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A synopsis of the liverwort family Schistochilaceae in New Caledonia

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In this study, we describe a new liverwort species, *Schistochila angulata* X.L. He & Rikkinen, from New Caledonia. It is morphologically allied to the New Caledonian endemics *S. gradsteinii* and *S. vitreocincta*, but also to *S. pinnatifolia* from New Zealand and Tasmania. By analysing all seven *Schistochila* species known from New Caledonia, along with other relevant taxa and available molecular evidence, we conclude that the regional flora of Schistochilaceae includes at least one ancient lineage comprising the endemics *S. angulata*, *S. gradsteinii* and *S. vitreocincta,* which likely evolved in the region, whereas *S. aligera*, *S. caledonica* and *S. integerrima* arrived later via independent long-distance dispersal events. We synonymise the name *S. nuda* Horik. with *S. integerrima* Steph., and *S. minor* C. Gao & Y. Huan Wu with *S. sciurea* (Nees) Schiffn. We provide illustrations of all species dealt with except for *S. gradsteinii*. Several patterns in adaptive morphology are discussed in detail, with new interpretations to be tested in future work.

Introduction

New Caledonia is a tropical archipelago in the southwest Pacific comprising the mountainous main island Grande Terre, which is nearly 400 km long and 50–70 km wide, and several smaller islands. It is located about 1200 km east of Australia and 2000 km north of New Zealand. The archipelago has a unique and species-rich flora with a remarkably high level of endemism (Morat *et al.* 2012, http://publish.plantnet-project.org/project/florical). Its bryophyte flora consists of over one thousand species, including 522 mosses, 529 liverworts and 14 hornworts; many of these are endemic to the archipelago (Thouvenot & Bardat 2010, Thouvenot *et al.* 2011, Thouvenot 2021, Thouvenot & Müller 2021). Notably, the number of liverwort species in New Caledonia accounts for approximately one-tenth of global liverwort diversity (Söderström *et al.* 2016). Especially the montane rainforests, which have relatively cool climates and pronounced diurnal temperature fluctuations, high rainfall and are regularly swept by clouds and mist, are very rich in bryophyte species.

The eminence of the New Caledonian biota is in part due to its complex geological history, including the separation from Gondwana in the late Paleozoic (Cluzel *et al.* 2012, Campbell *et al.* 2018), a prolonged submergence of the region of present Grande Terre, with re-emergences at different times, and the final uplift (Cluzel *et al.* 2012, Garrouste *et al.* 2021). While some features of the biogeographical history of New Caledonia remain incompletely understood, its present flora does contain both paleo- and neo-endemics (Nattier *et al.* 2017, Giribet & Baker 2019). Thus, the archipelago has acted both as a refugium for old lineages and as a source of new lineages, as exemplified by the exceptionally rich and unique gymnosperm flora (Condamine *et al.* 2017).

The liverwort family Schistochilaceae encompasses about 80 extant species and is among the earliest lineages to diverge within the leafy liverworts (Schuster & Engel 1977, 1985, He & Glenny 2010, Sun *et al.* 2014). More than two-thirds of *Schistochila* species occur in temperate to subantarctic South America and Australasia, and the remaining one third in the tropical mountain forests of Southeast Asia and the western Pacific Islands. Most plants in the family are relatively robust and form a prominent component of the ground layer of cool temperate forests or occur in montane tropical forests as epiphytes. A previous study on the biogeographic history of Schistochilaceae, based on molecular phylogenetic analysis, suggests that the family has a Gondwanan origin at approximately 100 Mya, with New Zealand as the centre of early radiation, and the major groups of the family already established before the Paleocene (Fig. 1, modified from Sun *et al.* 2014: fig. 2).

The morphology of Schistochilaceae is complex and highly distinctive, characterised by gametophytes with magenta rhizoids, stem paraphyllia, complicate-bilobed and winged leaves typically divided into two subequal lobes and having dentate and/or ciliate leaf margins, and a fleshy perigynium derived from stem tissue that encloses the sporophyte, which bears a cylindrical capsule deeply divided into four straight valves for spore dehiscence. However, at lower taxonomical levels, most species are morphologically highly variable, presumably due to environmental heterogeneity coupled with ample time for diversification and the evolution of adaptive strategies for survival in different environments (e.g. Buch 1939, So 2003a, b). While taxa of the Southern Hemisphere have been intensively studied (Schuster & Engel 1977, 1985), species of the tropical regions remain more poorly known. Since a global taxonomic treatment of Schistochilaceae is still lacking, we here follow the broad generic concept that recognises *Schistochila* as the sole genus of the family (He & Glenny 2010, He & Sun 2013, Sun *et al.* 2014, Söderström *et al.* 2016).

New Caledonia is known to harbour six species of *Schistochila*, including two endemics, *S. vitreocincta* (Herzog 1952 as *Perssoniella vitreocincta*, He & Glenny 2010) and *S. gradsteinii* (Thouvenot 2021). *Schistochila caledonica* also occurs in Fiji (Söderström *et al.* 2011), and *S. integerrima* in Vanuatu (So 2003b). The remaining two species are more widely distributed, with *S. aligera* occurring in Asia, Melanesia and Australasia, and *S. sciurea* in parts of the Pacific region and Asia. *Schistochila vitreocincta* is a rather extraordinary liverwort with a suite of unique morphological characters. Herzog (1952) placed it in the genus *Perssoniella*, and it was later assigned to a monotypic family, Perssoniellaceae, which was then thought to represent the only endemic bryophyte family in New Caledonia (Schuster 1963, 1964). However, molecular data have more recently suggested that the species falls within the Schistochilaceae (He & Glenny 2010).

The currently known species of *Schistochila* in New Caledonia have contrasting biogeographical histories. Two lineages have been shown to have originated from New Zealand, one including *S. vitreocincta* (Fig. 1, the clade Gottschea, modified from Sun *et al.* 2014: fig. 2) and the other including *S. sciurea* (Fig. 1, the clade Sciophila, modified from Sun *et al.* 2014: fig. 2); both lineages diverged in the Paleocene. Conversely, *S. caledonica* has close morphological affinities with a group of species that diverged in South America in the Eocene. *Schistochila aligera*, which closely resembles *S. integerrima* in morphology, appears to have diverged in New Guinea during the Neogene (Sun *et al.* 2014). The discovery of *S. gradsteinii*, which resem-



Fig. 1. A dated phylogeny of Schistochilaceae, modified from Sun *et al.* 2014 (fig. 2, with permission from the publisher). Names of the five major clades and species of the clade Gottschea are presented; species that occur in New Caledonia are marked with NC after each species name.

bles *S. vitreocincta* in many aspects (Thouvenot 2021), is noteworthy, as the latter species has been suggested to have survived the marine transgressions of Grande Terre in the Paleocene and Eocene (Sun *et al.* 2014).

During a field trip to Grande Terre, New Caledonia, in 2011, one of the authors (JR) collected a specimen of *Schistochila* with a unique set of morphological characteristics. The specimen was found on Mont Humboldt, the second-high-

est mountain of Grande Terre, in a dense mossy forest, growing on a tree trunk. A specimen of *S. vitreocincta* was also collected nearby in the same habitat. Through microscopic studies and careful comparison with morphologically similar species within the genus, we propose that the distinctive morphological characters of the specimen warrant recognition of a new species, which we describe below. The new species has affinities with *S. vitreocincta*, *S. gradsteinii* and *S. pinnatifolia*, a species from New Zealand and Tasmania. In addition, we studied other *Schistochila* species known to occur in New Caledonia using new specimens collected during the same field trip and other herbarium material. Based on these analyses, two new synonyms, one for *S. integerrima* and the other for *S. sciurea*, are proposed. We furthermore identified several new characteristics of *S. aligera*, *S. integerrima* and *S. vitreocincta* and present an overview of the biogeography of all currently known species of *Schistochila* in New Caledonia.

