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Three's a crowd: a revision of the monotypic family Goebeliellaceae (Porellales: Jungermanniopsida).

Matt A.M. Renner

National Herbarium of NSW, Royal Botanic Gardens and Domain Trust, Mrs Macquaries Road, Sydney, NSW 2000, Australia
matt.renner@rbgsyd.nsw.gov.au

Abstract

Three species of *Goebeliella* are here recognized on morphological evidence. The three species can be distinguished by a range of qualitative and quantitative characters, including width of the hyaline leaf-border, leaf lobe cell wall thickening and wall internal structure, horn shape and anatomy, and female bract shape and conformation.

The type specimen of *G. cornigera* was collected in New Zealand, and agrees in all respects with other individuals from that country. *Goebeliella cornigera* is endemic to New Zealand. The other two species are endemic to New Caledonia, and both are present in the syntype material of *G. bicornuta*, which is reinstated and lectotypified. No other names have been published within *Goebeliella*, leaving the second species from New Caledonia without a name. The name *Goebeliella glauca* is proposed for this new species.

Introduction

The Porellales is a speciose lineage of leafy liverworts comprising some 2500 species in seven families (Jubulaceae, Porellaceae, Radulaceae, Lepidolaenaceae, Lejeuneaceae, Frullaniaceae, Goebeliellaceae). These families share several distinctive morphological features, including incubously inserted fundamentally tri-lobed leaves (bi-lobed in Porellaceae and Radulaceae), rhizoids in fascicles, and a complete absence of branch production from the ventral merophyte. Species in most families bear a conspicuous perianth, and many lack associated stem-derived protective structures, though *Lepidogyna* is exceptional in its massive coelocaule topped by a perianth remnant (Schuster 1984).

The most striking feature is the possession of lobules, or 'water-sacs' on the leaves of the gametophyte in almost all species within the order. Lobule structure varies between lineages, and lobule form is a critically important source of morphological characters informing species circumscription (Renner et al. 2010, 2013; von Konrat et al. 2011).

Of the seven families, four have diversity in the hundreds of species, the Lejeuneaceae in particular probably comprises in excess of 1000 species, and the other three families have diversity lower by orders of magnitude. The Jubulaceae has four species in two genera (Patch et al. 2010; Larraín et al. 2015), the Lepidolaenaceae around 20 species in three genera, and the Goebeliellaceae a single species, *Goebeliella cornigera* (Mitt.) Steph.

Goebeliella cornigera was first described as *Frullania cornigera* Mitt. in the bryophyte treatment of Hooker's Flora of New Zealand (Mitten 1855). The specific epithet was chosen for the paired, horn like structures

present at the base of each leaf. *Frullania cornigera* was transferred to a new genus established for it by Stephani (1911) to reflect the uniqueness of Mitten's plant. Stephani (1911) also recognized a second species from New Caledonia. Both species treated by Stephani possess air-cells in the leaves and underleaves, hyaline leaf and underleaf border and heavy corrugated thickenings on the cell walls, in addition to these paired horns. These features make *Goebeliella* readily recognizable in both field and herbarium, and to some extent its uniqueness also obscures its relationships. *Goebeliella* was placed into its own family by Verdoorn (1932), who allied it to both Pleuroziaceae and Radulaceae. Affinities with Porellaceae and Radulaceae were posited by Evans (1939), while Schuster (1965) presented evidence for a relationship with the Frullaniaceae. Molecular phylogenetic studies have resolved *Goebeliella* sister to the Lepidolaenaceae (Davis 2004; He-Nygren et al. 2004; Heinrichs et al. 2005; Forrest et al. 2006).

In this paper morphological evidence supporting the recognition of three species of *Goebeliella* is presented. Two species are endemic to New Caledonia, and one endemic to New Zealand.

Materials and Methods

Specimens held in the herbaria F, G, NSW, and collections from New Caledonia made by M. von Konrat, B. Shaw and J. Larraín were examined for this study.

Structures were examined under Zeiss D125 dissecting microscope, and Zeiss DM2500 compound microscope following rehydration and slide-mounting in water. Dissections were performed by hand. Images were captured with Zeiss DFC295 and DFC420 digital cameras and the LAS application suite by Leica (Leica Microsystems, North Ryde, Sydney). SEM specimens were rehydrated for 24 hours in a humidity chamber, plunge-frozen in liquid nitrogen in a vacuum chamber and evacuated to Tor 10^{-2}, or as close to this as the evacuator could achieve. The specimens were then mounted on stubs, sputter coated with gold only, and examined.

Results

Three morphological groups are present within *Goebeliella cornigera*, each circumscribable by a suite of qualitative macro- and micro-morphological characters. These characters are illustrated and described in the figures accompanying the species treatments in the Taxonomic Treatment below, where hypotheses of relationship explaining the correlated distribution of character states among individuals are formally proposed. Two of these morphological groups occur only in New Caledonia, the third – which corresponds with the syntypes of *G. cornigera* – occurs only in New Zealand.

Discussion

The outstanding feature of *Goebeliella* is its possession of paired horn-like 'lobules' on each leaf. No other extant lineage consistently has more than one lobe modified into a 'lobule'. The only other examples of paired lobules are found in the Cretaceous fossil genus *Kaolakia*, which bears paired lobules on each leaf (Heinrichs et al. 2011), and in *Frullania* the first branch leaf may bear paired lobules (von Konrat & Braggins 2001).

The term 'lobule' is often loosely applied to two different structures. In 'lobules' of the Frullaniaceae, Jubulaceae and Lepidolaenaceae a space is enclosed by invagination of a leaf lobe, typically the second or third (or both), inward from the dorsal surface, so that the dorsal leaf surface is enclosed, and the ventral surface is on the outside of the lobule.

A transformation series from plane lobules to helms can be inferred from leaf-lobe variation in some *Frullania* species, particularly *Frullania explanata*, and in the underleaves of *Lepidolaena* species, whose underleaf lobes are often partially or completely modified into helms. In these genera the leaf margin forms the helm mouth, which is typically orientated toward the shoot base. That these lobules are not homologous with lobules of the Porellaceae and Radulaceae is well established (Schuster 1984). In the Porellaceae and Radulaceae, the lobules are formed by folding of the postical leaf-lobe under the antical. The inner lobule surface is therefore formed by the ventral side of both the dorsal and ventral leaf-lobes, and the dorsal surface is on the outside of the lobule, and actually sits against the substrate. In Radulaceae this surface gives rise to rhizoids. To reflect this non-homology the lobules enclosing the dorsal surface of a single lobe have been referred to as 'helms', while those that enclose the ventral leaf surface between two lobes have been referred to as 'lobules' (Schuster 1966), and this terminology is followed here.

The modified leaf-lobes of *Goebeliella* have been referred to as 'horns' and horn-like lobules, for instance in Schuster (1965). These horns in *Goebeliella* differ from the helms of the Frullaniaceae and Lepidolaenaeceae in several respects, including having their opening at the apex rather than the base, having a bulbous base, and being stalked. Which leaf surface do they enclose and how? The mouth of the horn in *Goebeliella* is surrounded by elongate thin-walled cells similar to those forming the margin on the dorsal leaf-lobe. The form of these cells is consistent with homology to lobe marginal cells, yet they appear to be limited to the horn apex. Normal leaf-lobes have a differentiated margin around their entire free portion, in leaves divided to near the base the margin extends all the way around the lobe. In *Frullania* helms the mouth corresponds with the entire free margin of the lobe, and can be traced from the end of the stem insertion line on one side, to the junction with the stylus on the other.

In contrast, the horns of *Goebeliella* are divided to one or two cells above the stem, yet marginal cells are present only at the very apex, how might this be possible? Some clues are provided by the leaves preceding female bract production. The middle and ventral lobes of female bracts and the preceding leaves have plane laminae. Other leaves separating those with plane lobes from those with fully formed horns bear lobes modified to varying degrees into horn-like structures (Fig. 1). The degree of modification is negatively correlated with proximity to the gynoecium. In some sense the sequence of leaves preceding gynoecia form a developmental transformation series between plane lobes and lobes taking the form of helms. This might not inform how horns evolved, but it may inform how parts of the horn relate to normal lobes.

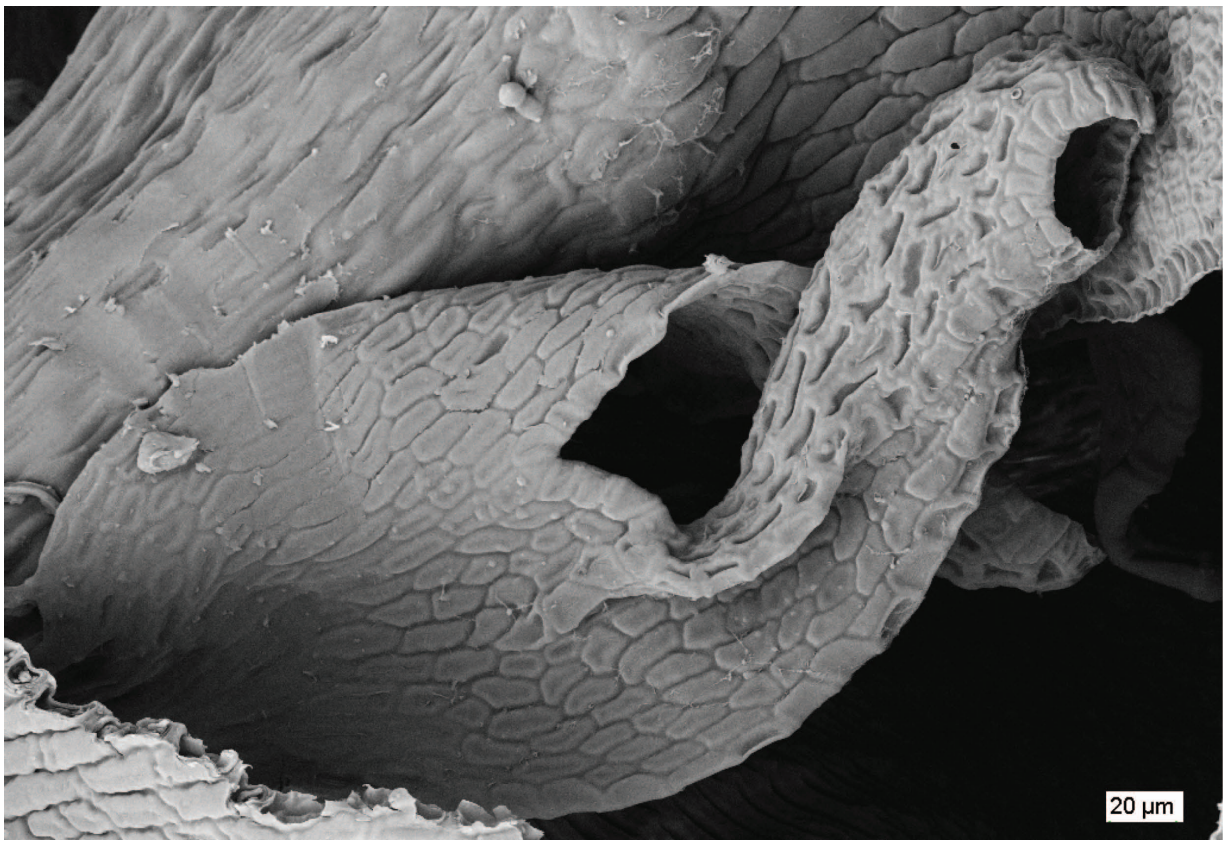

Fig. 1. Transitional lobule from a female bract in *G. bicornuta* (*Shaw 17204*).

