose, pale brownish, minutely roughened to nearly smooth, 12–18 µm in diameter. *Calyptra* conical, 1.5–1.8 mm long, mitrate to cucullate, brown, naked, smooth, 4–5-lobed at base.

Etymology: The new species is dedicated to Rodney D Seppelt, Hobart, Tasmania, in recognition of his great contribution to Australasian and Antarctic bryology. During his many years as a bryologist, he has made large collections of bryophytes in Tasmania, sub-Antarctica, and Antarctica, which resulted in many valuable bryophyte discoveries. He also completed the first descriptive moss flora in the sub-Antarctic for Macquarie Island and contributed some taxa to the “Flora of Australia” project. This is also a tribute to his exquisite activity as an excellent illustrator of bryophytes.

Habitat: *Bucklandiella seppeltii* is a rupicole, occurring on ledges, scree, boulders, scoria, blocks, outcrops, and ridge crests and growing on various types of acidic rocks, including schist, greywacke, sandstone, gneiss, gabbro, granite, dolerite, and other igneous rocks. Only occasionally it thrives on light or peaty soil over rocks and scoria, and once it was collected from a log in a forest. The species grows in xeric, mostly open and exposed, sometimes heavily insolated sites in subalpine and alpine tussock lands, herb fields, grasslands, heaths, scrubs, and forests dominated in New Zealand by *Chionochloa flavescens* Zotov, *Ch. pallens* Zotov, *Ch. rigida* (Raoul) Zotov, *Dracophyllum longifolium* (J.R.Forst. & G.Forst.) R.Br., *D. uniflorum* Hook.f., *D. rosmarinifolium* R.Br., *Phormium cookianum* Le Jol., *Pseudopanax arboreus* Phillipson, and *Podocarpus alpinus* Hook.f. Sometimes it is found to grow in shaded and moist sites, near and in streams, on periodically inundated rocks, and on boulders in streams above water level. It usually forms pure patches without admixture of other mosses, but sometimes it has been found with such species as *Racomitrium pruinosum* (Wilson) Müll.Hal.; *R. lanuginosum* (Hedw.) Brid.; *Bucklandiella pycnotricha* (Müll.Hal.) Bednarek-Ochyra, Ochyra & Seppelt; *B. elegans* (Müll.Hal.) Bednarek-Ochyra & Ochyra; and *Rhacocarpus purpurascens* (Brid.) Paris, as well as various species of liverworts and lichens. *Bucklandiella seppeltii* occurs at various elevations, ranging from 360 m a.s.l. on the Auckland Islands in the south-cool-temperate zone at one of its southernmost localities to 1650 m a.s.l. on the South Island of New Zealand.

Distribution: *Bucklandiella seppeltii* is a south-cool-temperate species, endemic to Australasia (Figure 4). It occurs in Tasmania and New Zealand and so far it has not been recorded from mainland Australia. It seems to be the most widespread on the South Island of New Zealand

(Figure 5), occurring throughout the whole territory from the Tasman and Nelson/Marlborough region in the north to the Southland region in the south, with the highest concentration of records in the Tasman, Marlborough, and northern Canterbury regions in the northern part of the island. Its altitudinal range extends on the South Island from 800 to 1650 m a.s.l., although the majority of the records have been made at 1250–1400 m a.s.l. In contrast, the species is rare and widely scattered in the mountainous areas on the North Island of New Zealand, occurring at elevations from 1310 to 1525 m a.s.l. Likewise, *B. seppeltii* seems to be rare and widely scattered in Tasmania, but possibly it is undercollected in this area because half of the collections was made only in 2013 after special search for this species. Like in New Zealand, it occurs here at higher elevations, from 920 to 1270 m a.s.l. in alpine fellfields. The frequency of the species decreases southwards. It was only occasionally collected on Stewart (Rakiura) Island, as well as on the Auckland and Campbell Islands. On the latter archipelago it was collected only once and this is the southernmost record of the species at about 52°30'20"S. Although the elevation is not given on the label, the species was collected on the slopes of Mount Azimuth, whose summit has an altitude of 445 m a.s.l. *B. seppeltii* occurs on the Auckland Islands at similar elevations of 360–610 m a.s.l. At these latitudes, climatic conditions are very severe and resemble those occurring in alpine zone in the mountains at lower latitudes. On the sub-Antarctic Prince Edward Islands at around 47°S, Zinderen Bakker (1978) estimated that at 250 m above sea level the temperature just above the soil surface falls below 0 °C on about half of the nights during year, compared to about one-third at sea level. On Macquarie Island, at 54°S, the adiabatic lapse rate is 1 °C for every 100 m increase in altitude, whereas in Tasmania, at 43°S, it is around 1 °C for every 250 m increase in altitude. Moreover, strong winds contribute much to the severity of the climate in these regions because they cause drought stress and wind abrasion of the plants, and therefore the fellfields on these islands are often designated as “wind-deserts” (Schenck, 1905).