Material and methods

Five fresh specimens of *Schistochila* were photographed *in situ* and then collected in New Caledonia by one of the authors (JR). These and numerous specimens held in the herbaria G, GOET, H and HIRO (herbarium acronyms according to *Index Herbariorum*, https://sweetgum.nybg.org/science/ih/), were examined. The herbarium specimens included type specimens of *S. caledonica*, *S. integerrima*, *S. nuda* and *S. yakushimensis*, and other specimens of *S. aligera*, *S. berteroana*, *S. nuda*, *S. pinnatifolia*, *S. reflexa, S. stratosa*, *S. sciurea* and *S. tuloides*.

A Leica MD1000 LED compound microscope (Leica Microsystems, Germany) and a Leica Wild M3B stereomicroscope (Wild Heerbrugg AG, Switzerland) were used to document and measure morphological characteristics of each species studied. Images were taken using a Flexacam C3 microscope camera, a Leica Z16 APO macroscope and a Leica MD2500 compound microscope of Leica Microsystems. The imaging and analysis software for widefield microscope Leica LAS X was used. A few images were taken with a 26 mm wide camera of an iPhone 13 manually attached to the microscopes.

Results and discussion

Of the five newly collected samples, two were identified as *S. vitreocincta*, and one each as *S. aligera* and *S. caledonica*. The fifth specimen possessed a previously unknown combination of characters that did not match any currently accepted species, and this specimen is described and illustrated in detail below. This is followed by taxonomic discussions of all the other *Schistochila* species known to occur in New Caledonia, with an overview of their biogeographical history in the region. Each species is illustrated, except for *S. gradsteinii*, which was recently well illustrated by Thouvenot (2021).

Schistochila angulata X.L. He & Rikkinen, *sp. nova* (Fig. 2)

Type: New Caledonia. Province Sud: Réserve spéciale botanique du Mont Humboldt, close to Mont Humboldt refuge, dense moss forest near spring, on tree trunk, 1345 m a.s.l., 21°52′58″ S, 166°24′45″ E, 9 November 2011, *J. Rikkinen 38484* (holotype H, barcode H3254966; isotype P!).

Etymology. The specific epithet *angulata* refers to the species' distinctive leaf cell type with angular collenchymatous cells resulting from unevenly thickened cell walls, and with angular thickenings at each corner of the cell.

Plants up to 1.5 cm long, in small patches tightly adherent to substrate with upper portions becoming ascending, epiphytic on tree bark, green to yellowish green, golden or reddish brown in older portions when fresh, dried plants light yellowish brown to brown. Shoots up to 7 mm wide. Branches mostly of *Frullania*-type, sporadically lateral intercalary. Stem 380–540 µm in diameter, 13–15 cells across, paraphyllia absent. Stem epidermal cells in surface view slightly rectangular to irregular, 27.5–55 × 22.5–25 µm, in cross-sectional view 30–52 × 23–40 µm, hyaline, translucent, and thin-walled. Medullary cells with walls strongly thickened, collenchymatous, cell lumen reduced, surrounded by massive thickenings. Stems completely hidden by leaves in dorsal view, partially or entirely hidden in ventral view. Rhizoids magenta, dense, scattered along ventral side of stems in middle and basal portions of shoots but absent from apical regions, rhizoid tips occasionally branched. Leaves widely spreading,

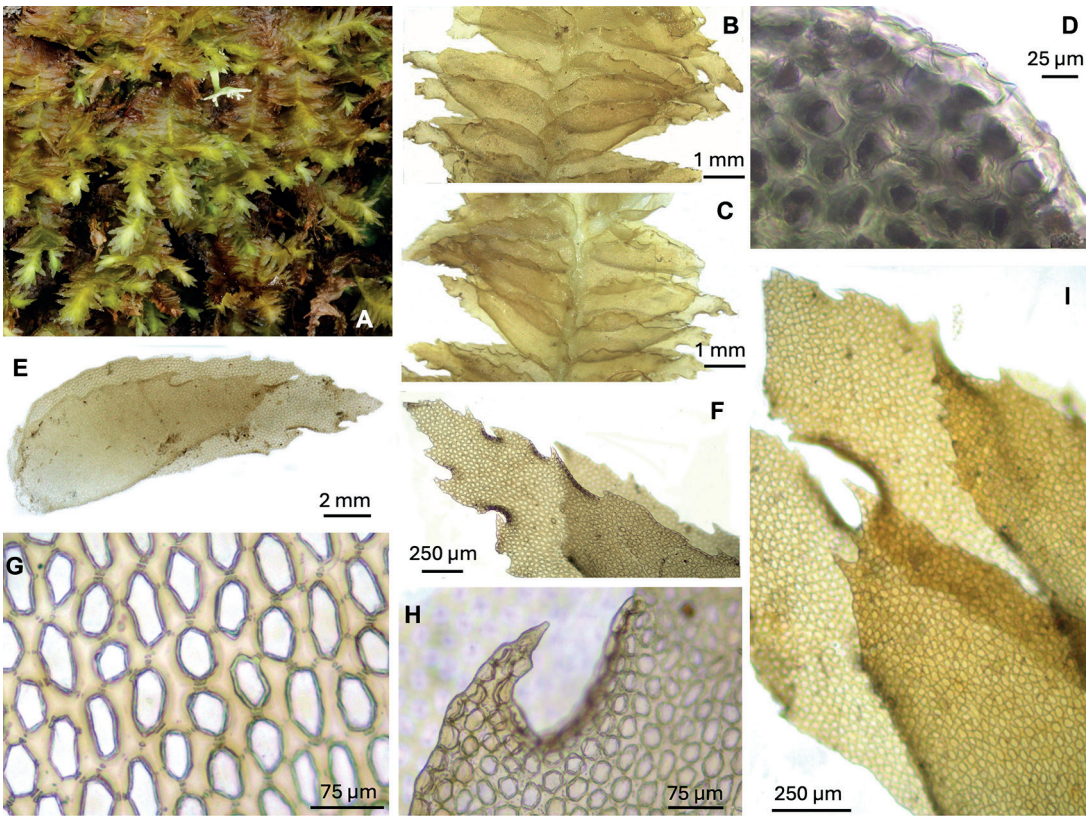


Fig. 2. *Schistochila angulata* (from the holotype). — **A**: Habit. — **B**: A portion of shoot, dorsal view. — **C**: A portion of shoot, ventral view. — **D**: Part of cross-section of stem. — **E**: A leaf, dorsal view. — **F** and **H**: Upper portion of ventral lobe of a leaf, showing pinnate-incised ventral lobe. — **G**: Leaf cells of the middle portion of the ventral lobe of a leaf. — **I**: Upper portion of toothed dorsal lobes.