Normal lobes are cucullate, with a continuous margin of differentiated cells. Transitional lobes have a sac in the upper half of the lobe, with a circular opening bordered by differentiated marginal cells. The lower half of the lobe is plane, and the base on either side is bordered by differentiated cells. Unlike plane lobes, transitional lobes have a discontinuous border of differentiated cells, broken at the transition between plane and saccate halves. The lobe lamina in some transitional leaves is spiraled through almost 360°, with the dorsal leaf surface on the inside of the spiral.

One possible way to homologize horns with plane lobes is through sac formation in the upper part of lobe by fusion of margins of a twisted or spiraled lobe. This could explain the opening at the top being bordered by marginal cells, and the absence of other marginal cells on the sides of the resulting cylinder of tissue, perhaps

by incorporation into the cylinder walls. What happens to marginal cells at the junction between plane and saccate portions of transitional lobes is unclear. Under this model of horn formation the anatomical dorsal surface of the lobe would be enclosed within the 'helm'. The lobe base may remain plane to varying degrees, as in transitional lobes on female bracts, in fully formed horns the plane portion is reduced to the stalk. If this model is robust there are three non-homologous modifications to leaf-lobes that involve formation of lobules in the broad sense. Three different terms would best reflect this hypothesized non-homology, so I advocate using the term 'horn' when referring to leaf lobes that have been putatively spiraled and fused to enclose a space, in addition to the terms helm and lobule.

However, these are not the only structures that enclose spaces within the Porellales. In *Neotrichocolea* individual subsidiary lobes invaginate. More broadly across the Jungermanniales in the relatively unrelated genera *Delavayella* and *Tetracymbaliella* the lobe and underleaf margins may elaborate and invaginate to form a 'sac', and in *Plagiochila* the leaf base may inroll to the same end.

Just as helms and lobules are a source of critically important species circumscribing characters in other families of Porellales, including Frullaniaceae and Radulaceae, so they are in *Goebeliella*. Diagnostic differences between species are found in the horns, including cell shape, stalk length, and the presence of papilliform cells at the helm apex.

Stylus-like structure: at the base of the stalk on the ventral horn, between stalk and stem, there is a stylus-like structure. Is this the remnant of a highly reduced leaf-lobe, as it is in Frullaniaceae? In leaves with transitional morphology or plane lobules, there is no evidence of a stylus. This is consistent with the hypothesis that the stylus-like structure in *Goebeliella* is a by-product of horn formation on the ventral leaf-lobe. Further evidence for this hypothesis comes from ventral lobes of transitional morphology found on leaves immediately preceding the female bracts. At the base of these lobes a projecting ear of lamina is present, whose margin is separated from the rest of the lobe by a shallow notch. The depth of this notch increases with helm expression. So, the stylus-like appendage at the base of the ventral horn is not fully homologous with the stylus of Frullaniaceae species in that it is derived from only part of a lobe, rather than being equivalent to a lobe in its entirety. For this structure I propose the term pseudo-stylus.

Species concept: Schuster (1965) in his treatment of *Goebeliella* examined specimens from New Caledonia and New Zealand. Though he commented on differences between them, notably the opacity of medial cell walls in some of the New Caledonian specimens, he did nothing further with these observations, probably because his primary task in that treatment was to establish the relationships of what was still, then, an unusual and isolated element whose phylogenetic placement had not been firmly resolved.

The three morphological groups identified within *Goebeliella* are circumscribed by macro- and micro-morpholoical characters from all facets of their form. Though some characters, such as the presence of papilliform cells above the mouth of the horn are subtle, they are consistently correlated with other different character states such as, in this specific instance, the border of the dorsal leaf-lobe being one cell tier deep and formed by quadrate cells whose radial walls bear heavy thickening. Other characters, such as colour and the correlated manifestation of cell wall structure, are obvious at lower levels of magnification. The morphological groups are geographically structured, one is found in New Zealand, the other two in New Caledonia. The best explanation for the correlated distribution of character states among individuals is the existence of three tokogenetic groups within which character states have diverged and become fixed (Fitzhugh 2005). The stability of morphological character states separating the three morphological groups, their number, and their distribution in all aspects of plant form suggest that the three species hypotheses proposed below will fulfill many other species criteria, including those posited by phylogenetic and biological species concepts. The morphologically based species hypotheses outlined below can be tested against data relevant to these additional criteria.

Figures 2-73 illustrating the three species of *Goebeliella* recognized in this treatment are placed at the end of the paper. Plates are not devoted to single species, rather they are designed to show various structures from the three species side-by-side to facilitate comparison and reference. On each plate the figures are arranged into three columns, each column corresponds to one species, from left to right *G. cornigera*, *G. bicornuta* Steph., and *G. glauca* M.A.M.Renner.

Taxonomic Treatment

Goebeliellaceae Verdoorn *Manual of Bryology* 425. 1932.

= Goebelielloideae (Verdoorn) Hamlin *Records of the Dominion Museum* 7: 348. 1972.

Goebeliella Steph. *Hedwigia* 51: 61. 1911.

Type: *Goebeliella cornigera* (Mitt.) Steph. *Hedwigia* 51: 62. 1911.

Basionym: *Frullania cornigera* Mitt. in Hooker, *Flora Novae Zelandiae* 2: 163. 1855.

Morphological circumscription of the family Goebeliellaceae and its constituent genus was treated by Schuster (1965). The family as circumscribed by Schuster (1965) and authors before him (Verdoorn 1932) has been corroborated by molecular phylogenetic studies (e.g. Heinrichs et al. 2005), and remains current. To the characters currently accepted as distinctive of the family Goebeliellaceae could be added the horn-like form of the middle and ventral leaf-lobes. As hypothesized in the discussion above, the form of these leaf-lobes is not homologous with the helms and lobules of other families in the Porellales, and is indeed unique within Jungermanniopsida.

Key to species of *Goebeliella*

1. Plants with grey-red bloom when dry. Underleaf width half or less that of dry shoots, horns visible almost in entirety in ventral view. Leaf-lobe medial cells with more or less evenly-thickened cell walls. Cell walls with rugose 'ornamentation'. Pseudo-stylus reduced to a two- or three-celled spur capped by a slime papilla. Female bracts cucullate when hydrated, dorsal margin of innermost bract lobe almost perpendicular to shoot axis, bract medial and ventral lobe apices rounded ..... ***Goebeliella glauca* M.A.M.Renner**

1: Plants green, brown or red when dry. Underleaf width nearly equal to dry shoot width, horns mostly obscured by under-leaves in ventral view. Leaf-lobe medial cells with sinuous cells walls. Leaf-lobe cell walls with granular ornamentation. Pseudo-stylus with distinct lamina. Female bracts concave or flat, not cucullate when hydrated, dorsal margin of innermost bract inclined at about 45° to shoot axis, bract medial and ventral lobe apices rounded or obtuse **2**

2. Leaf-lobe margin with one tier of hyaline cells, whose radial walls bear heavy thickening. Horns with two bulging cells at mouth projecting at right angles to one another. Postical horn with long stalk. Underleaves plane, occasionally weakly concave in ventral view. Shoot systems regularly and closely pinnate. Female bracts spreading from perianth surface, bract medial and ventral lobe apices obtuse ..... ***Goebeliella bicornuta* Steph.**

2: Leaf lobe margins with two or three tiers of hyaline cells, the outer most differentiated into thin-walled long rectangular cells. Horns without papillae above the opening. Postical horn with short stalk. Underleaves concave in ventral view. Shoot systems regularly and openly pinnate. Female bracts appressed to perianth surface, bract medial and ventral lobe apices rounded ..... ***Goebeliella cornigera* (Mitt.) Steph.**

Goebeliella cornigera (Mitt.) Steph., *Hedwigia* 51: 62. 1911.

Frullania cornigera Mitt. in Hooker, *Flora Novae Zelandiae* 2: 163. 1855.

Type: New Zealand, Northern and Middle Islands: Bay of Islands, amongst *Sendtnera attenuata*, *Dr J.D. Hooker* (lectotype here designated: BM000969465!); New Zealand, Port Cooper, *Lyall.* (paralectotype: BM000969464!)

Shoot systems green to orange-red to red or red-black, openly pinnately branched with widely spaced secondary shoots, dried primary shoots 795–1135 μm wide, dried secondary shoots 675–845 μm wide; branching of *Frullania*-type, first branch leaf with a pair of horns. **Stems** cordate in transverse section around 200 μm diameter on primary shoots, with medial furrow on dorsal surface, cortical cells in 1 tier, smaller than medulla cells, walls bearing heavy, warm-brown pigmented thickenings contricting the lumen to a narrow cylinder, medulla cells with bulging, confluent yellow to orange-brown pigmented thickenings more or less continuous over cell walls. **Leaf-lobes** on primary shoots elliptic, 1100–1180 μm long by 900–960 μm wide, postical margin straight other margins curved, densely imbricate, concave, margin entire, differentiated marginal cells continuous around the margin except in antical and postical base, insertion J-shaped. Leaf-lobe cells divided into three zones. Marginal cells in two or three tiers of hyaline cells devoid of contents, outermost tier long short to long rectangular, 7.5–18.3 μm long 5.4–12.1 μm wide, long axis oriented perpendicular to lobe margin, walls hyaline and unthickened; inner tier cells with elliptic to rounded-oblong lumena due to heavy thickening of cell walls, walls hyaline but with heavy concave to triangular trigones and cell angles and continuously thickened medial cell walls, often differentially thickened at middle, long axis orientated perpendicular to lobe margin; lobe median cells occupying antical half of lobe between marginal cells above and basal cells below, dimorphic, with air-cells scattered among normal chlorophyllous cells, air-cells clear, devoid of content, rounded-oblong to elliptic, 12.1–16.4 μm long, 8.1–9.7 μm wide, walls evenly and continuously rounded, without rounded projection into the lumen; normal cells 12.4–24.3 μm long, 6.4–10.4 μm wide, walls heavily