Additional specimens examined (paratypes): AUSTRALIA. TASMANIA. Cradle Mountains: Marions Lookout, alt. 1120 m, 14 Feb 2013, *Bednarek-Ochyra & Ochyra* 684/13 (HO, KRAM); Cradle Plateau, alt. 1270 m, 14 Feb 2013, *Bednarek-Ochyra & Ochyra* 710a/13 (HO, KRAM); Southwest National Park: saddle between Mt Eliza and Mt Anna, alt. 1250 m, 21 Feb 1989, *Croft 10239 & Richardson* (HO, KRAM, NY); SW slope of St Valentines Peaks, SSW of Burnie, alt. 920–1100 m, 19 Mar 1977, *Engel 15622* (NY).

NEW ZEALAND. NORTH ISLAND. Gisborne: Mt Hikurangi, 27 Oct 1941, *Teague s.n.* (WELT). Ruapehu: Tongariro Ecological Region and District, Mount

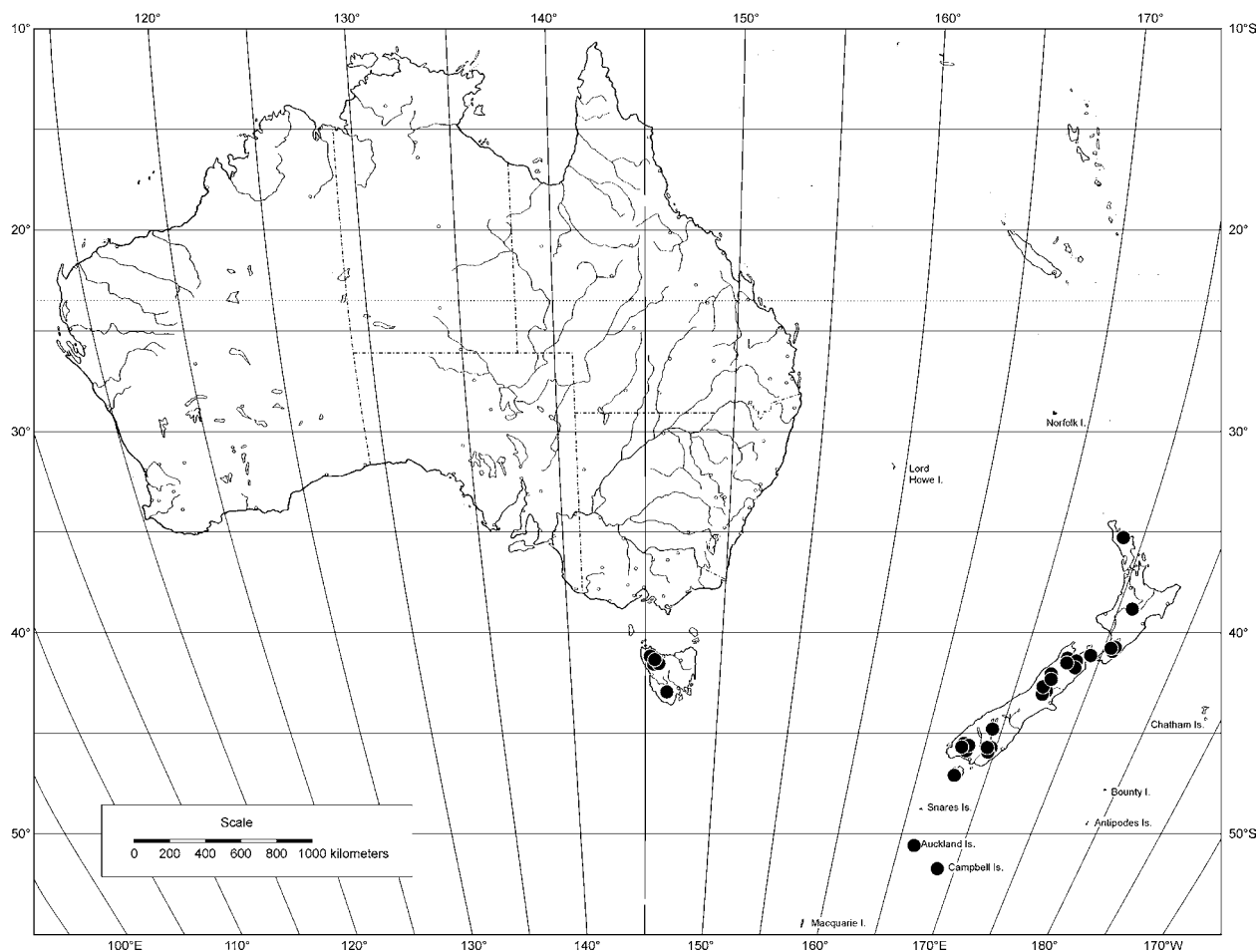


Figure 4. Global distribution map for *Bucklandiella seppeltii*.

Ruapehu, Site A, Bruce Road, alt. 1525 m, Jan 1978, *Bartlett s.n.* (AK). **Wellington:** Tararua Range, Mt Hector, 31 Dec 1933, *Zotov s.n.* (CHR); same area, watercourse on N face of Mt Hector, alt. ca. 1310 m, 31 Dec 1933, *Zotov s.n.