imbricate, asymmetrically bilobed, with ventral and dorsal lobes unistratose throughout, wing single, leaf insertion to stem narrow, leaf margins dentate, teeth serrate to spinose, distal portion of ventral lobe pinnately incised, commonly with two conspicuous incisions on both dorsal and ventral margins, base of incisions recurved, leaf apex acutely triangular to acuminate, with tip terminating in an elongated, thickened, often hyaline cell. Ventral lobe 2.8–4.5 mm long, 0.6–1.8 mm wide, oblong-lanceolate, dorsal margin undulate in proximal half when fully developed, with several 1–2-celled teeth from lobe base to middle of dorsal leaf margin, becoming conspicuously incised-lobulate towards apex, lobules with 1–2-celled spinose teeth, ventral margin entire or rarely toothed until middle of ventral margin, then similar to dorsal margin in becoming conspicuously incised-lobulate towards lobe apex. Dorsal lobe asymmetrically oblong to lanceolate, triangular to narrowly triangular distally, smaller than ventral lobe, 1.2–3.3 mm long, 0.6–1.5 mm wide, 0.7–0.8 of ventral lobe length, free portion of dorsal lobe 0.17–0.30 of its length, slightly convex, margin plain or rarely undulate, apex typically oblique, rarely truncate, with several 1–2-celled and a few broad-based teeth (2–4 cells wide) along free margin to apex, none or rarely incised, apex acuminate, with a hyaline terminal tooth often elongated and thick-walled. Leaf cells of ventral lobe collenchymatous, at apex isodiametric to oval, 22–38 × 20–25 µm, at medial cells 35–63 × 25–32 µm, basal cells 40–70 × 25–28 µm, oval to irregularly hexagonal, trigones conspicuous, irregularly triangular to rectangular, separated by thin-walled pits or confluent, occasionally trigones appear massive due to shrinkage and delamination of protoplast, leaf surfaces

slightly striolate. Underleaves lacking. Reproductive organs and sporophytes not seen.

Diagnostic characters of *Schistochila angulata* are hyaline, translucent epidermal stem cells; massively thickened walls of the medullary cells; reduced cell lumen; condensed and usually darkly pigmented cell content (Fig. 2D); absence of stem paraphyllia; leaves with pinnately incised ventral lobes in the distal portion of the lobe and undulate proximal half of dorsal margin of the ventral lobe (Figs. 2B and C); angular collenchymatous leaf cells with conspicuous, irregularly triangular to rectangular trigones, separated by thin-walled pits or becoming confluent (Fig. 2G); and slightly striolate leaf surfaces.

Schistochila angulata shows affinities with species of the clade Gottschea (Fig. 1), which has a New Zealand origin and dispersed once to southern South America, with more recent back-dispersals to New Zealand (Sun *et al.* 2014). Most species in this clade were previously placed in the genus *Paraschistochila* (Schuster 1971, Schuster & Engel 1985) and most of them are epiphytes. The new species shares the unique pattern of stem epidermal and medullary cells described above with the other two New Caledonian endemics, *S. gradsteinii* and *S. vitreocincta*. Moreover, shrinkage of the protoplast of leaf cells is seen in all three species (Herzog 1952, Thouvenot 2021). Our proposed explanation for this peculiar cellular phenomenon is given in the discussion of *S. vitreocincta*, in which it was first reported (Herzog 1952).

The leaf characteristics of *S. angulata,* including pinnate-incised and undulate ventral lobes, cell shape of leaves and pattern of wall thickening, suggest a connection to *S. pinnatifolia*, which belongs to a subclade of the Gottschea clade comprising species with a more recent back-dispersal to New Zealand from a southern South American ancestor (Fig. 1, modified from Sun *et al*. 2014: fig. 2). However, plants of *S. pinnatifolia* are much more robust and possess stem paraphyllia, thin-walled stem cells, densely ciliate and spinose-toothed leaf margins and smooth leaf surfaces (Schuster & Engel 1985). *Schistochila pinnatifolia* occurs in New Zealand and Tasmania and grows on the ground, rocks and the forest floor or as an epiphyte, from lowland and submontane forests to subalpine and alpine environments (Schuster & Engel 1985). Likewise, *S. angulata* differs markedly in leaf shape and structure from both *S. gradsteinii* and *S. vitreocincta*. *Schistochila gradsteinii* resembles *S. tuloides* of New Zealand and Tasmania, a species also belonging to the Gottschea clade and sister to a group of Southeast Asian species, including both *S. aligera* and *S. integerrima* (Fig. 1, modified from Sun *et al.* 2014: fig. 2).

Distribution. Endemic to New Caledonia. Known only from the type locality.

Selected specimens examined. — *Schistochila pinnatifolia*: **New Zealand**. South Island, *J.-P. Frahm 15-5* (GOET), *J. Engel 18513* (H3183067). **Australia**. Tasmania, *J. Engel 19619* (H3254972). — *Schistochila tuloides*: **Australia.** Tasmania, *J. Engel 14833* (H3183070). **New Zealand**. South Island, *J. Engel 19073* (H3183071).

Schistochila vitreocincta (Herzog) X.L. He & Glenny (Fig. 3)

Aust. Syst. Bot. 23(4): 237. 2010. — *Perssoniella vitreocincta* Herzog, Ark. Bot. 2: 265. 1952. — Type: New Caledonia, Montagnes des Sources, in humid *Araucaria muelleri* forest, alt. 800 m, 1949, leg. *O. H. Selling B145* (holotype S, not seen).

Knowledge of this species, extraordinary in morphology and cellular structure, has gradually accumulated since it was described by T. Herzog (Herzog 1952, Schuster 1964, Kitagawa 1983, Schuster & Engel 1985, He & Glenny 2010, Thouvenot 2021). The species is characterised by the stems having a layer of hyaline epidermal cells and strongly thickened medullary cells (Fig. 3A); the presence of a vitreous border of hyaline cells on the leaves, with the cells becoming progressively smaller towards the leaf margins, where they typically lack chloroplasts (Figs. 3B–E); and the trigones of leaf cells being large, white-shiny and nodose (Figs. 3F and G). Herzog (1952: 269) described the peculiar cellular structure, which he had not seen in any other liverwort: "When dissecting the very fragile leaf, the content of the cells of the thick-walled central region is released in well-defined flakes, which correspond exactly to a cast of the cell lumen, and appear to be still covered with the innermost thickening layer of the cell walls" (translated