thickened and sinuous due to pronounced rounded medial thickenings, typically one thickening present on each side of the medial wall, either alternating or opposing the thickening on the other side, long axis of cell orientation variable, but often parallel with radial lines from leaf base to margin; lobe basal cells long rectangular, 24.3–44.2 μm long, lumen 4.9–9.9 μm wide between heavily thickened cell walls bearing 3–6 confluent nodular thickenings on longitudinal walls, secondary thickenings orange pigmented, transverse walls unthickened. Cell walls of leaf-lobe medial portion appearing granular, basal and marginal cells without apparent texture. **Horns** falcate, antical margin evenly curved or slightly more curved toward apex, 417–520 μm long, postical margin straight at base, curved through 90° in upper half, 237–315 μm long, base 101–127 μm wide, both stalks short, antical horn stalk longer, to 20–27 μm, cells of mouth thin-walled and hyaline, long rectangular, papilliform cells above mouth absent, cells of horn body long rectangular, cell surfaces lacking pitted sculpting along cell walls. Pseudo-stylus at base of antical horn leaf-like, small, 4–6 cell tiers tall and wide. **Underleaves** transversely broad-elliptic, contiguous, concave particularly in upper half in ventral view when wet, fan-shaped when dry due to recurving of lateral and basal margins, 393–523 μm long, 595–804 μm wide on dry primary shoots, 303–433 μm long, 426–616 μm wide on dry secondary shoots, insertion shallowly curved, base on either side of insertion with small auricle, marginal cells in three or four tiers, outermost cells 10.1–22.5 μm long, 5.7–11.6 μm wide, quadrate to long rectangular, thin-walled, hyaline, long axis oriented perpendicular to margin, inner cells quadrate to rectangular, with weakly thickened, sinuous, hyaline walls; median cells narrow oblong 14.3–19.2 μm long, 6.7–9.8 μm wide, walls heavily thickened and sinuous due to pronounced rounded medial thickenings, orientation of long axis variable, air cells present, scattered throughout medial portion, basal cells long, cell lumen constructed by heavy confluent nodular thickening on medial walls, walls orange pigmented, basal cells forming zone in medial base of leaf above stem insertion. **Oil-bodies** not seen. **Asexual reproduction** absent. **Dioicous**. **Gynoecia** terminal on secondary shoot, female bracts in three or four pairs, increasing in stature toward gynoecium, closely adherent to perianth when wet and dry, air cells present in outer third of bract lobe only. Middle and ventral lobes on bracts transitioning from horn-like to plane, fused for one third their length in lower bracts, to fused for nearly their entire inner margin in upper bracts, upper bract folded, along lamina joining dorsal and medial lobes, dorsal lobe ligulate 1700–2400 μm long, 800–1100 μm wide, apex rounded, middle and ventral lobes ligulate, separated by a shallow sinus, concave, apex of both lobes rounded. Bracteole ligulate, folded medially, lamina either side of fold appressed to ventral perianth keel, bracteole apex rounded, around 2300 μm long and 700 μm wide, margins below midpoint recurved, insertion linear, broad. **Perianth** trigonous, ventral and lateral keels sharp and pronounced in upper half, perianths around 3450–4100 μm long and 950 μm wide at widest point, narrowing slightly in upper half toward mouth where 400 μm wide, mouth bordered by rectangular, thin-walled, hyaline cells plate-like appendages comprised of thin walled hyaline cells present; dorsal perianth surface with conspicuous medial furrow extending from the basal quarter to the mouth; incipient shoot calyptra present below perianth, sporophyte foot penetrating the stem apex to the level of the second leaf pair preceding the perianth; calyptra bistratose. **Androecia** not seen.

Distribution: *Goebeliella cornigera* is endemic to New Zealand, where it widespread in cool hyper-humid environments from around 100 m to more than 1200 m asl. *Goebeliella cornigera* is particularly common on the West Coast of the South Island, and is also common at higher elevations on ranges in the North Island.

Habitat: *Goebeliella cornigera* grows in all major forest types in New Zealand, including *Nothofagus* dominated, podocarp-broadleaf, broadleaf-dominated, and podocarp-dominated forests. It also grows above the treeline in alpine scrub and shrublands. Throughout its range *G. cornigera* is an epiphyte on the trunks and branches of a wide range of hosts including *Nothofagus* species, species of Podocarpaceae, and many broadleaf species. It may, in situations of suitable insolation grow as a lithophytic and even a terrestrial, for example on exposed banks in full sun. *Goebeliella cornigera* co-occurs with a suite of bryophytes typical of well-lit, epiphytic habitats, including species of the moss family Orthotrichaceae, and the liverwort genera *Lepicolea attenuata*, *L. scolopendra, Radula multiamentula, R. pseudoscripta, R. uvifera*, *Frullania ptychantha*, *Lepidolaena* spp., *Plagiochila circumdentata*, and on rock and soil with *Adelanthus occlusus*, *Kurzia calcarata*, and *Lepidozia obtusiloba* (as in *Engel 18548B*).

Recognition: *Goebeliella cornigera* is distinctive in its leaf margin with long-rectangular, thin-walled cells in the outer of two tiers of hyaline cells, the inner tier cells are similar in size, shape, and cell wall thickening to the adjacent medial cell walls but are hyaline. The horns lack a long stalk, the longest stalks on the antical horn are up to 30 μm long. The antical horn has at its base a small pseudo-stylus. The female bracts are closely appressed to the perianth in both wet and dry states.

Goebeliella cornigera can be separated from *G. glauca* by a suite of characters, listed below in order of decreasing accessibility.

1. The plants not having a glaucous bloom, which is a conspicuous feature of *G. glauca*.
2. In dry shoots the lateral leaves of *G. cornigera* are rolled inward and contact the underleaves, so completely obscuring the horns in ventral view; while in *G. glauca* no contact between leaves and underleaves is made in dry shoots, and the horns are visible in the intervening space as they project well beyond the underleaf margin.
3. The female bracts of *G. cornigera* are closely apressed to the perianth in both wet and dry shoots and the female bract dorsal lobe is ligulate, in *G. glauca* the female bracts are not appressed to the perianth, the dorsal lobe is falcate and strongly concave so spirals downward around the perianth.
4. The horns of *G. cornigera* are falcate, the antical margin is evenly curved and the horn turns through around 90° in the upper half; the horns of *G. glauca* are more sickle-shaped, the antical margin increases curvature in the upper half, and the horn turns through anything between 90° and 180° in the upper half.
5. The hyaline margin on the leaf lobe is two cell tiers deep in *G. cornigera*, cells of the outer tier are long rectangular and thin-walled; the hyaline margin in *G. glauca* is 2 or 3 tiers deep and cells in the outer tier are rectangular and thick-walled.
6. The walls of lobe medial cells of *G. cornigera* are sinuous due to their bearing pronounced, alternating, rounded medial thickenings, in *G. glauca* the lobe medial cell walls are evenly thickened.
7. Under light microscope, the leaf lobe medial cell surfaces of *G. cornigera* appear densely, yet irregularly, granular; in *G. glauca* the cell surfaces appear to have conspicuous ruminate ornamentation. Note that the causative structures are associated with the wall internal structure, rather than its surface.
8. The horns of *G. cornigera* are nearly sessile, their basal stalks are short and inconspicuous in both horns in each pair; in *G. glauca* the stalk on the antical horn is conspicuous, up to 90 μm long.
9. The pseudo-stylus at the base of the horn pair has a distinct lamina in *G. cornigera*, but in *G. glauca* consists of a three or four-celled spur only.
10. In *G. cornigera* cells of the horn are long rectangular cells, while in *G. glauca* they are short rectangular cells.

Goebeliella cornigera is more similar to *G. bicornuta* than *G. glauca*, both being green to wine-red plants whose horns are obscured by the underleaves, and leaves in dry shoots, and having female bracts adherent to the perianths. As such *G. cornigera* and *G. bicornuta* share the same state in the three most accessible characters described above. Closer examination, and accessing micromorphological characters is necessary to differentiate *G. cornigera* and *G. bicornuta*, in order of decreasing accessibility these characters and their states are:

1. The hyaline margin on the leaf lobe is two cell tiers deep in *G. cornigera*, the outer cells of which are long rectangular with thin walls; in *G. bicornuta* the margin is one cell thick, and the cells are quadrate to rectangular and have heavily thickened radial walls and a contrasting unthickened external wall.
2. The horns of *G. cornigera* have the antical and to a lesser degree the postical, margins of the horn continuously and nearly evenly curved from their base to their apex; in *G. bicornuta* the antical and postical margins are shallowly curved in the basal half, and have pronounced curvature in their apical half.
3. The horn apex of *G. cornigera* is bounded by cells whose surfaces are all plane; in *G. bicornuta* two cells above the opening are mamilliform, these two cells are orientated at around 45° to the horns line of bilateral symmetry on either side.
4. The stalk on both horns in *G. cornigera* is short, the horns are nearly sessile against the stem; in *G. bicornuta* the antical horn is stipitate, the stalk is long and distinct, being up to 90 μm long.
5. Female bract medial and ventral lobes rounded to obtuse in *G. cornigera*; obtuse to acute in *G. bicornuta*.
6. Underleaves are contiguous to loosely imbricate in *G. cornigera*, while they are closely imbricate in *G. bicornuta*.

Representative specimens examined: NEW ZEALAND: North Island: Auckland Province, Kaimai-Mamaku Forest Park, Mt Te Aroha, 37°32'S 175°44'E, 880–890 m, 15 Feb 2003, *J.J. Engel 23821 & M.J. von Konrat* (F); South Auckland Province, Southern extent of Herangi Range, W of cushion bog in vicinity of plateau area south of Te Whakapatiki, 38°29.9'S 174°46.2'E, 720–750 m, 18 Mar 2003, *J.J. Engel 25173*, *M.J. von Konrat & J.E. Braggins* (F); Gisborne province, Urewera National Park, Panekiri Range, summit area of Pukenui in vicinity of Punekiri Bluff, south of Lake Waikaremoana, 38°47'S 177°4'E, 1180 m, 24 Mar 1997, *J.J. Engel 23319* (F); Wellington Province, Ruahine Range, Pohangina Valley, 40°10'S 175°50'E, 16 Nov 1969, *J. Child H199* (F1033440); Wellington Province, northern Tararua Mountains Schormanns Track, eastern slopes of Mt

Hines, 10–12 miles west of Eketahuna, c. 1000 m, 15–16 Nov 1961, *R.M. Schuster 49163a* (F); South Island: Nelson Province, Paparoa National Park, Inland Pack track, SW of terminus of Bullock Creek Road, 42°7'S 171°24'E, 35 m, 24 Feb 1995, *J.J. Engel 21641* (F); Westland Province, Paparoa Range, road to Sewell Peak, 42°25'S 171°20'E, 710 m, 3 Feb 1983, *J.J. Engel 19062* (F); Paparoa Range, ridge immediately north of Sewell Peak, 42°24'S 171°20'E, 910 m, 3 Feb 1983, *J.J. Engel 19051* (F); Camp Creek, west of the Alexander Range, 42°42'S 171°33'E, 1010 m, Dec 1982, *A. Reif C129F* (F1062836); Westland Province, Jacksons Bay, between confluence of Jackson River and Arawata River and Lake Ellery, off Jackson River Road, 44°4'S 168°E, 30 m, 21 Dec 1982, *J. Child H4224* (F1086604); Cascade Road, Cascade ultramafic moraine, west of Martyr Saddle, 44°9'S 168°36'E, 135 m, 9 Mar 1997, *J.J. Engel 23011* (F); Arthurs Pass National Park, Kelly Range, off track to Carroll Hut, above Kellys Creek, north of Otira, 42°47'S 171°33'E, 1040–1110 m, 6 Jan 1983, *J.J. Engel 18418* (F); Arthurs Pass National Park, Bealey Valley track, 42°55'S 171°33'E, 875–900 m, 5 Mar 1997, *J.J. Engel 22858* (F); Canterbury Province, Arthurs Pass National Park, Scotts track to Avalanche Peak, w of Arthurs Pass township, 42°56'S 171°33'E, 950 m, 5 Mar 1995, *J.J. Engel 22084* (F); Southland Province, Fiordland National Park, Stuart Mountains, western shore of Lake Thomson north of stream draining from Lade Wade, 45°02'S 167°32'E, 300 m, 22 May 1986, *A.J. Fife 7665* (F1096273); Stewart Island (Rakiura), Rakiura National Park, Mt Rakeahua summit area, 46°56'S 167°52'E, 600–690 m, *J.J. Engel 24560A, M.J. von Konrat & J.E. Braggins* (F1173079).