* (CHR); same area, without closer locality data, Jan 1948, *Robbins 1337* (AK, PC). **Wairarapa:** Mt Holdsworth, 12 Feb 1948, *Robbins s.n.* (WELT).

SOUTH ISLAND. Tasman. Allen Range: NW end of Allen Range, route from Little Wanganuito Mt Zetland, alt. 1140 m, 8 Feb 1987, *Fife 8050* (CHR). **Peel Range:** Mt Peel, alt. 1525 m, 8 Jan 1981, *Child 5090 & 5114* (BM). **Arthur Range:** NE flank Mt Arthur above MA Hut, alt. 1340 m, 1 Feb 1988, *Fife 8405* (CHR); above Mt Arthur Hut, alt. 1310 m, 6 Mar 2013, *Bednarek-Ochyra & Ochyra 2856/13, 2856/13, 2868/13, 2874/13, 2883/13, 2885/13, 2886/13, & 2888/13* (CHR, KRAM); same locality, alt. 1350 m, 1 Dec 2010, *Shevock & Malcolm 36525* (KRAM). **Lookout Range:** E of Mt Owen, alt. ca. 1310 m, 25 Jan 1972, *Cave 164073* (MO); W flank of summit, alt. 1525–1585 m, 24 Jan 1983, *Fife 5136* (CHR). **Nelson/Marlborough. Richmond Range:** Patriarch, alt. ca. 1650 m, 2 Feb 1980, *Child 4953*