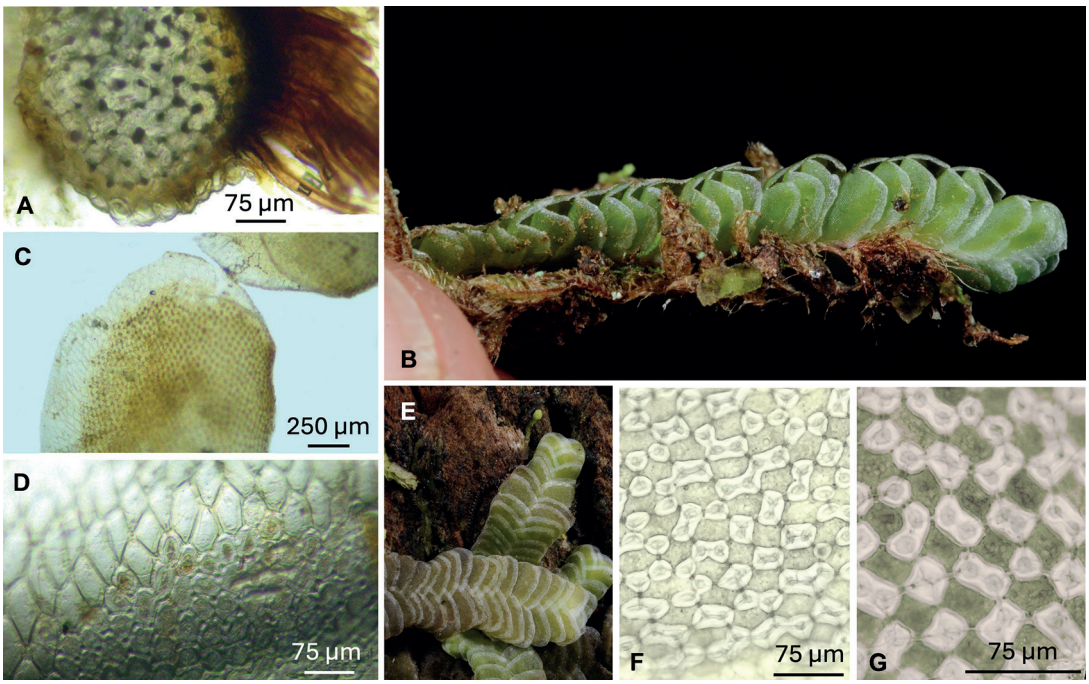


Fig. 3. *Schistochila vitreocincta* (from *J. Rikkinen 38483*). — **A**: Cross-section of stem showing epidermal and medullary cells and rhizoids. — **B** and **E**: Habit and growth form showing symmetrically bilobed leaves with a hyaline margin. — **C** and **D**: Leaves with a border of 3–5 marginal cells. — **F** and **G**: Leaf cells with contracted protoplasts, leaving a whitish empty space, surrounding trigones.

from German). Later, Schuster (1964) claimed that the large trigones were formed of three strata and separated by narrow, pit-like, thin areas.

Kitagawa (1983) explained the formation of the three strata of the trigones proposed by Schuster (1964). According to Kitagawa (1983), each leaf cell contains an endogenous daughter cell that acts as a single-celled gemma. It was further explained by Kitagawa (1983) that the innermost layer contains a real, relatively small trigone, the middle layer is an empty space, and the outermost layer is the newly formed thick wall of the daughter cell. The protoplast detaches from the cell wall at the cell corners and becomes densely aggregated into a stellate form with 4–6 arms, around which a thick wall develops on its concave side at a later stage. Kitagawa (1983) proposed that the development of the endogenous daughter cell is a plasmolysis-like phenomenon, with the stellate cell nested inside the mother cell functioning as a gemma to endure adverse environmental conditions, and the truncate ends of the stellate arms functioning as germ pores. Previously, Kitagawa and Kodama (1975) had described and illustrated similar endogenous gemmae in *Bazzania kokawana* collected from Borneo, and later also in *Acromastigum homodictyon* and *A. stellare* (Kitagawa 1985). All three liverwort species occur in New Caledonia, with the latter two species being endemic (Kitagawa 1985). However, while the idea of endogenous gemmae is elegant, new shoots germinating from these structures have never been reported. In other leafy liverworts, endogenous gemmae are only known in *Endogemma caespiticia* (Buch 1911, as *Haplozia caespiticia*, Vilnet *et al.* 2011, Pöltl *et al.* 2022). According to Buch (1911), the leaves of this species are not involved in gemma formation. Gemma cells arise in massive numbers from cells of the swollen apex of the stem, consisting of meristematic gemma parent cells. Each parent cell produces 2–4 gemma cells, which are liberated when the parent cell wall ruptures (Buch 1911).

The cell pattern we observed in *S. vitreocincta* and, to a lesser degree, in *S. angulata*

suggests that the unique cells are partially plasmolysed and have undergone concave plasmolysis, which represents one of two major types of plasmolysis (Oparka 1994). In this type, some sites of the plasma membrane retain adhesion to the cell wall, indicating strong adhesion between the plasma membrane and cell wall in *S. vitreocincta*. Plasmolysis is generally reversible (Oparka 1994, Cheng *et al.* 2017). When plant cells are exposed to hyperosmotic stress, they lose hydrostatic pressure, causing a decrease in cell volume due to water transport out of the protoplasts and detachment of the plasma membrane from the rigid cell wall. However, a physical linkage between the plasma membrane and the cell wall through fine, thread-like strands (Hechtian strands, Hecht 1912, Oparka 1994), which form mostly at plasmodesmata, can limit the shrinkage and ensure plasma membrane continuity. The Hechtian strands can act as anchor points and transduce cell wall stress signals to receptors located in the plasma membrane (Liu *et al.* 2015, Cheng *et al.* 2017, Yoneda *et al.* 2020). The stellate arms described by Kitagawa (1983) representing projections against the pits between the angular thickenings seem to correspond with the connecting sites between the plasma membrane and cell wall in *S. vitreocincta* plasmodesmata. The clear, whitish, empty-looking space at the conjunction of three adjacent cell corners in *S. vitreocincta* would then represent the space retreated from protoplasts of the partially plasmolysed cells, and not a portion of the trigones. We also observed that the contracted protoplasts tend to become darker in colour. The escaped "flakes" that Herzog observed, are the dead protoplasts that are released from plasmolysed cells during dissection, presumably because the sites of connection between the plasma membrane and the cell wall are quite limited, and entire protoplasts can thus be readily detached from the wall by even a slight force.

We therefore do not support the endogenous gemma hypothesis for *S. vitreocincta* and comparable liverwort species (Kitagawa & Kodama 1975, Kitagawa 1983, 1985). We interpret the phenomenon as a cellular-level adaptive strategy, in which liverworts, by being able to undergo plasmolysis-deplasmolysis cycles, can tolerate extreme desiccation and other stressful events. We expect that, with careful observation, many other liverwort species will also be found to exhibit similar phenomena.

The great age of the lineage subtending *S. vitreocincta* (Sun *et al.* 2014) and the putative phylogenetic positions of *S. angulata* and *S. gradsteinii*, discussed in the preceding section, suggest the possibility that the striking stem cellular features shared by the three endemic species reflect early diversification of the clade Gottschea within Grande Terre, which has played a crucial role as a biotic source for further diversification into surrounding regions such as Melanesia and Southeast Asia. The new and recent findings of *S. angulata* and *S. gradsteinii* support the hypothesis that the *S. vitreocincta* lineage has persisted through geological time (Sun *et al.* 2014), and may have survived on remained ephemeral islands in the vicinity of New Caledonia during the Paleogene (Condamine *et al.* 2017, Heads 2019). New Caledonia may thus have served as a refugium for liverwort flora.

Distribution. Endemic to New Caledonia, South Province, on tree trunks of Araucariaceae species at 200–1400 m a.s.l. (Thouvenot 2021).

Specimens examined. **New Caledonia.** Province Sud, *J. Rikkinen 38483* (H3254967), *38735* (H3254968).

Schistochila gradsteinii Thouvenot

Cryptog. Bryol. 42(2): 13. 2021. — Type: New Caledonia. North Province, Hienghène, Ouaïème rocks, UTM 58K: 0485 E, 7717 N (20°38′ S, 164°51′ E), 22 September 2019, *Thouvenot NC2807* (holotype PC0712100, not seen).