Goebeliella bicornuta Steph., *Hedwigia* 51: 64. 1911.

Type: Mt Mou, Jul 1909, *Le Rat 156*, ex herb Steph. as *Goebeliella bicornuta St.* (lectotype here designated: G00051143!); Mont Mou, *Le Rat 271*, as *Goebeliella bicornuta* St. n.sp., (paralectotype: G00067854!).

Shoot systems green to orange-red to red, pinnately branched with closely spaced secondary shoots, dried primary shoots 950–1300 µm wide, dried secondary shoots 635–910 µm wide; branching of *Frullania*-type, first branch leaf with a pair of horns. **Stems** elliptic in transverse section around 200 µm diameter on primary shoots, with medial furrow on dorsal surface, cortical cells in 1 tier, smaller than medulla cells, walls bearing heavy, warm-brown pigmented thickenings contricting the lumen to a narrow cylinder, medulla cells with bulging, confluent yellow to orange-brown pigmented thickenings more or less continuous over cell walls. **Leaf-lobes** on primary shoots elliptic, 1280–1460 µm long by 960–1010 µm wide, postical margin straight other margins curved, densely imbricate, concave, margin entire, differentiated marginal cells continuous around the margin except in antical and postical base, insertion J-shaped. Leaf-lobe cells divided into three zones. Marginal cells in a single tier of hyaline cells devoid of contents, quadrate to rectangular, 7.1–12.1 µm long 6.8–10.7 µm wide, long axis oriented perpendicular to lobe margin, walls hyaline, external wall unthickened, thin and often partly collapsed, radial walls heavily and continuously thickened by colourless secondary thickening that tapers toward the lobe margin; medial cell walls often differentially thickened at middle, sinuous, long axis orientated perpendicular to lobe margin; occupying antical half of lobe between marginal cells above and basal cells below, dimorphic, with air-cells scattered among normal chlorophyllous cells, air-cells clear, devoid of content, rounded-oblong to elliptic, 14.9–21.6 µm long, 7.8–10.8 µm wide, walls sinuous or evenly and continuously rounded; normal cells 10.9–23.4 µm long, 9.1–12.2 µm wide, walls heavily thickened and sinuous due to pronounced rounded medial thickenings, typically one thickening present on each side of the medial wall, either alternating or opposing the thickening on the other side, long axis of cell orientation variable, but often parallel with radial lines from leaf base to margin; lobe basal cells long rectangular, 35.7–64.4 µm long, lumen 6.5–8.9 µm wide between heavily and evenly thickened radial cell walls, secondary thickenings orange pigmented, transverse walls unthickened. Cell walls of leaf-lobe medial portion granular, basal and marginal cells without texture. **Horns** falcate, antical margin shallowly curved or straight between bulbous base and apex, curvature increasing at apex where curved abruptly through 90°, 389–540 µm long, postical margin straight nearly its entire length or shallowly curved above the bulbous base, then abruptly curved through 90° at the apex, 251–344 µm long, base 85–118 µm wide, stalks differing in length, antical horn stalk longer, to 51–81 µm, postical horn nearly sessile, cells of mouth thin-walled and hyaline or orange pigmented, long rectangular, two papilliform cells above mouth present, orientated at 45° either side of the line of bilateral symmetry, cells of horn body rectangular, cell surfaces with pitted sculpting along cell walls. Pseudo-stylus at base of antical horn leaf-like, small, 3–4 cell tiers tall and wide, capped by a papilla. **Underleaves** transversely broad-elliptic, imbricate, plane or concave particularly in upper half in ventral view when wet, fan-shaped when dry due to recurving of lateral and basal margins, 375–416 µm long, 697–851 µm wide on dry primary shoots, 299–358 µm long, 394–606 µm wide on dry secondary shoots, insertion shallowly curved, base on either side of insertion with small auricle, marginal cells in two or three tiers, outer cells quadrate to long rectangular, 7.9–17.8 µm long, 5.5–10.5 µm wide, thin-walled, hyaline, long axis oriented perpendicular to margin, inner cells quadrate to rectangular, with weakly thickened, sinuous, hyaline walls; median cells narrow oblong 12.5–14.6 µm long, 5.7–8.9 µm wide, walls heavily thickened and sinuous due to pronounced rounded medial thickenings, orientation of long axis variable, air cells present, scattered throughout medial portion,

basal cells forming zone in median and basal region of underleaf, cells long rectangular, 21.7–44.9 μm long, 6.1–8.4 μm wide, lumen constructed by heavily and continuously thickened, orange-brown pigmented cell walls. **Oil-bodies** not seen. **Asexual reproduction** absent. **Dioicous**. **Gynoecia** terminal on secondary shoot, female bracts in three or four pairs, increasing in stature toward gynoecium, spreading from the perianth when wet and dry, air cells present in outer third of bract lobe only. Middle and ventral lobes on bracts transitioning from horn-like to plane, fused for one third their length in lower bracts, to fused for nearly their entire inner margin in upper bracts, upper bract folded along lamina joining dorsal and medial lobes, dorsal lobe ligulate 2820–2900 μm long, 820–980 μm wide, obtuse or actute, middle and ventral lobes ligulate, separated by a shallow sinus, concave, apex of both lobes obtuse. Bracteole ligulate, folded medially, lamina either side of fold appressed to ventral perianth keel below but spreading ventrally from perianth in upper half, bracteole apex rounded, to 2300 μm long and 800 μm wide, margins below midpoint recurved, insertion linear, broad. **Perianth** trigonous, ventral and lateral keels sharp and pronounced in upper half, perianths at least 2500–3000 μm long and 860–940 μm wide at widest point, narrowing slightly in upper half toward mouth where 200–400 μm wide, mouth bordered by rectangular, thin-walled, hyaline cells plate-like appendages comprised of thin walled hyaline cells absent; mature perianths not seen. **Androecia** not seen.

Distribution; *Goebeliella bicornuta* is endemic to New Caledonia, where it grows in forests on and around mountain summits between 1000 and 1300 m asl.

Habitat: *Goebeliellla bicornuta* is an epiphyte on tree trunks and branches, and has been collected on trees with trunks as small as 2 cm dbh. *Goebeliella bicornuta* co-occurs with a wide range of epiphytic bryophytes, including species of the genera *Bazzania*, *Drepanolejeunea, Frullania*, and *Microlejeunea*.

Recognition: *Goebeliella bicornuta* is distinctive in the hyaline border on leaf lobe being 1 cell tier deep; the horns straight, or nearly so, in their lower half; the horns have a pair of papilliform cells above the mouth; the female bract lobes have an obtuse to acute apex.

Goebeliella bicornuta can be separated from *G. glauca* by many of the same characters that separate the latter from *G. cornigera*, and these are listed below in order of decreasing accessibility.

1. The plants do not have a glaucous bloom, which is a conspicuous feature of *G. glauca*.
2. In dry shoots the lateral leaves of *G. bicornuta* are rolled inward and contact the underleaves, so obscuring the horns in ventral view; while in *G. glauca* no contact between leaves and underleaves is made in dry shoots, and the horns are visible in the intervening space as they project well beyond the underleaf margin.
3. The female bracts of *G. bicornuta* are falcate and spread away from the perianth, but are plane; in *G. glauca* the female bracts are not appressed to the perianth, the dorsal lobe is falcate and cochleariform so envelops the perianth.
4. The horns of *G. bicornuta* are weakly falcate, the antical margin is nearly straight, but turns through about 90° in the upper half; the horns of *G. glauca* are more sickle-shaped, the antical margin increases curvature in the upper half, and the horn turns through anything between 90° and 180° in the upper half.
5. The hyaline margin on the leaf lobe is one cell tier deep in *G. bicornuta*; the hyaline margin in *G. glauca* is 2 or 3 tiers deep.
6. The walls of lobe medial cells of *G. bicornuta* are sinuous due to their bearing pronounced, alternating, rounded medial thickenings, in *G. glauca* the lobe medial cell walls are evenly thickened.
7. Under light microscope, the leaf lobe medial cells of *G. bicornuta* appear densely, yet irregularly, granular; in *G. glauca* the cell surfaces appear to have conspicuous ruminate ornamentation.
8. The horns of *G. bicornuta* have a pair of papilliform cells above the mouth; papilliform cells are absent from the horns of *G. glauca.*
9. The pseudo-stylus at the base of the horn pair has a small but distinct lamina in *G. bicornuta*; in *G. glauca* it consists of a three or four celled spur only.

Typification: No type indicated by Stephani (1911). The only detail given in the protologue regarding specimens examined is 'Hab. Novae-Caledoniae'. There are three specimens from New Caledonia in Stephani's herbarium in Geneva annotated '*G. bicornuta* St.' or '*G. bicornuta* St. n.sp.' by Stephani, all collected by Le Rat, probably on the same trip given the proximity of Le Rat's specimen numbers, which have a range of 120 across the specimens. One specimen bears the date 'July 1909'. The most reasonable assumption regarding Stephani's receipt of these specimens, in the absence of other evidence, is that all three were received in the same consignment, as all three had been collected by Le Rat in New Caledonia, and bear a range of numbers

compatible with collection within a short space of time. Stephani probably had access to all three specimens when composing his protologue.