(BM); Mt Fishtail, alt. ca. 1650 m, 23 Dec 1979, *Child 5000 & 5008* (BM); Mt Richmond, alt. ca. 1615 m, 7 Jan 1983, *Child 6141* (CHR). **Marlborough Sounds:** Mount Stokes Scenic Reserve, 23 km NNE of Picton, Mt Stokes, alt. 1180 m, 6 Feb 1993, *Streimann 51502* (KRAM, MO). **Westland. Papahaua Ranges, Denniston Plateau:** Mt Rochfort, 11 km ESE of Westport, alt. 990 m, 2 Feb 1993, *Streimann 51178* (CHR, H, KRAM, L, MO) [Musci Australasiae Exsiccati No 194]; Mt Rochfort summit, Ngakawau, alt. 1020 m, 18 March 2008, *Glenny 10215 & Ford* (CHR). **Paparoa Range:** North Westland Ecological Region, Maimai Ecological Distr., Mount Uriah, alt. 1260 m, 17 Feb 2003, *Renner 255 & 226* (AK); Paparoa Range, 7 Jan 1981, *Visch s.n.* (CHR); NW flank Mt Euclid, saddle above Morgan Tarn, alt. ca. 1275 m, 22 Feb 1984, *Beever 24-2* (CHR). **Canterbury. Arthur's Pass National Park:** Kelly Range, along summit Ridge WSW of Carroll Hut, alt. 1200 m, 14 March 1993, *Fife 10058 & Meurk* (CHR); Stockton Plateau, Mt Frederick, 5 Jan 1987, *Polly s.n.* (WELT); Kelly's Hill, Jan 1945, *Martin s.n.* (CHR); Westland Pegleg Creek, ca. 7 km N of Arthur's Pass, alt. 840 m, 1 Feb 1986,

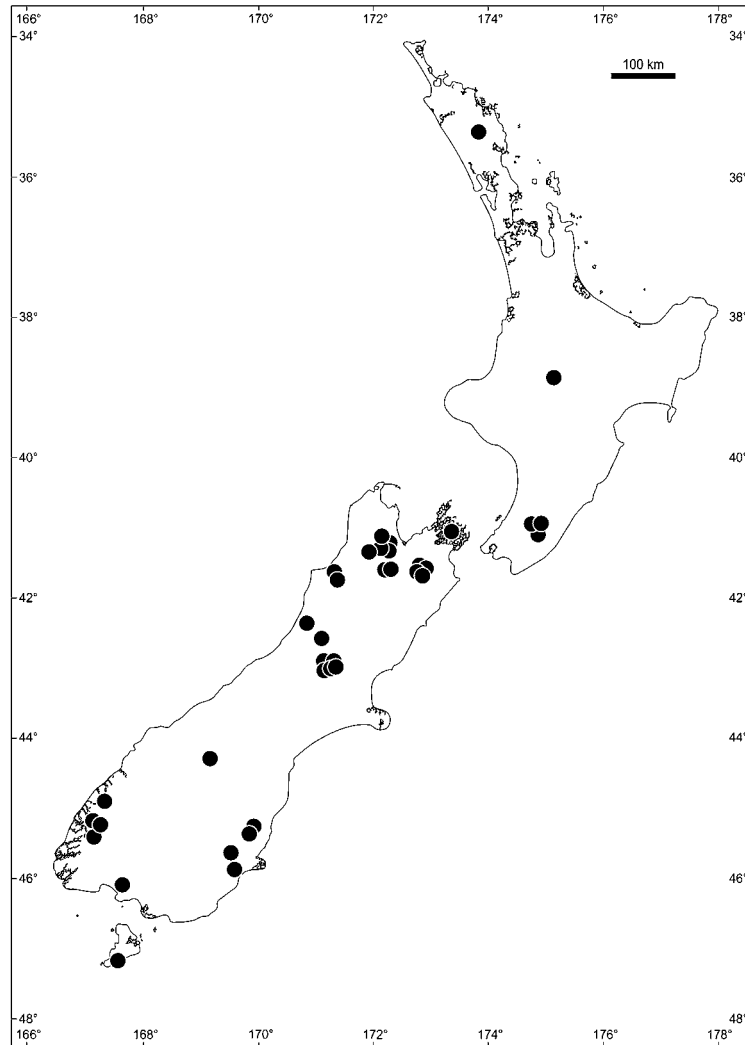


Figure 5. Distribution map for *Bucklandiella seppeltii* in New Zealand.