Schistochila gradsteinii was recently discovered in a cloud forest on a mountain ridge in the North Province of New Caledonia, growing on trunks of small trees (Thouvenot 2021). Except for its distinctive stem and leaf cellular characteristics, which are also present in *S. vitreocincta* and *S. angulata*, *S. gradsteinii* is characterised by leaves with oblong-lanceolate to oblong-ovate ventral lobes with an acuminate-acute apex terminating in a row of up to six uniseriate cells, oblong-ovate dorsal lobes nearly 0.7 of the length of the ventral lobe and with a truncate to rounded apex, and entire leaf margins. These leaf features suggest an affinity with *S. tuloides* (Schuster

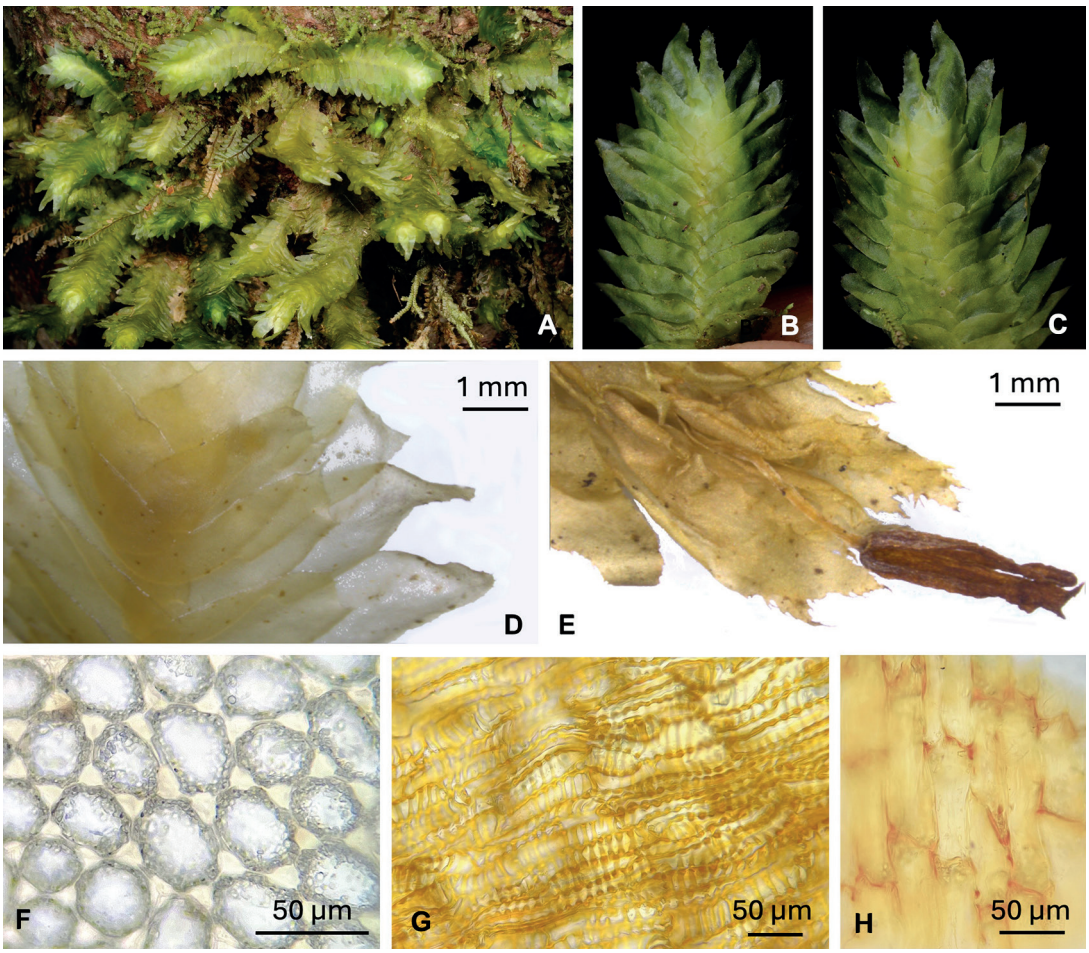


Fig. 4. *Schistochila aligera* (from *J. Rikkinen 38520*). — **A**: Habit. — **B**: Portion of a shoot, ventral view. — **C** and **D**: Portion of a shoot, dorsal view. — **E**: A sporophyte and surrounding gynoecial bracts. — **F**: Leaf cells with distinct trigones. — **G**: Innermost layer of sporophyte capsule showing wall thickenings. — **H**: Outermost layer of sporophyte capsule showing wall thickening pattern.

& Engel 1985). Thouvenot (2021) reported the occurrence of a perianth in *S. gradsteinii*, but no true perianth develops in *S. tuloides* (Schuster & Engel 1985). More detailed comparisons between the two species are clearly needed.

Distribution. Endemic to New Caledonia. Known only from the type locality (Thouvenot 2021).

Schistochila aligera (Nees & Blume) Jack & Steph. (Fig. 4)

Hedwigia 31: 12. 1892. — *Jungermannia aligera* Nees & Blume, Nova Acta Acad. Leop.-Carol. 11: 135. 1823. — *Notarisia aligera* (Nees & Blume) Trev., Mem. Real. Ist. Lombardo Ser. 3, 4: 392. 1877. — *Schistochilaster aliger* (Nees & Blume) H.A. Miller, Phytologia 20: 318. 1970. — *Paraschistochila aligera* (Nees & Blume) R.M. Schust., Bull. Nat. Sci. Mus. 14: 650. 1971. — Type: Indonesia. Java, "Tjerimai" (Mount Ciremai), *Junghuhn s.n.* (holotype STR, not seen).

Schistochila philippinensis (Mont.) Steph., Bot. Jahrb. Syst. 23: 308. 1896. — *Fide* Stephani (1909).

Schistochila sumatrana Steph., Sp. Hepat. 4. 74. 1909. — Synonymised by So (2003a).

Schistochila samoana Steph., Sp. Hepat. 4. 78. 1909. — Synonymised by So (2003b).

For more synonyms *see* So (2003a, b).

The morphological variation of *S. aligera* is considerable, both in shoot size, shape and

dentation of leaves, and presence or absence of underleaves. The plants are usually robust, up to 15 cm long and 2 cm wide, smaller sized shoots less than 4 cm long and slightly over 1 cm wide; paraphyllia form turfs on the ventral side of the stem, also laterally on the stem in axils of lateral leaves. The ventral lobes are narrowly ovate or lanceolate and taper to the apex, bearing a few coarse marginal teeth at the distal half, otherwise they are entire. The apex is rounded to acuminate, ending in a 1–3-celled tooth. The wing is ca. 0.4–0.6 of ventral lobe length; the dorsal lobe is plane or with slightly incurved margins and the shape varies from rectangular with apex transversely truncate bearing a tooth on the angle towards the keel or a few toothed, to triangular with the dorsal margin tapering gradually to merge with ventral lobe. Underleaves are absent on sterile shoots, which bear paraphyllia, but are present on fertile shoots just below the gynoecia. The leaf cells are collenchymatous, with distinct angular thickenings and conspicuous trigones, the cuticle is smooth or occasionally roughened, as an ornamentation of the outer cell wall. The gynoecia are terminal on the main stem, with 3–6 pairs of bracts and bracteoles, bracts are equal in size to leaves on sterile shoots or larger, but with numerous coarse and longer teeth, irregularly 2–5-lobed, with deeply dissected margins, the bracteoles are bilobed, with the innermost deeply divided, and the lobes laciniate.

The specimen of *S. aligera* newly collected from New Caledonia was fertile, revealing the sporophyte characters of this species for the first time. The capsule is ellipsoidal, brown, 4-valved to the base with valves straight (Fig. 4E); the wall is 45–65 µm thick, 2–3-cell-layered, the outer wall cells are elongate and their tangential walls thin or weakly thickened with brownish wall material, better developed at the angles where cells join (Fig. 4H), the innermost cells are obliquely rectangular to oblong, with many nodulose radial wall thickenings with extended complete bands across free tangential walls (Fig. 4G). The elaters are ca. 550 µm long and 10 µm wide, non-tortuous. The spores are 20–25 µm in diameter, light brown, and the surface is finely granular to papillose.