Two morphological entities are represented in the following three specimens:

1. Mt Mou, leg. *Le Rat 271*, G00067854. This specimen contains both a fuscous and a glaucous element.
2. Pic du Sources, *Le Rat 264*, G00067853. This specimen contains only the glaucous element.
3. Mt Mou, July 1909, leg. *Le Rat 156*, G00051143. This specimen comprises the fuscous element only.

Do characters described and illustrated in the protologue identify one morphological entity, or are they a mixture of features from both? Considering the major elements of the description: sterilis – ambiguous; fusca – an unambiguous reference to the red-brown element, rather than the glaucous element; irregularly pinnately branched – ambiguous; branches simple – ambiguous; rarissime pinnula auctis [very rarely branches increasing in stature] – ambiguous; leaf description – mostly ambiguous, though "hyalinae uniseriatae rectangulares (18 μm)" unambiguously refers to the fuscous plant; the description of horns could refer to either element; the underleaf description 'gigantea reniformia' and '1.21 mm lata' both suggest the fuscous plant, the measurement was probably taken from hydrated, slide mounted material, so is larger than the measurement from dehydrated material in the description above.

The figures in the protologue provide additional evidence. Figure 2 shows a leaf and adjacent underleaf attached to a short stem sector, within which the underleaf obscures the horns. This is consistent with the fuscous plant. The horns in Figure 2 have straight or nearly straight antical and postical margins in their lower halves, they are not S-shaped, and the apex does not curve through more than 90°, again consistent with the fuscous element. Figure 3 is ambiguous. Figure 4 again shows horns with nearly straight lower antical and postical margins, and an abrupt curve through around 90° close to the apex, all consistent with the fuscous element.

In summary, several features described and illustrated in the protologue of *G. bicornuta* unambiguously match the fuscous element. These include the width of the hyaline lobe margin, and horn shape. A couple of additional characters *suggest* the fuscous plant, but are not definitive, including underleaf size, and the horns obscured behind the underleaf in ventral view. Many characters are ambiguous and fit both plants equally as well. Critically, no character fits the glaucous element better than the fuscous element. I conclude that the protologue is a better match with the fuscous element and the name *G. bicornuta* must be lectotypified accordingly. The Pic du Sources specimen does not match the protologue, leaving two specimens, *Le Rat 156* and *271*, from which to select a lectotype. We may choose among these two specimens on their merits. *Le Rat 156* contains more copious material and is pure, and on these bases is selected as lectotype. This lectotypification leaves the glaucous element without a name.

Frullania bicornuta Steph. ex Paris was published in 1910, so a year before Stephani's name (Paris 1910). Paris cited specimens from Pic du Source and Mt Mou, in that order. Though the specimens cited are both *Goebeliella*, the name is invalid because no description was presented. Even if validly published, and based on the first cited specimen (which contains only the glaucous element) a combination for this species under *Goebeliella* would be blocked by Stephani's *Goebeliella* species published the following year.

Frullania bicornuta Steph. was published in 1911. The protologue of *Frullania bicornuta* Steph. describes a fairly typical *Frullania* subg. *Microfrullania* or subg. *Australes* species (Stephani 1911). Stephani's choice of epithet in this instance can be found in the second to last sentence of the diagnosis 'laciniae apicales anguste lanceolatae, torte valide dentatae quasi cornutae' [apical laciniae (on the female bracteole lobes) narrowly lanceolate, twisted strongly toothed resembling horns]. The lobes on the bifid female bracteole resemble horns, hence *bicornuta*. Stephani's descriptions and derivation of the same epithet from quite different structures emphasise the fact that he regarded his *Goebeliella bicornuta* and *Frullania bicornuta* as different species. Confusion between the two species sharing the same epithet seems to originate with Paris, and is probably due to the fact that his name was published before the genus *Goebeliella* had been described. Possibly it was published before Stephani had reached a decision to describe a new genus, and this late decision may explain the absence of *Goebeliella* from his *Species Hepaticarum*, a fact noted with some derision by Schuster (1965).

Specimens examined: NEW CALEDONIA: Epiphyte, le long d'un tronc entre 0.5 et 1.8 m au-dessus du sol, foret hygrophile de montagne, chaine de l'Ignambi pres du point culminant de la "Route do Gomen", 1200 m, 17 Aug 1951, *H. Hurlimann*, Franco Suisse Expédition botanique en Novell Calédonie No. 2849 (G); Northern Province: trail to the summit of Mont Panié by southern slopes, 20°35'44"S 164°45'34"E, 1280 m, 9 Oct 2012, *J. Larraín 35904* (F); Reserve Speciale Botanique du Mont Panie, along ridge trail between hut (Blaffart Refuge) and Bwa Tean, 20.62446°S 164.77503°E, 780 m, 9 Oct 2012, *B. Shaw 17204* (DUKE, NSW); Mont Panié, Aufsteig entland de Wanderwegs von der Straße RPN 3 bis zum Gipfel, c. 1100 m, 13 Sep 2001, *F. Müller NC144* (DR); Southern Province: near summit of Mont Dzumac, by the vehicle road, 22°00'32"S 166°27'36"E, 1100 m,

26 Sep 2012, *J. Larraín 35388* (F); Province Sud, near summit of Mont Dzumac, 22°00'33"S 166°27'36"E, 1100 m, 26 Sep 2012, *J. Larraín 35379B* (F); sur le tronc d'un Weinmannia monticola, foret hygrophile de montagne, crete entre le Mt Dzumac et la Mt Ouin, 1000 m, 17 May 1951, *H. Hurlimann*, Franco Suisse Expédition botanique en Novell Calédonie No. 2591b (G); sur la tige d'un Dracophyllum, forest hygrophile de montage, au NW du sommet du Mt Dzumac, 1150 m, 19 May 1951, *H. Hurlimann*, Franco Suisse Expédition botanique en Novell Calédonie No. 2627 (G); New Caledonia, Epiphyte, sure une tige de Freycenitia sp. pea au-dessus du sol, foret meso-hydorophile de montagne, crete Sud-Ouest du Mt. Colnett, 1300 m, 13 Sep 1951, *H. Hurlimann* Franco Suisse Expédition botanique en Novell Calédonie No. 2941 (G-073699).

Goebeliella glauca M.A.M.Renner *sp. nov.*

Diagnosis: *Goebeliella glauca* differs from *G. bicornuta* and *G. cornigera* by its distinct glaucous hue, which overlays green, red-green, red or even purple-red shoot colour; by the horns visible between the underleaves and leaf lobes in dry shoots of primary and secondary order; by the horns evenly curved through 90–180° in their upper halves and having S-shaped antical and postical margins, and lacking papilliform cells above the mouth; by the round to transversely elliptic, remote to contiguous underleaves whose hyaline border is 2–4 cell tiers wide; by the leaf lobe cell walls evenly and continuously thickened in medial and basal divisions; by the hyaline border on the leaves 2 or 3 cell tiers wide; by the walls appearing to bear distinct ruminate ornamentation; by the cochleariform female bracts that envelope the perianth base when a perianth is present, or wrap around each other to form a structure resembling a strobilus that projects above the patch.

Type: New Caledonia, Southern Province, Noumea area, Montagne du Sources, along road to Pic Buse area, 22.14966°S 166.59033°E, 600 m, 28 Sep 2012, *B. Shaw 16737* (holotype: NOU; isotypes: DUKE, F, NSW)

Shoot systems glaucous-green to glaucous-purple, irregularly pinnately branched, dried primary shoots 850–1400 μm wide, dried secondary shoots 735–1025 μm wide; branching of *Frullania*-type, first branch leaf with a pair of horns. **Stems** elliptic in transverse section around 200 μm diameter on primary shoots, with medial furrow on dorsal surface, cortical cells in 1 tier, smaller than medulla cells, walls bearing heavy, warm-brown pigmented thickenings constricting the lumen to a narrow cylinder, medulla cells with bulging, confluent yellow to orange-brown pigmented thickenings more or less continuous over cell walls. **Leaf-lobes** on primary shoots elliptic, 1120–1220 μm long by 660–760 μm wide, postical margin straight other margins curved, densely imbricate, concave, margin entire, differentiated marginal cells continuous around the margin except in antical and postical base, insertion J-shaped. Leaf-lobe cells divided into three zones. Marginal cells in two or three tiers of hyaline cells devoid of contents, outer cells variable in shape, quadrate to long rectangular, 9.9–21.3 μm long 9.1–15.9 μm wide, long axis oriented perpendicular to lobe margin, walls hyaline, external wall unthickened, thin and often partly collapsed, radial walls heavily and thickened, bulging trigones present at cell angles, confluent with adjacent trigones across thickened medial walls, thickening colourless, inner cells round, elliptic or ovate with evenly thickened hyaline walls, similar in size to medial cells; medial cells occupying antical half of lobe between marginal cells above and basal cells below, dimorphic, with air-cells scattered among normal chlorophyllous cells, air-cells clear, devoid of content, rounded-oblong to elliptic, 10.9–14.4 μm long, 7.1–10.3 μm wide, normal cells variously round, elliptic, ovate or rounded-oblong, 14.4–21.9 μm long, 8.0–12.9 μm wide, walls in both cell types evenly and continuously thickened, occasionally weak medial thickening present, long axis of cell orientation variable, but often parallel with radial lines from leaf base to margin; lobe basal cells long rectangular, 23.1–40.1 μm long, lumen 6.8–9.7 μm wide between heavily and evenly thickened radial cell walls, secondary thickenings pale tan pigmented, sinuous, transverse walls unthickened or weakly thickened. Cell walls of leaf-lobe medial portion ruminate, including internal walls, basal and marginal cell walls without texture. **Horns** falcate, antical margin shallowly curved or straight between bulbous base and half way, then evenly curved through 90–180° in upper half, 445–622 μm long, postical margin S-shaped never straight, or straight only close to the middle, curved below, and above evenly curved through 90–180°, 311–428 μm long, base 97–115 μm wide, stalks differing in length, antical horn stalk longer, to 60–87 μm, postical horn sessile, cells of mouth thin-walled and hyaline or orange pigmented, long rectangular, papilliform cells above mouth absent, cells of horn body rectangular, cell surfaces with pitted sculpting along cell walls. Pseudo-stylus at base of antical horn a spur of, 3-4 cells, capped by a papilla. **Underleaves** rotund to transversely elliptic, imbricate, plane, 245–346 μm long, 469–540 μm wide on dry primary shoots, 203–323 μm long, 344–421 μm wide on dry secondary shoots, insertion shallowly curved, base on either side of insertion with small auricle, marginal cells in two to four tiers, outer cells quadrate to elliptic, 7.1–14.3 μm long, and wide, thin-walled, hyaline, long axis oriented perpendicular to margin, inner cells quadrate to rectangular, with continuously thickened, hyaline walls with bulging trigones; median cells narrow oblong 10.5–22.2 μm long, 7.9–11.5 μm wide, walls evenly and continuously thickened, orientation of long axis variable, air cells present, scattered throughout medial portion, basal cells forming zone in median and basal region of underleaf, cells long rectangular, 17.6–27.7 μm long, 8.8–12.4 μm wide, lumen not

constructed, cell walls evenly and continuously thickened. **Oil-bodies** not seen. **Asexual reproduction** absent. **Dioicous**. **Gynoecia** terminal on secondary shoot, female bracts in three or four pairs, increasing in stature toward gynoecium, spreading from the perianth when wet and dry, air cells present in outer third of bract lobe only. Middle and ventral lobes on bracts transitioning from horn-like to plane, fused for one third their length in lower bracts, to fused for nearly their entire inner margin in upper bracts, upper bract folded along lamina joining dorsal and medial lobes, dorsal lobe ligulate, falcate, and cochleariform 2000–2540 µm long, 760–860 µm wide, apex rounded, middle and ventral lobes ligulate, separated by a shallow sinus, concave, apex of both lobes rounded. Bracteole ligulate, folded medially, lamina either side of fold appressed to ventral perianth keel below but spreading ventrally from perianth in upper half, bracteole apex rounded, to 1800 µm long and 800 µm wide, margins below midpoint recurved, insertion linear, broad. **Perianth** trigonous, ventral and lateral keels sharp and pronounced in upper half, perianths 2200–3000 µm long and 780–900 µm wide at widest point, narrowing close to mouth where 250–400 µm wide, mouth bordered by rectangular, thin-walled, hyaline cells plate-like appendages comprised of thin walled hyaline cells present; dorsal perianth surface plane. **Androecia** not seen.