Brownsey s.n. (HO, WELT); Arthur's Pass, Jan 1944, *Martin* 383.20 (CHR); Otira River Gorge, alt. 884–1004 m, 19 Feb 2013, *Bednarek-Ochyra & Ochyra* 890/13, 907/13, 972a/13, 982/13, 986/13, 998/13, 991/13, & 996/13 (CHR, KRAM); Otira River Gorge near parking area for track to Mt Rolleston, alt. ca. 915 m, 13 March 1983, *Fife* 5414 (MO); Temple Basin, alt. 1300 m, 31 Jan 1986, *Brownsey s.n.* (WELT). **Otago. Crown Range:** Wanaka, Cardrona Skifield, Captain's Basin, alt. 1632 m, 11 Jan 2001, *Beveridge s.n.* (WELT). **Rock and Pillar Range:** Museum Rock, alt. 1280 m, 6 Dec 1972, *Vitt* 8649 (MO, UC), alt. 1365 m, 14 Feb 1971, *Child* 2386 (BM) and alt. 1370 m, 19 May 1969, *Child* 109 (BM); Summit Rock, alt. 1410 m, 27 Feb 2013, *Bednarek-Ochyra & Ochyra* 2056/13 (CHR, KRAM). **Lammermoor Range:** ca. 6 km NE of Ailsa Craig, alt. 980 m, 24 Nov 1998, *Fife* 11418 (CHR). **Maungatua Range:** S of Dunedin, alt. ca. 610 m, 11 Nov 1946, *Allison* 1609 (CHR). **Southland. Fiordland National Park:** Franklin

Mountains, Narrows Creek, alt. 800 m, 22 April 2002, *Paul s.n.* (CHR); Murchison Mountains: north of Takahe Valley, alt. 1330 m, 25 Jan 1994, *Fife* 10272 (CHR); same area, western end of Lake Orbell in Takahe Valley, 25 Jan 1994, *Fife* 10244 (CHR); Borland Saddle, alt. ca. 915 m, 20 April 1970, *Child* 1516 (BM). **Longwood Range:** Bald Hill west of Otautau, west of the Southland Plains, ca. 40 km northwest of Invercargill, alt. 800–804 m, 1 Mar 2013, *Bednarek-Ochyra & Ochyra* 2171/13, 2174/13, 2182/13, 2186a/13, 2189/13, 2191/13, 2194/13, 2195/13, 2197/13, 2200/13, 2206/13, & 2209/13 (CHR, KRAM).

STEWART ISLAND (RAKIURA). Rock summit of Tin Range, 7 Jan 1949, alt. ca. 535 m, *Martin* 383.45 & 383.46 (CHR) and 14 Jan 1949, *Martin* 383.35 (CHR); same locality, alt. ca. 535 m, 13 Jan 1949, *Martin s.n.* (HO).

AUCKLAND ISLANDS. Auckland Islands Ecological Region and Distr., ridge S of Lake Speight, alt. 360 m, 20 Feb 1973, *Johnson* 20/2 (AK); Tower of Babel, alt. 550 m,

20 Feb 1973, *Johnson 20/18* (AK) & 20/27 (AD); around summit of mountain to south of Mt Easton, alt. 610 m, 20 Dec 1972, *Vitt 9180* (ALTA).

CAMPBELL ISLANDS. Slopes of Mt Azimuth, 4 Jan 1970, *Vitt 2397* (S).

4. Discussion

Bucklandiella seppeltii is a distinct species that can hardly be mistaken for any other moss in Australasia. It can be readily distinguished in the field by the somewhat hoary appearance of the plants, which form usually extensive, loose, or compact mats, patches, or turves with a characteristic golden or golden-brown coloration, at least in the upper part. The stems are typically erect or ascending and only at the edges of the patches are they prostrate. All the leaves, including the lowest ones in the dense cushions or tufts, have a long, hyaline, capillaceous hair point, to 0.5 mm or occasionally as long as 0.7 mm, which is erect, strict, straight, or recurved. Apart from the external features of the habit, the species is recognized by a set of microscopic characters, including (1) lanceolate to narrowly ovate-lanceolate leaves; (2) elongate-rectangular and smooth cells throughout the lamina, with strongly incrassate, sinuose to sinuose-nodulose lateral walls; (3) broadly recurved leaf margins on 1 side in the distal portion giving a characteristic outline of leaf cross-sections of an arm broken at a 90° to obtuse angle; (4) narrow costa, bistratose throughout, with 3–4 enlarged guide cells on the adaxial side in the proximal part and 2 adaxial cells in the median and upper parts; (5) biseriate basal marginal border composed of 10–20 hyaline, esinuose, translucent cells; (6) elongate basal cells with strongly nodulose lateral walls; (7) epilose perichaetial leaves with strongly modified areolation in the innermost ones, consisting of rectangular to irregular cells with strongly incrassate walls.