Phylogeographic analyses suggest that *S. aligera* belongs to a recent radiation of the genus in New Guinea (Sun *et al.* 2014), which started to develop in the early Miocene with mountain uplift that continues to the present day. The mid- and upper-montane forests of New Guinea, at 2000–3000 m a.s.l., share climatic similarities with the cool-temperate montane forests of New Zealand and southern South America (Löffler 1982). Although the taxonomy of *S. aligera* was assessed previously (So 2003a, b), a more comprehensive analysis is in progress by the first author of the morphologically similar but less studied New Guinean endemics, including *S. antara* (Grolle 1966), *S. brassii* (Grolle 1968), *S. crinita* (Grolle 1968) and *S. lacerata* (Stephani 1924).

In Western Melanesia, *S. aligera* commonly occurs in mountain forests and mossy cloud forests up to 3200 m a.s.l. (Piippo 1984) but can also be found in tropical lowlands. It inhabits tree trunks, logs, climbers and humus on the forest floor. In New Caledonia, it grows on tree trunks at 110–300 m a.s.l. in hygrophilous forests and at 600–980 m a.s.l. in mountain forests (Engel 1975, Hürlimann 1998, So 2003a, b). More information on the habitats and substrates is provided in So (2003a, b) and Thouvenot *et al.* (2011).

Distribution. *Schistochila aligera* is the most widespread species of its genus, spanning East and Southeast Asia and some regions of South Asia, including India, Nepal and Sri Lanka, as well as Melanesia and northeast Queensland in Australia (Buch 1939, Grolle 1966, Piippo 1984, So 2003a, b).

Specimens examined. **New Caledonia.** Province Sud, *J. Rikkinen 38520* (H3254969). **Australia**. Queensland, *H. Streimann 28632* (H3192049). **Papua New Guinea.** Morobe Prov., *T. Koponen 28956* (H3173040). **Philippines.** Luzon, *N. Jacobs B135* (H3192044). **American Samoa.** Tutuila, *E. Christophersen 3518/a* (H3191954). **Solomon Islands**. Kolombangara, *D. H. Norris & G. L. Roberts 49973* (H3196691).

Schistochila integerrima Steph. (Fig. 5)

Sp. Hepat. 6: 492. 1924. — Type: New Hebrides (now Vanuatu), *W. Gunn s.n.* 1911, *ex herb*. Lillie, *herb*. Stephani 274 (holotype G020425!).

Schistochila nuda Horik., *syn. nov*., J. Sci. Hiroshima Univ. ser. B, div. 2, 2: 215. 1934. — *Paraschistochila*

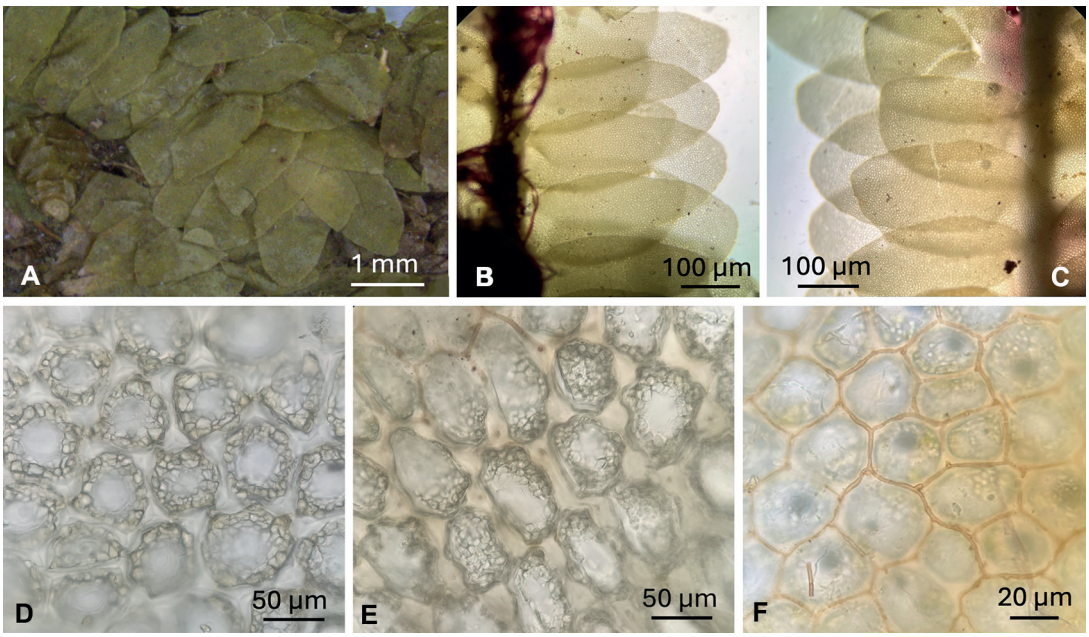


Fig. 5. *Schistochila integerrima* (**A**–**D**, from the holotype) and *Schistochila nuda* (**E**–**F**, from the holotype). — **A**: Habit, plants when dry, dorsal view. — **B**: Plant when wet, showing magenta rhizoids, entire margined leaves, ventral view. — **C**: Dorsal view showing dorsal lobes. — **D** and **E**: Leaf cells with distinct trigones, roughened surface cuticle. – **F**: Fungal association, a fungal species around the walls of leaf cells.

nuda (Horik.) Inoue, Illustr. Jap. Hepat. 2: 179. 1976. — Type: China. Taiwan, Taito, between Shinsuiei and Shuchou-Kyokai, 3 January 1933, *Y. Horikawa 10626* (holotype HIRO!).

Schistochila integerrima was described by Stephani (1924) based on a specimen collected from Vanuatu. As suggested by its name, this species has entire leaf margins and is also characterised by an oblong-elliptic ventral lobe with a rounded apex, truncate apex of the dorsal lobe which is nearly or more than half the length of the ventral lobe, and the absence of underleaves on sterile shoots. The plants are soft-textured, small to medium sized, 2–4 cm long, 5–6 mm wide, the stem is 0.45–0.50 mm in diameter, about 15 cells in cross-section, the epidermal cells are quadrate to rectangular, and the medullary cells are larger, irregular in shape and with thin walls. Paraphyllia are absent. The rhizoids are magenta and densely distributed on the stem from the base to nearly the apex; the ventral lobe is ovate to ovate-oblong, 1.9–3.8 mm long, 1.1–1.7 mm wide, and its apex is rounded or obtuse, the leaf margin is entire, occasionally with a few small teeth on the apex in the leaves near the shoot apex; the dorsal lobe is ovate to obliquely oblong, 1.8–2.6 mm long, 1.1–1.8 mm wide, 0.6–0.8 of ventral lobe length, its apex is obtuse or obliquely truncate, and the margins are entire. Cells in the upper portion of leaves are isodiametric, quadrate to rounded and 15–30 µm in diameter, middle cells are 30–42.5 × 25–37.5 µm, and basal cells 35–50 × 30–37.5 µm; all leaf cells are collenchymatous, with distinct, small to medium-sized trigones, otherwise the walls are thin; the cuticle is roughened from cell wall ornamentation. Reproductive organs and sporophytes were not seen by us.