Etymology: glaucous, in reference to the distinctive colour of this species.

Distribution: *Goebeliella glauca* is endemic to New Caledonia.

Habitat: *Goebeliella glauca* has been collected between 500 and 900 m asl, generally at lower altitudes than *G. bicornuta*. *Goebeliella glauca* grows as an epiphyte on tree trunks and branches with a wide range of xerophytic associates such as mosses of the family Orthotrichaceae, and many other liverworts including *Radula scariosa*, *Chiastocaulon caledonicum*, *Mastigophora caledonica*, many species of Lejeuneaceae, and *Frullania*. *Goebeliella glauca* also grows as a lithophyte on naked rocks or on thin humus over rock, again with xerophytic species including *Herbertus leratii*, *Mastigophora caledonica*, and *Acromastigum adaptatum* among others.

Recognition: *Goebeliella glauca* is distinctive in its glaucous hue, which overlays green, red-green, red or even purple-red shoot colour. The horns are visible between the underleaves and leaf lobes in dry shoots, and are evenly curved through 90–180° in their upper halves. The underleaves are round to transversely elliptic, and remote to contiguous on primary and secondary shoots. Leaf lobe cell walls are evenly and continuously thickened in medial and basal divisions, and the walls appear to bear distinct ruminate ornamentation, though this texture seems integral to wall structure rather than wall ornamentation. The female bracts are cochleariform, and envelope the perianth base if a perianth is present, otherwise they wrap around each other to form a structure resembling a strobilus, and this is held above the patch. See the recognition sections of *Goebeliella bicornuta* and *G. cornigera* for more detailed descriptions of character states differentiating *G. glauca* from these two species.

Remarks: With light microscope conspicuous rugose cell 'ornamentation' is visible. Under SEM no ornamentation was noted. In transverse sections of the leaf these "laminations" are observable in all walls, above, below and between adjacent cells in internal walls. This suggests these structures are integral to the wall, rather than deposits on the external walls only. Plants from New Caledonia illustrated by Schuster (1965) belong to *G. glauca*.

Specimens examined: NEW CALEDONIA: Montagne des Sources, in *Araucaria muelleri* forest, 800–850 m, 30 Mar 1962, *R.M. Schuster 52309a* (F); South Central, Pic Buse near Montagne des Sources, above St Louis, 650–750 m, open burned *Dacrydium araucarioides-Callitropsis* scrub forest, 30 Mar 1962, *R.M. Schuster 52273b* (F); ibid, *R.M. Schuster 52273c* (F); Sur un tronce en forest mesophile d'altitude moyehne, crete au NE du P. 576 a l'Ouest de la vallee du Boulari vers le P. 784, env. 530 m, 5 Feb 1951, *H. Hurlimann* Franco Suisse Expédition botanique en Novell Calédonie No. 2347 (G); Epiphyte sur lat tige d'une Scaevola, forest hygrophile de montagne, vallée derrière la mine Sunshine (Dumbea), 700 m, 15 Mar 1951, *H. Hurlimann*, Franco Suisse Expédition botanique en Novell Calédonie No. 2416 (G); Sur un tronce de *Podocarpus*, en forest hygrophile de montagne, fond de la vallée derrière la mine Sunshine (Dumbea), 730 m, 15 Mar 1951, *H. Hurlimann*, Franco Suisse Expédition botanique en Novell Calédonie No. 2431 (G); Epiphyte, ave *Mastigobryum* et *Radula* sur le tronc d'un *Calophyllum caledonicum* en foret mesophile, pente N des collines entre la Riviere Bleue et la Riviere Blanche (Yate), 500 m, 14 Jun 1951, *H. Hurlimann*, Franco Suisse Expédition botanique en Novell Calédonie No. 2692 (G); Pic du Sources, *Le Rat 264*, (syntype of *G. bicornuta* G00067853).

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Anders Hagborg and Lars Söderström provided advice on *Frullania bicornuta* Steph. and *Frullania bicornuta* Steph. ex Paris. Matt von Konrat, Juan Larraín and Blanka Shaw collected *Goebeliella* on New Caledonia and made their specimens available for study. Sue Lindsey (as Microscopy and Microanalysis Laboratory Manager at the Australian Museum) performed SEM examination of *Goebeliella*.

References

Davis EC (2004) A molecular phylogeny of leafy liverworts (Jungermanniidae: Marchantiophyta). *Monographs in Systematic Botany from the Missouri Botanical Garden Volume* 98: 61–86

Evans AW (1939) The classification of the Hepaticae. *Botanical Review* 5: 49–96 http://dx.doi.org/10.1007/BF02899993

Fitzhugh K (2005) The inferential basis of species hypotheses: the solution to defining the term 'species'. *Marine Ecology* 26: 155–165

Forrest LL, Davis EC, Long DG, Crandall-Stotler BJ, Clark A, Hollingsworth ML (2006) Unraveling the evolutionary history of the liverworts (Marchatiphyta): multiple taxa, genomes and analyses. *The Bryologist* 109: 303–334 http://dx.doi.org/10.1639/0007-2745(2006)109[303:UTEHOT]2.0.CO;2

He-Nygren X-L, Ahonen I, Juslén A, Glenny D, Piippo S (2004) Phylogeny of liverworts – beyond a leaf and a thallus. *Monographs in Systematic Botany from the Missouri Botanical Garden Volume* 98: 87–118

Heinrichs J, Gradstein SR, Wilson R, Schneider H (2005) Towards a natural classification of liverworts (Marchantiophyta) based on the chloroplast gene *rbc*L. *Cryptogamie, Bryologie* 26: 215–233

Heinrichs J, Reiner-Drehwald ME, Feldberg K, Grimaldi DA, Nascimbene PC, von Konrat MJ, Schmidt AR (2011) *Kaolakia borealis* nov. gen. et sp. (Porellales, Jungermanniopsida): a leafy liverwort from the Cretaceous of Alaska. *Review of Palaeobotany and Palynology* 165: 235–240 http://dx.doi.org/10.1016/j.revpalbo.2011.04.002

Larraín J, Carter B, Shaw B, Hentschel J, Strozier L, Furuki T, Heinrichs J, Crandall-Stotler BJ, Engel JJ, von Konrat MJ (2015) The resurrection of *Neohattoria* Kamim. (Jubulaceae, Marchantiophyta): a six decade systematic conflict resolved through a molecular perspective. *PhytoKeys* 50: 101–122 http://dx.doi.org/10.3897/phytokeys.50.4940

Mitten W (1855) Hepaticae, in Hooker JD, *Flora Novae Zealandiae, 2*. London: Reeve

Paris EG (1910) Hépatiques de la Nouvelle Calédonie. *Revue Bryologique* 37: 128–132

Pätsch R, Hentschel J, Linares-Palomino R, Zhu R-L, Heinrichs J (2010) Diversification and taxonomy of the liverwort *Jubula* Dumort. (Jungermanniopsida: Porellales) inferred from nuclear and chloroplast DNA sequences. *Systematic Botany* 35: 6–12 http://dx.doi.org/10.1600/036364410790862515

Renner MAM, Brown EA, Wardle GM (2010) The *Lejeunea tumida* species group (Lejeuneaceae: Jungermanniopsida) in New Zealand. *Australian Systematic Botany* 23: 443–462 http://dx.doi.org/10.1071/SB10037

Renner MAM, Devos N, Brown EA, von Konrat MJ (2013) New records, replacements, reinstatements and four new species in the *Radula parvitexta* and *R. ventricosa* species groups (Jungermanniopsida) in Australia: cases of mistaken identity. *Australian Systematic Botany* 26: 298–345 http://dx.doi.org/10.1071/SB13027

Schuster RM (1965) Studies on Antipodal Hepaticae VII. Goebeliellaceae. *Journal of the Hattori Botanical Laboratory* 28: 129–138

Schuster RM (1966) The Hepaticae and Anthocerotae of North America. Volume 1. New York: Columbia University Press

Schuster RM (1984) Evolution phylogeny and classification of the Hepaticae, Marchantiophyta. pp 21–70 in Schuster RM (ed) *New Manual of Bryology, Volume 2*. Nichinan: The Hattori Botanical Laboratory

Stephani F (1909–1912). *Species Hepaticarum 4*. Geneve et Bale: Mme Maison a Lyon

Verdoorn F (1932) Classification of Hepaticae. *in* Verdoorn F (ed) *Manual of Bryology.* M. Nijhoff: The Hague