All the aforementioned traits are very stable and constant. There are a few populations collected in shaded habitats that have dark green to blackish-green plants (e.g., *Bednarek-Ochyra* & *Ochyra 2182/13*, CHR, KRAM) or green to olive-green (e.g., *Bednarek-Ochyra* & *Ochyra 2182/13*, CHR, KRAM). There is also some variation in the length of the hair point, although in the majority of the plants it is 0.3–0.4 mm long. Only 1 specimen from the Auckland Islands (*Vitt 9180*, ALTA) has a very long hair point, to 0.7 mm.

A characteristic feature of *Bucklandiella seppeltii* is the very rare production of sporophytes. Although sexual organs, especially perichaetia, have been observed fairly often in the species, of about 100 studied specimens (including duplicates), sporophytes were discovered only in 1 specimen from the Southland region on South Island. It was collected in Narrows Creek in the Fiordland National Park at an altitude of 800 m on 22 April 2002 by T Paul (CHR).

In the large and strongly morphologically diversified genus *Bucklandiella*, *B. seppeltii* is morphologically and anatomically most closely related to *B. heterostichoides* (Cardot) Bednarek-Ochyra & Ochyra, in which the stems are prostrate and closely appressed to the substrate with numerous short, erect-ascending lateral branchlets that give the plants a cristate appearance. Putting aside the differences in the overall aspect, the 2 species show a remarkable similarity in structural characters. They share the same size and shape of leaves and their areolation, leaf hair points, costal anatomy, perichaetial leaves, and all details of sporophytes.

The only real differences between *Bucklandiella heterostichoides* and *B. seppeltii* are the strongly pseudopapillose laminal cells in the former due to numerous longitudinal cuticular ridges densely covering both adaxial and abaxial surfaces of the laminal cells and giving them a papillose appearance when viewed in transverse section. In contrast, the leaf lamina is entirely smooth or only occasionally slightly pseudopapillose in *B. seppeltii* because it lacks the lengthwise cuticular ridges over leaf cells. A second difference is the plane or only narrowly recurved, or deflexed on one side, leaf margin in *B. heterostichoides*. Conversely, in *B. seppeltii* the leaf margins are broadly recurved on one side in the distal portion and this gives a characteristic shape of the leaf cross-sections which in outline resemble a “broken arm” with a bend on one side at a 90° or obtuse angle. Moreover, the hyaline hair point in *B. heterostichoides* is flexuose, whereas that in *B. seppeltii* is strict and straight. The differences in the habit of the plants are also evident, although in some populations of *B. heterostichoides* the stems are also erect or ascending and the plants may resemble those of *B. seppeltii*. The plants of *B. heterostichoides* are mostly dark yellow-green and blackish-brown in older regions, whereas those in *B. seppeltii* are mostly bright golden or olive-yellow throughout and only seldom they are blackish-brown below. Interestingly, as is the case with *B. seppeltii*, *B. heterostichoides* very seldom produces sporophytes and so far only 2 fertile populations of this species, mostly with immature capsules, have been detected.

Bucklandiella seppeltii and *B. heterostichoides* are Holantarctic allopatric species since their geographical ranges are strongly isolated. The former is a south-temperate species restricted in its distribution to Tasmania and New Zealand, including the Auckland and Campbell Islands, the 2 small archipelagos in the south-cool-temperate zone. For over a century, *B. heterostichoides* was known only from southern South America, being restricted in its distribution to Tierra del Fuego and the Falkland Islands (Roivainen, 1955). It was reported from Tristan da Cunha in the South Atlantic Ocean (Dixon, 1960), but the voucher specimen proved

to be *B. striatipila* (Cardot) Bednarek-Ochyra & Ochyra (Bednarek-Ochyra and Ochyra, 2010, 2011; Ellis et al., 2011a). *Bucklandiella heterostichoides* is very widespread on South Georgia, a sub-Antarctic island in the South American sector of this biome (Bell, 1974). Exploration of other islands and archipelagos in the Southern Ocean resulted in the discovery of the species on Gough Island in the south-cool-temperate zone (Ellis et al., 2012a) and in Îles Kerguelen (Blockeel et al., 2009b) and on isolated Heard Island. These discoveries established *B. heterostichoides* as a sub-Antarctic ampho-Atlantic species.