Very similar diagnostic characteristics have also been described for *S. nuda* (Horikawa 1934), an Asiatic species known from China (Guangxi, Sichuan, Taiwan, Yunnan), Japan, the Philippines and Thailand (Horikawa 1934, So 2003a, b, Gao & Wu 2004, Juengprayoon *et al.* 2015, Wang *et al.* 2024). The relationship of these two taxa has until now been obscure (So 2003a, b, Juengprayoon *et al.* 2015, Thouvenot 2021). We examined the type specimens of both *S. integerrima* and *S. nuda*, and additional herbarium specimens

of the latter species. We found that shoot size, the sizes of both ventral and dorsal leaf lobes, as well as the size of leaf cells overlap between the two taxa. The taxa also share several other features, including the soft-textured shoots when wet and their opaque appearance when dry, the pattern of cell wall thickness and leaf-surface ornamentation. Based on these observations, we conclude that the two taxa are conspecific, thus synonymising *S. nuda* with *S. integerrima*, which is the older legitimate name.

We observed that *S. integerrima* possesses the following characteristics that have not been previously described. The plants are dull, yellow-green and opaque when dry (Fig. 5A). This colour is obviously due to leaf-surface ornamentation, which can be seen in both type specimens under a light microscope (Figs. 5D and E). Interestingly, we observed a similar type of fungal associate in both type specimens: a tightly attached filamentous fungus grew over large areas of the leaf surface, tracing around cell walls (Fig. 5F). Döbbeler (1978) found the bryophilous ascomycete *Bryomyces jungermanniae* (current name *Bryobroma jungermanniae*; Greiff & Döbbeler 2024), an obligate parasite, with its ascomata within the outermost cell walls of the leaves in the type specimen of *S. aligera*. More studies are needed to establish whether the two unknown fungal associates are related, and their relationship with *Bryobroma jungermanniae*.

Schistochila integerrima was first reported ffom New Caledonia by Herzog (1953) at Montagne des Sources, South Province, in humid *Araucaria muelleri* forest, and later from the North Province from collections by Hürlimann in 1949 (So 2003b) and by Thouvenot in 2019 (Thouvenot 2021).

Distribution. China, Japan, New Caledonia, the Philippines, Thailand, Vanuatu (Horikawa 1934, So 2003a, b, Thouvenot 2021).

Selected specimens examined. — *Schistochila nuda*: **China.** Taiwan, *M. J. Lai 6808* (H3173095). **Japan**. Ryukyu, *T. Yamaguchi 143* (H3254971).

Schistochila caledonica Steph. (Fig. 6)

Sp. Hepat. 4: 77. 1909. — Type: New Caledonia. Noumea, 1906, *Le Rat s.n.*, *herb*. Gen. Paris 92 (holotype G027496, not seen); 1907, *Le Rat 214* (G00265814!, original material).

Schistochila balansae Gottsche *ex* Lacout., Gen. Hep. 27. 1910. — *Fide* So (2003b).

Schistochila flavicans Steph., Sp. Hepat. 6: 490. 1924. — Synonymised by Kitagawa (1973).

For further synonyms *see* So (2003b) and Thouvenot *et al.* (2011).

Plants medium sized, 2–5.5 cm long, 1.1–1.5 mm wide, light green to light yellowish green, soft-textured when fresh, becoming rigid and fragile when dry; shoots dorsiventrally compressed, with epidermal cells smaller than medullary cells in cross-section, paraphyllia lacking, rhizoids magenta, long and dense, on lower portion of stem at underleaf and ventral lobe bases; ventral lobe narrowly ovate to oblong, a single wing confluent distally with it, occasionally with a vestigial lamella always associated with a slight marginal incision; wing margins usually entire, margins of ventral lobe dentate usually with 1-celled, occasionally a few broad-based (2–3 cells) teeth with thick-walled cells, terminating in a sharp projection; apex acuminate to narrowly rounded; dorsal lobe half of ventral lobe length, margins as for ventral lobe, apex obtuse to acuminate, or truncate, marginal teeth at distal portion of both leaf lobes are more conspicuous; underleaves small, distantly scattered on stem, bilobed to one-third to half of their length, margins armed with sparse 1–few-celled teeth; leaf cells collenchymatous, trigones distinctive, thickened at cell corners, otherwise walls thin, cuticle smooth. Reproductive organs and sporophytes not seen.

Morphologically, *S. caledonica* is quite distinct from all congenerics in Southeast Asia and the Pacific. Instead, it strongly resembles two species from southern South America, *S. stratosa* and *S. reflexa*. The close relationship of the two latter species is also supported by molecular data, which resolve them in the clade Isoschistochila (Sun *et al.* 2014). Schuster and Engel (1985) placed *S. caledonica*, the two South American species mentioned above and a fourth species, *S. berteroana*, which is endemic to the Juan Fernández Islands, in the subgenus *Eoschistochila*. The latter species differs from the other three taxa in the absence of a perianth and bracteolar antheridia, the frequent occurrence of spinose teeth on the dorsal lobe, and