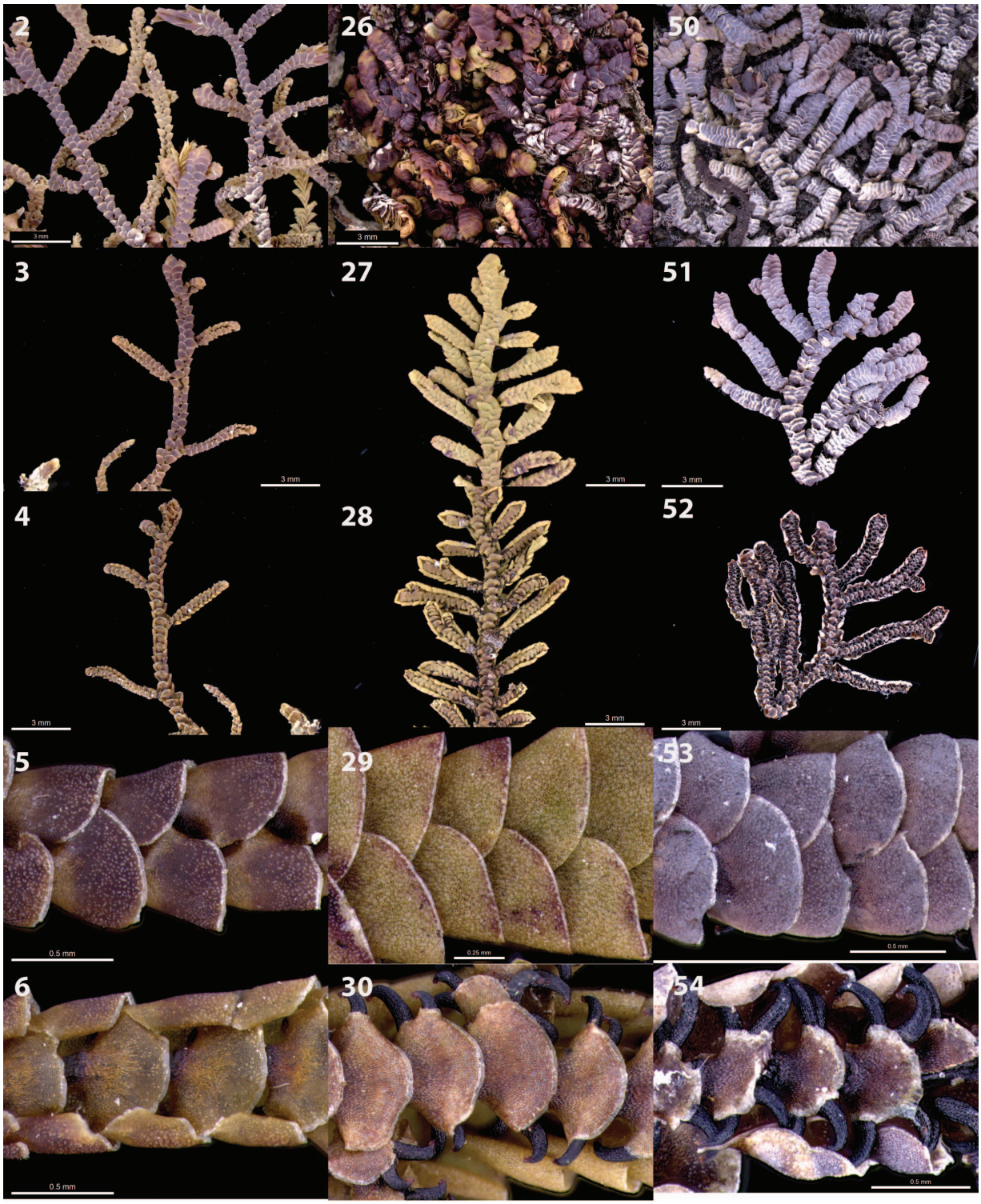
von Konrat MJ, Braggins JE (2001) A taxonomic assessment of the initial branching appendages in the liverwort genus *Frullania* Raddi. *Nova Hedwigia* 72: 283–310

von Konrat MJ, Hentschel J, Heinrichs J, Braggins JE (2011) Deep southern hemisphere connections: a revision of *Frullania* sect. *Amphijubula*. *The Bryologist* 114: 52–66 http://dx.doi.org/10.1639/0007-2745-114.1.52

Figs 2–25. *Goebeliella cornigera* (Mitt.) Steph. 2: Shoot systems. **3**: Single shoot system in dorsal view. **4**: Single shoot system in ventral view. **5**: Primary shoot dorsal view. **6**: Primary shoot ventral view. **7**: Secondary shoot dorsal view. **8**: Secondary shoot ventral view. **9**: Leaf-lobe cell wall texture. **10**: Transverse section of primary shoot stem. **11**: SEM of primary shoot ventral view. **12**: Horn mouth. **13**: Cell surface of horn body. **14**: Three horn-pairs. **15**: Stalks. **16**: Pseudostylus. **17**: SEM of horn mouth. **18**: Branches in ventral view. **19**: Perianth and female bracts, dorsal view. **20**: Perianth and female bracts, ventral view. **21**: SEM of perianth and female bracts, ventral view. **22**: Leaf lobe marginal cells. **23**: Leaf lobe medial cells. **24**: Leaf lobe basal cells. **25**: Underleaf marginal cells. All from *Schuster 49163a* (F).

Figs 26–49. *Goebeliella bicornuta* Steph. 26: Shoot systems. **27**: Single shoot system in dorsal view. **28**: Single shoot system in ventral view. **29**: Primary shoot dorsal view. **30**: Primary shoot ventral view. **31**: Secondary shoot dorsal view. **32**: Secondary shoot ventral view. **33**: Leaf-lobe cell wall texture. **34**: Transverse section of primary shoot stem. **35**: SEM of primary shoot ventral view. **36**: Horn mouth. **37**: Cell surface of horn body. **38**: Three horn-pairs. **39**: Stalks. **40**: Pseudostylus. **41**: SEM of horn mouth. **42**: Branches in ventral view. **43**: Perianth and female bracts, dorsal view. **44**: Perianth and female bracts, ventral view. **45**: SEM of perianth and female bracts, ventral view. **46**: Leaf lobe marginal cells. **47**: Leaf lobe medial cells. **48**: Leaf lobe basal cells. **49**: Underleaf marginal cells. All from *Shaw 17204* (NSW).