The close relationship of *Bucklandiella seppeltii* and *B. heterostichoides* is well supported by molecular data (Figure 1). Together with *B. allanfifei* and *B. striatipila* they form a distinct, well-supported group. Morphology indicates *B. heterostichoides* as the closest relative of *B. seppeltii*. MP analysis resolved the new species as a sister to the *B. allanfifei*-*B. heterostichoides* group, but Bayesian analysis leaves this clade unresolved. Moreover, molecular species delimitation methods used in the barcoding projects point out *B. striatipila* as the closest species to *B. seppeltii*. The evolutionary relationships among these 4 species remain unclear and will require more plastid and nuclear regions to be sequenced. However, all applied methods revealed the molecular distinctiveness of each species from this group, including the newly described *B. seppeltii*.

Bucklandiella seppeltii may be confused with some ascending plants of *B. allanfifei*, a widely distributed New Zealand endemic species (Bednarek-Ochyra and Ochyra, 2010) with which it shares a hoary appearance. However, this species has much longer leaf hair points, to 1.5 mm, which are flat throughout and usually distantly serrulate, making the plants strongly hoary to canescent. Moreover, *B. allanfifei* has either mostly prostrate stems, closely appressed to the substrate with numerous short, erect-ascending branchlets giving the plants a cristate aspect, or the stems are pinnately branched because of many short, tumid, close lateral branchlets. The latter species differs also markedly in leaf areolation with short, mostly irregular cells in the distal part; anatomy of the costa, which is 3–4-stratose with 4–5(–7) guide cells in the proximal part; and entirely unistratose laminal cells including the margins.

Bucklandiella allanfifei is morphologically a sibling species of *B. striatipila*. The latter has a similar geographical range to *B. heterostichoides* but, in contrast to *B. allanfifei*, it is an ampho-Atlantic south-cool-temperate species. It is widely distributed in the *Nothofagus* zone on the western coast of southern South America, ranging from the Valdivian region in central Chile to Tierra del Fuego and the Falkland Islands, with an isolated station in Islas Juan Fernández (Bednarek-Ochyra and Ochyra, 2010) and, additionally, extending to sub-Antarctic South Georgia (Bell, 1974). In recent years, *B. striatipila* has been discovered in the archipelagos of Îles Crozet (Blockeel et

al., 2009b) and Îles Kerguelen (Ellis et al., 2010) in the sub-Antarctic, on Tristan da Cunha (Ellis et al., 2011a) and Gough Island (Ellis et al., 2012a) in the middle of the South Atlantic Ocean in the temperate zone, and on the Western Cape in South Africa (Bednarek-Ochyra and Ochyra, 2013b).

All the aforementioned species are closely related morphologically and their relationship is confirmed by molecular data. They are classified in *Bucklandiella* sect. *Marginatae* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra, which is characterized by the presence of the basal marginal border, the elongate basal leaf cells with strongly nodulose lateral walls, the innermost perichaetial leaves with the distal areolation of cells with strongly incrassate and porose cells, and the elongate upper laminal cells (Bednarek-Ochyra and Ochyra, 2010).

The other species in New Zealand likely to be confused with *Bucklandiella seppeltii* is *B. angustissima* Bednarek-Ochyra & Ochyra, which has the main center of its occurrence on the Auckland and Campbell Islands in the south-cool-temperate zone and on sub-Antarctic Macquarie Island (Bednarek-Ochyra and Ochyra, 2011). This species is easily distinguished from *B. seppeltii* by having small, subglobose capsules, 0.5–0.8 × 0.45–0.6 mm, very short and stout setae, 0.8–1.2 mm, unistratose leaf margins, and a very narrow bistratose costa with 2 adaxial guide cells throughout its whole length. This species also has strongly modified, hyaline innermost perichaetial leaves, which indicate its placement in a different section, *Bucklandiella* sect. *Emersae* (Bednarek-Ochyra) Bednarek-Ochyra & Ochyra.