Figs 50–73. *Goebeliella glauca* M.A.M.Renner. 50: Shoot systems. **51**: Single shoot system in dorsal view. **52**: Single shoot system in ventral view. **53**: Primary shoot dorsal view. **54**: Primary shoot ventral view. **55**: Secondary shoot dorsal view. **56**: Secondary shoot ventral view. **57**: Leaf-lobe cell wall texture. **58**: Transverse section of primary shoot stem. **59**: SEM of primary shoot ventral view. **60**: Horn mouth. **61**: Cell surface of horn body. **62**: Three horn-pairs. **63**: Stalks. **64**: Pseudostylus. **65**: SEM of horn mouth. **66**: Branches in ventral view. **67**: Perianth and female bracts, dorsal view. **68**: Perianth and female bracts, ventral view. **69**: SEM of perianth and female bracts, ventral view. **70**: Leaf lobe marginal cells. **71**: Leaf lobe medial cells. **72**: Leaf lobe basal cells. **73**: Underleaf marginal cells. All from *Larraín 35388* (NSW).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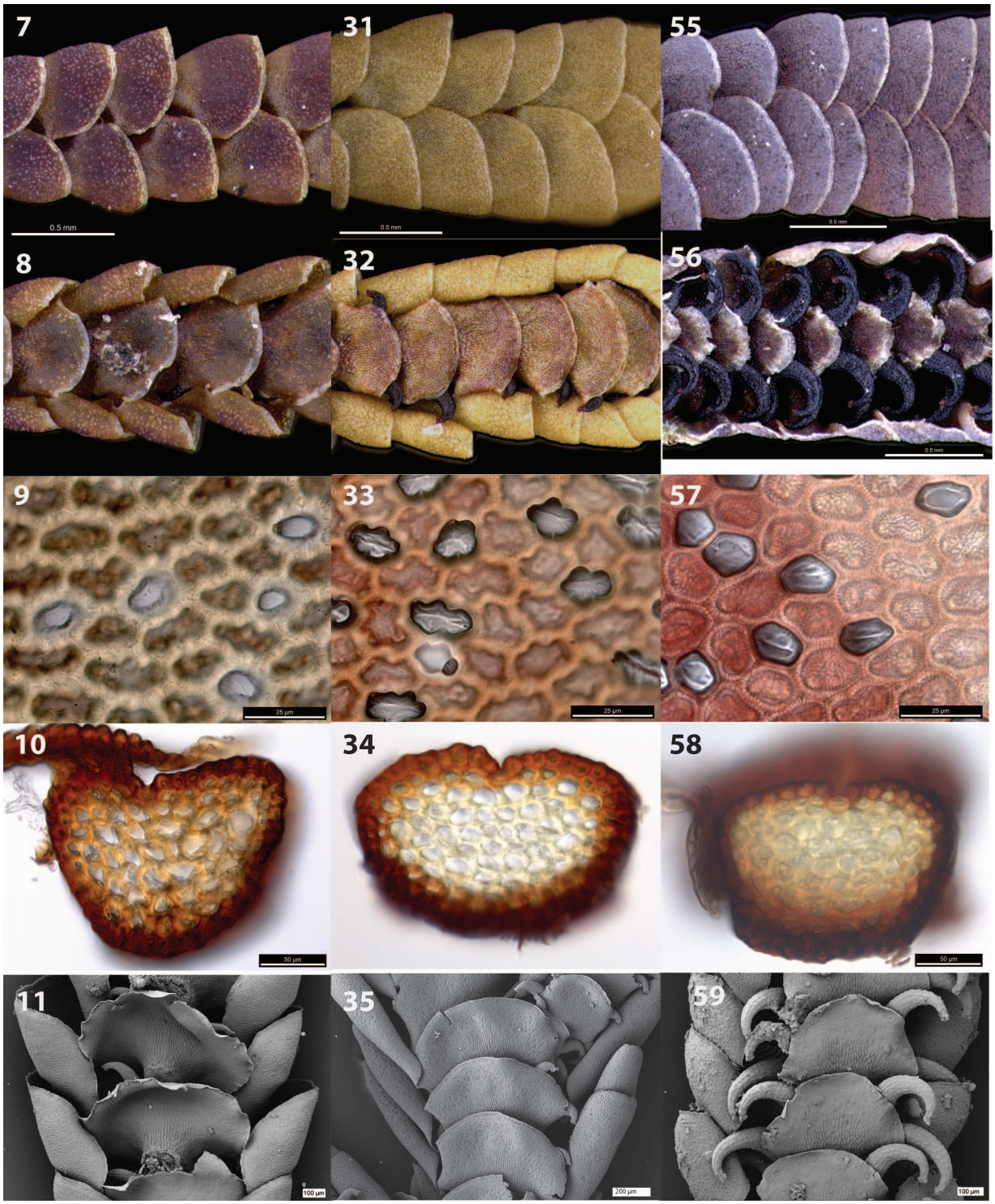
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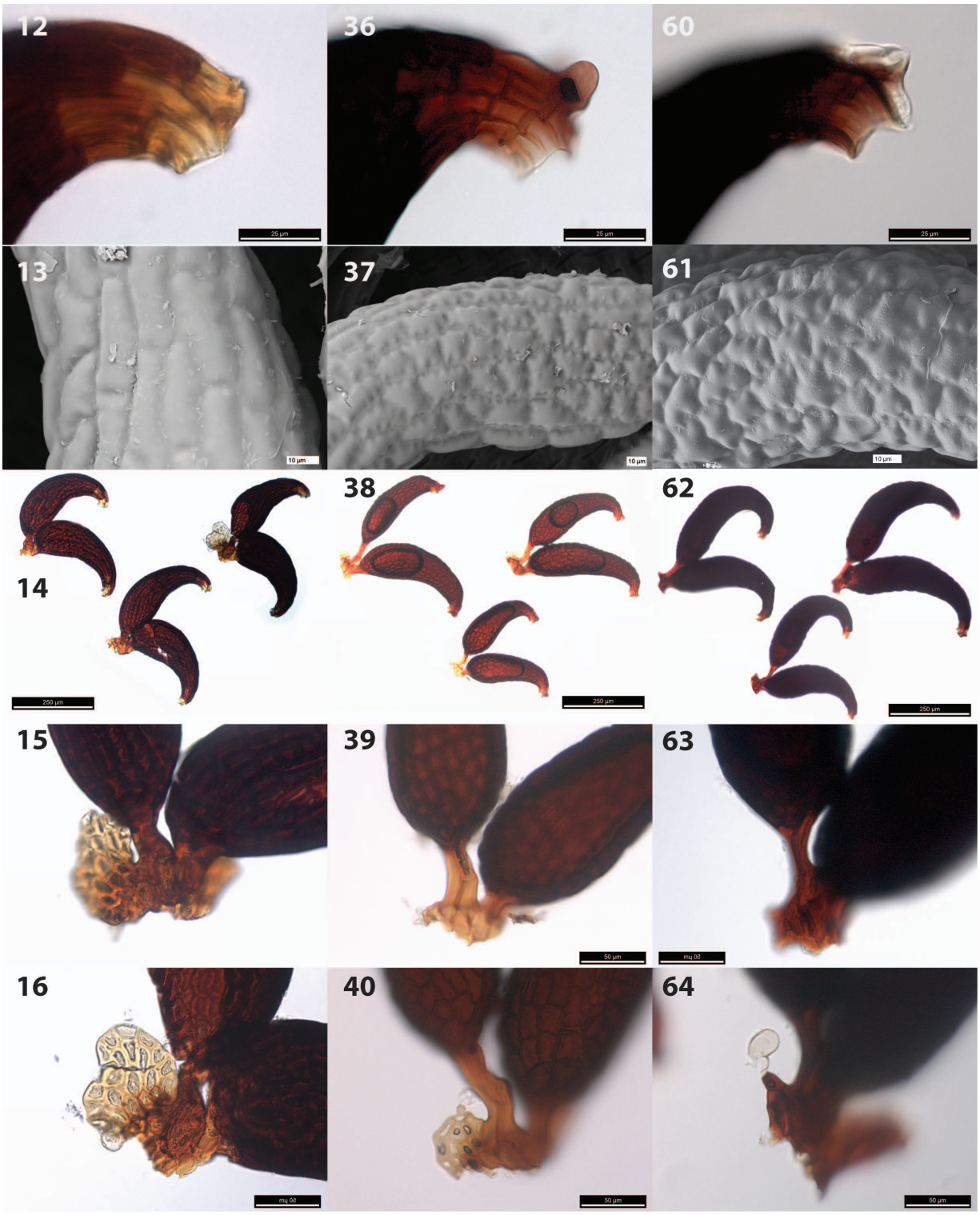
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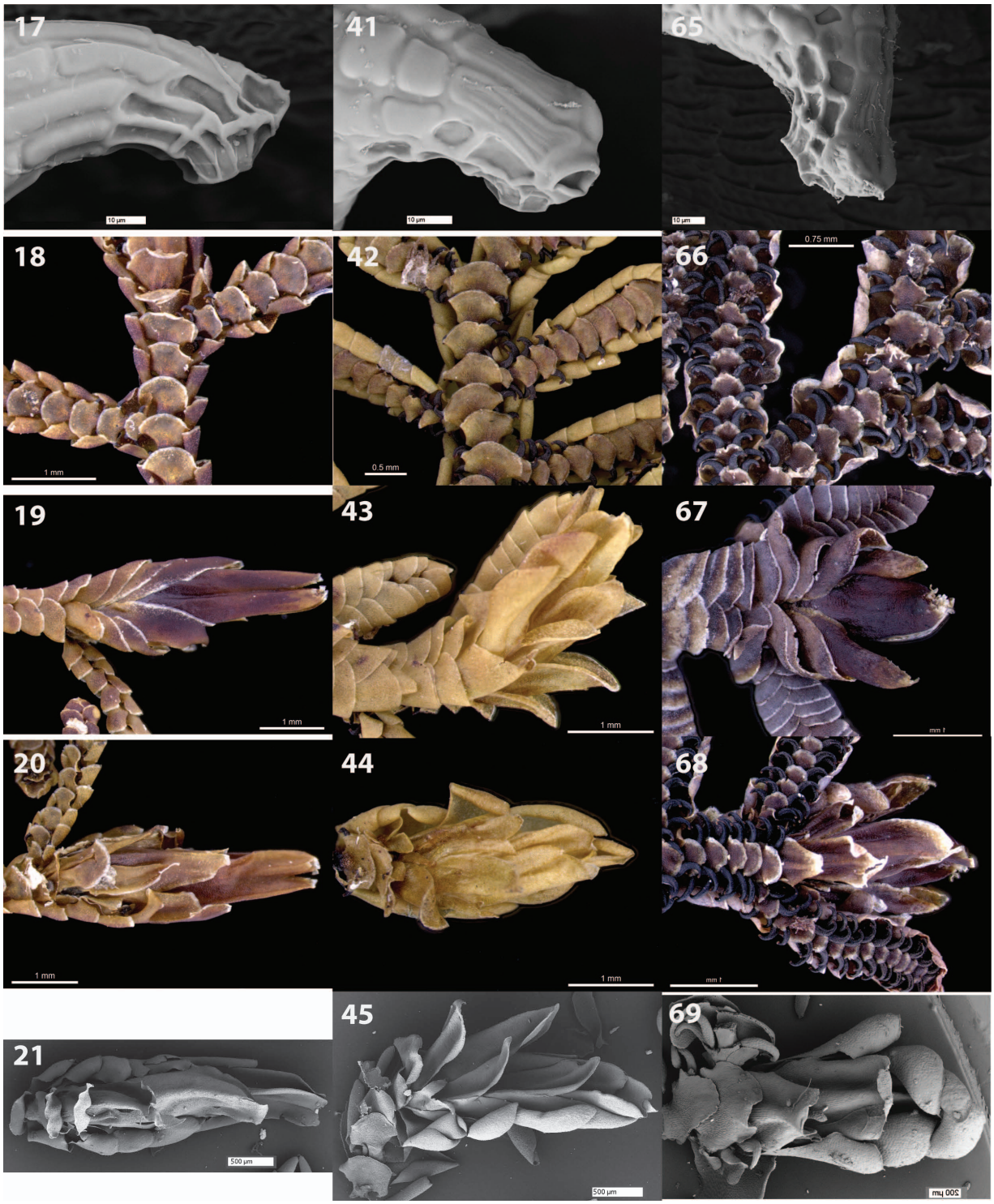
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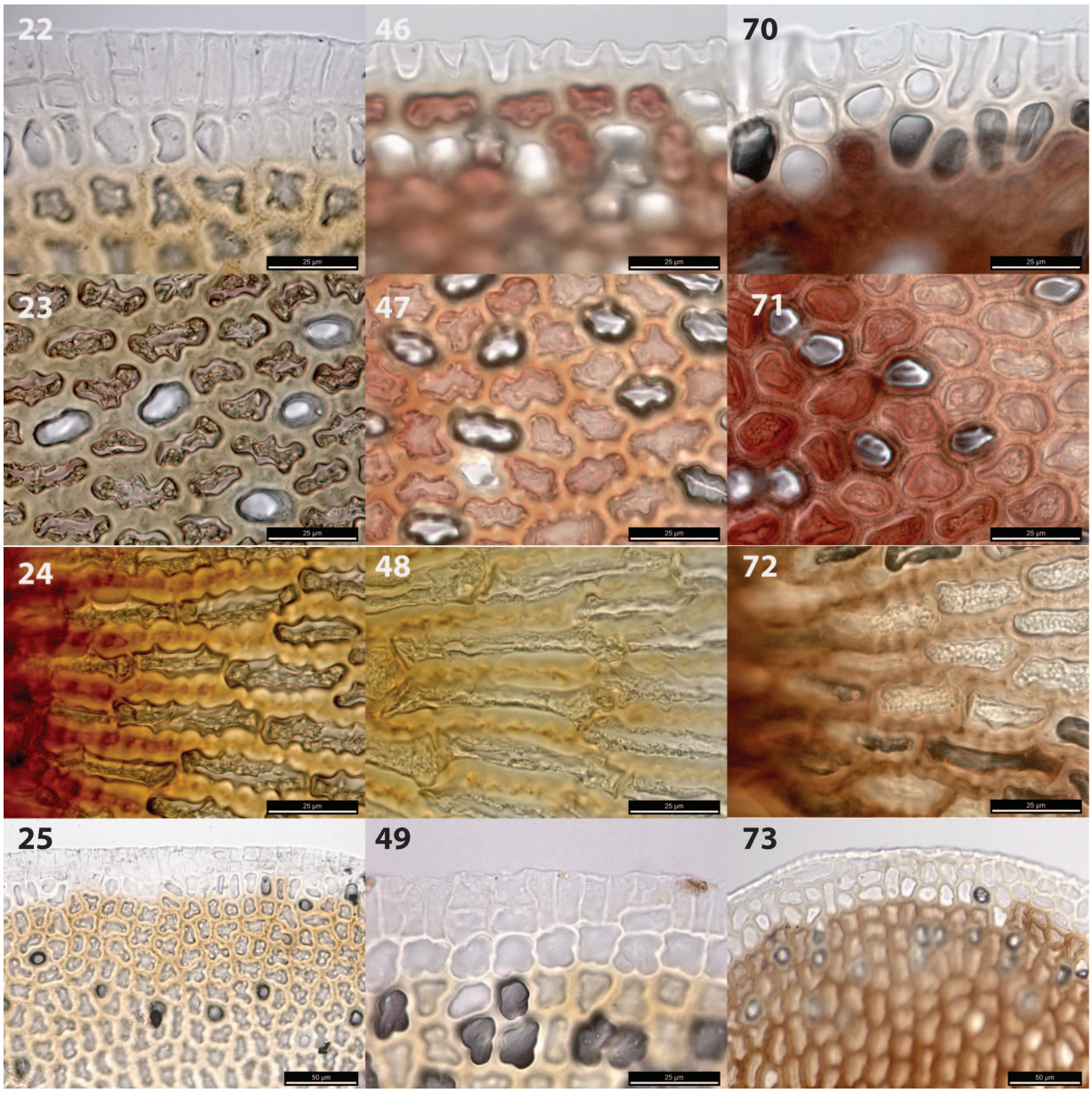

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