One Australasian species that could be mistaken with *Bucklandiella seppeltii* is *B. pycnotricha* (Müll.Hal.) Bednarek-Ochyra, Ochyra & Seppelt. It has long been known only from Tasmania and only recently was it discovered in New Zealand (Ellis et al., 2014). These species share some external similarity, including relatively gracile and hoary plants, but the stem is prostrate and many-branched, the leaf hair point is flexuose and distinctly denticulate, the leaf margin is plane on 1 side and only narrowly recurved on the other side in the proximal part, and the spores are large, 18–28 µm in diameter.

Other Australasian species of *Bucklandiella*, for example *B. crispula* (Hook.f. & Wilson) Bednarek-Ochyra & Ochyra and *B. didyma* (Mont.) Bednarek-Ochyra & Ochyra (Blockeel et al., 2008, 2010), are unlikely to be misidentified as *B. seppeltii*. They are clearly differentiated by their brownish leaf hair point and multiserial bistratose marginal borders in the distal part of leaf.

At present, 13 species of *Bucklandiella* are known from Australasia. Of these, 7 species occur in Australia, including Tasmania and sub-Antarctic Macquarie Island, and 12 species have been detected so far in New Zealand, including offshore islands (Stewart Island, Antipodes Islands, Auckland Islands, Campbell Islands).

Key to species:

1. Leaves with distinctive, fragile, deciduous propaguloid apices **B. crumiana**
1. Leaves lacking differentiated, fragile, deciduous apices 2
2. Leaves deeply multiplicate on either side of the costa 3
2. Leaves smooth throughout or with a single plica near the costa in the proximal part 4
3. Leaves auriculate, with a very long, strongly spinose, hyaline hair point, long-decurrent down the leaf margins
..... **B. curiosissima**
3. Leaves nonauriculate, epilose or with a very short, diaphanous hyaline tip **B. ptychophylla**
4. Innermost perichaetial leaves similar to vegetative leaves; costa semiterete, tristratose distally **B. sudetica**
4. Innermost perichaetial leaves strongly modified, lax and hyaline throughout or with some sturdy laminal cells near the costa in the apical part; costa in transverse section elliptical, reniform to lunate, bistratose distally 5
5. Basal marginal border absent **B. lamprocarpa**
5. Basal marginal border present, composed of pellucid, straight-walled cells 6
6. Costa in transverse section with 2 ventral guide cells throughout; seta very short, 0.8–1.2 mm **B. angustissima**
6. Costa in transverse section with 3–7 ventral guide cells; seta longer, more than 1.5 mm 7
7. Leaf hair point hyaline throughout 8
7. Leaf hair point yellowish to yellowish-brownish throughout, sometimes hyaline on the tip only 10
8. Leaf margin bistratose; leaf hair point erect and strict **B. seppeltii**
8. Leaf margin unistratose; leaf hair point flexuose, straight to recurved 9
9. Basal marginal border 3–4-seriate; costa reniform to crescent-shaped, tristratose near the base, in transverse section with 4–7 ventral guide cells **B. allanfifei**
9. Basal marginal border uniseriate; costa elliptical, bistratose throughout, in transverse section with 3–4 ventral guide cells **B. pycnotricha**
10. Leaf hair point capillaceous, 0.2–0.6 mm long, yellowish to yellowish-brownish throughout, sometimes with a hyaline tip, smooth or nearly so **B. crispula**
10. Leaf hair point broad and massive, to 0.2 mm long, never hyaline, distinctly sharply or bluntly serrate ..
..... 11
11. Basal marginal border 2–3-seriate; spores (20–)25–30(–40) μm in diameter **B. chlorocarpa**
11. Basal marginal border uniseriate; spores 10–23(–25) μm in diameter 12
12. Leaf lamina including the margin always unistratose; leaf margin recurved on both sides to two-thirds or three-quarters of the way up the leaf; peristome teeth to 500 μm long; spores 10–15 μm in diameter **B. elegans**
12. Leaf lamina 1–2-stratose; leaf margin irregularly recurved on 1 or both sides to halfway up the leaf; peristome teeth to 400 μm long; spores (17–)22–23(–25) μm in diameter **B. didyma**

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