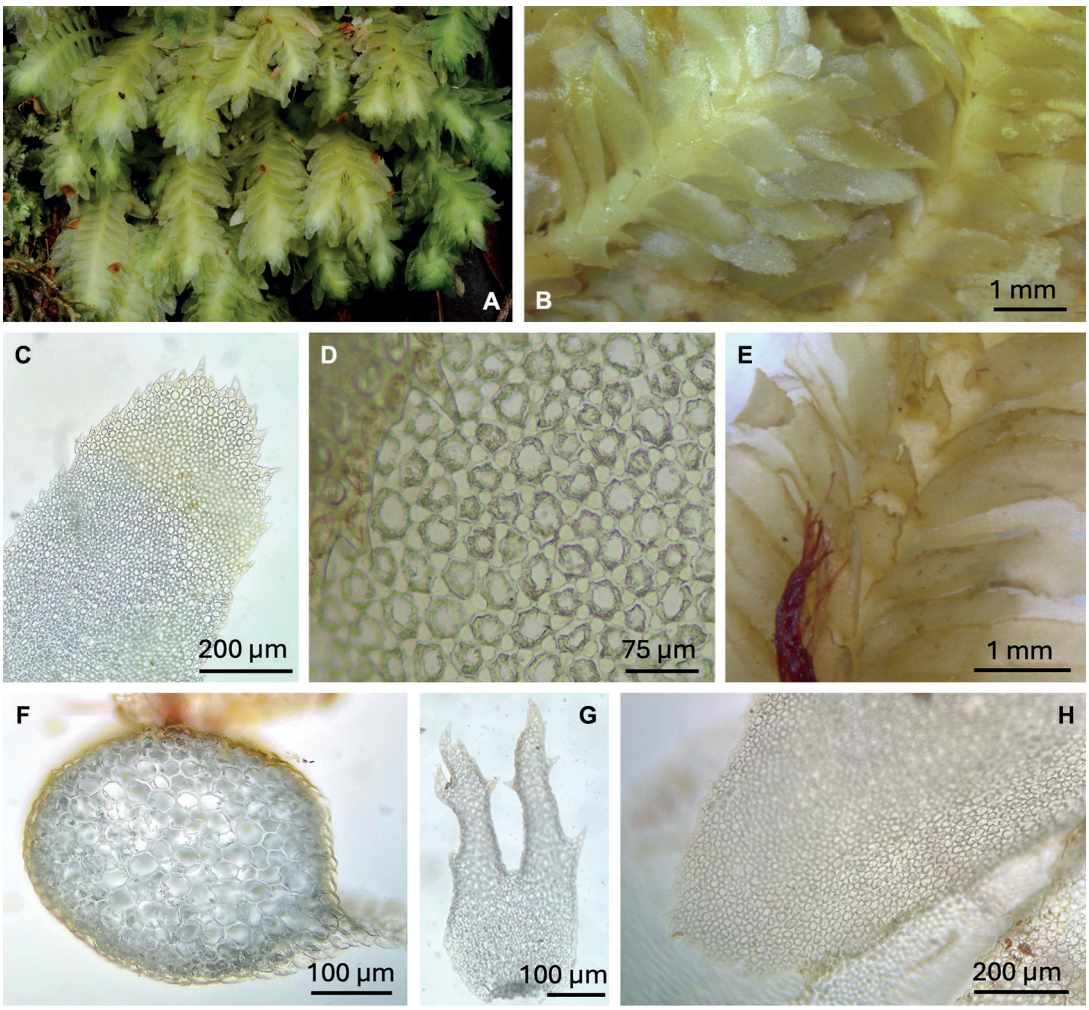


Fig. 6. *Schistochila caledonica* (from *J. Rikkinen 38967*). — **A** and **B**: Habit, dorsal view. — **C**: Upper portion of ventral lobe of leaf showing toothed margin. — **D**: Collenchymatous leaf cells in the middle portion of leaf, also marginal teeth of dorsal lobe of leaf on the left. — **E**: Habit, ventral view, showing rhizoids and underleaves scattered along the stem. — **F**: Cross-section of stem. — **G**: An underleaf from a younger shoot. — **H**: Apical portion of dorsal lobe of leaf showing truncate and toothed apex.

the extraordinary number of antheridia produced in bract axils, up to 120 per bract (Schuster & Engel 1985). *Schistochila caledonica* can be readily distinguished from *S. reflexa* by conspicuous teeth on the proximal half of the dorsal lobe (Fig. 6B) and the dorsal wing, both of which are present in the latter species but absent in *S. caledonica*, and from *S. stratosa* by having more marginal serrations on both ventral and dorsal lobes (Fig. 6C). *Schistochila reflexa* and *S. stratosa* are proposed to only have diverged during the Neogene (Sun *et al.* 2014), and in the light of our current study, it appears likely that *S. caledonica* shared a South American ancestor with these two species and later colonised New Caledonia by long distance dispersal.

Schistochila caledonica occurs in both the North and South Provinces of Grande Terre in various habitats from hygrophilous forests at 450–550 m a.s.l. on decaying or living tree trunks to mountain forests at 700–1250 m a.s.l. on humus, moist peridotite rock, tree trunks or tree bases (Hürlimann 1998). More details are given in Thouvenot *et al.* (2011).

DISTRIBUTION. New Caledonia and Fiji (Hürlimann 1998, Thouvenot *et al*. 2011).

SPECIMENS EXAMINED. **New Caledonia**. Province Sud, *J. Rikkinen 38967* (H3254970), *É.F. Deplanche 551* (G00265813), *A.J. Le Rat 221* (G00265817).

SELECTED SPECIMENS EXAMINED. — *Schistochila berteroana*: **Juan Fernández Islands**. Quebrada Damajuana, *C. & I. Skottsberg 16* (H3191653); Masafuera, *C. & I. Skottsberg H127* (H3191654) as *S. skottsbergii*; Quebrada Damajuana, *C. & I. Skottsberg H283* (H3191656); Masatierra, *C. & I. Skottsberg H272* (H3191659); Valle Colonial, *C. & I. Skottsberg H328* (3191657). — *Schistochila reflexa*: **Argentina**. Tierra del Fuego, *U. Drehwald 970075* (Herbar-Nr.: 3111, GOET); Isla Grande, *J. Hyvönen 3082* (H3191940). **Chile**. Prov. Valdivia, *J. Engel 11163* (H3191943). — *Schistochila stratosa*: **Chile**. Prov. Chiloe, *J. Engel 11872* (H3192025); Prov. Valdivia, *J. Engel 12293* (H3192027).

Schistochila sciurea (Nees) Schiffn. (Fig. 7)

Nova Acta Acad. Leop.-Carol. 60: 251. 1893. — *Jungermannia sciurea* Nees, Hepat. Javan. 34. 1830. — *Ptilidium sciureum* (Nees) Nees, Syn. Hepat. 251. 1845. — TYPE: Indonesia. Java (holotype STR, not seen).

Schistochila minor C. Gao & Y. Huan Wu, J. Hattori Bot. Lab. 95: 267. 2004, *syn. nov.* — TYPE: China. Taiwan: Xinzhu County, Yuanyang Lake Natural Reserve, *C. Gao & T. Cao 980318* (holotype IFS8H, isotype JE, not seen), *980455* (paratype IFS8H, not seen).

Schistochila javanica (Nees) Steph., Sp. Hept. 4. 72. 1909. — *Fide* Buch (1939).

Schistochila inversa Herzog, Hedwigia 66: 342. 1926. — Synonymised by So (2003a).

Schistochila yakushimensis N. Ohnishi & Deguchi, Bryologist 106: 451. 2003. — Synonymised by Katagiri *et al.* (2022).

For further synonyms, *see* So (2003a).

The species has a unique combination of characters. These include soft-textured and pellucid shoots, typically bright red to dark-brownish red, or green when growing in shade; leaves with two parallel wings along their midline, each fused with the margin of the dorsal lobe and the margin of the ventral lobe, respectively; and, unlike most of the species of the genus, which have larger ventral leaf lobes, two leaf lobes of subequal size, with the narrowly to broadly ovate dorsal lobe typically larger and broader than the ventral lobe and thereby entirely covering the ventral lobe in dorsal view. The ventral lobe and wing are often divided into a few smaller lobes, with their margins bearing abundant single-rowed cilia 4–11 cells long, with the lower end of the wing extending far down along the stem. The dorsal lobe may resemble the ventral lobe in being irregularly pinnated and with abundant cilia around the entire margins or unlobed, with only some cilia on the apex and at the base and wing margins. Underleaves are deeply divided into two lobes, which may further divide into smaller lobes with long ciliate margins, and with 0–2 wings. The cilia are often furcate and then refurcate. The dense cilia of the leaves and underleaves make the shoots, particularly their ventral sides, appear densely and tangledly hairy (Fig. 7A). Reproductive organs and sporophytes were not seen by us.

Buch (1939) already pointed out that the morphology of *S. sciurea* varies considerably: many types of intermediate forms are found, ranging from those with strongly pinnately lobed and long-ciliate ventral lobes to those with an almost unlobed and short-ciliate or dentate ventral lobes, and the morphology of the dorsal lobe can vary in a similar manner. Over the last two decades or so, two species morphologically close to *S. sciurea* were described: *S. yakushimensis* from Japan and Thailand (Ohnishi & Deguchi 2003), subsequently reported also from Vietnam (Shu *et al.* 2017), and *S. minor* from Taiwan (Gao & Wu 2004). The former species differs from *S. sciurea* mostly in the degree of marginal ciliation of the leaf: in *S. yakushimensis*, both the dorsal and ventral lobes are entire or have only few cilia (Ohnishi & Deguchi 2003). *Schistochila minor* is characterised mainly by its smaller size, with both leaf lobes being ovate to oblong and not further divided into smaller lobes, as well as by having irregular cilia on the margins of both leaf lobes, or with the dorsal lobe occasionally being entire in its basal half (Gao & Wu 2004). The morphological features shared by all three species are the decurrent and variably ciliate leaves with two distinct wings (Figs. 7B, E and I), the copious cilia on the margins of the underleaves (Figs. 7C and H) and leaf cells with conspicuous trigones (Figs. 7F and G). A molecular phylogenetic analysis including *S. yakushimensis* (a sample from Thailand) and samples of *S. sciurea* did not resolve *S. yakushimensis* as distinct from *S. sciurea*, leading to the syn-

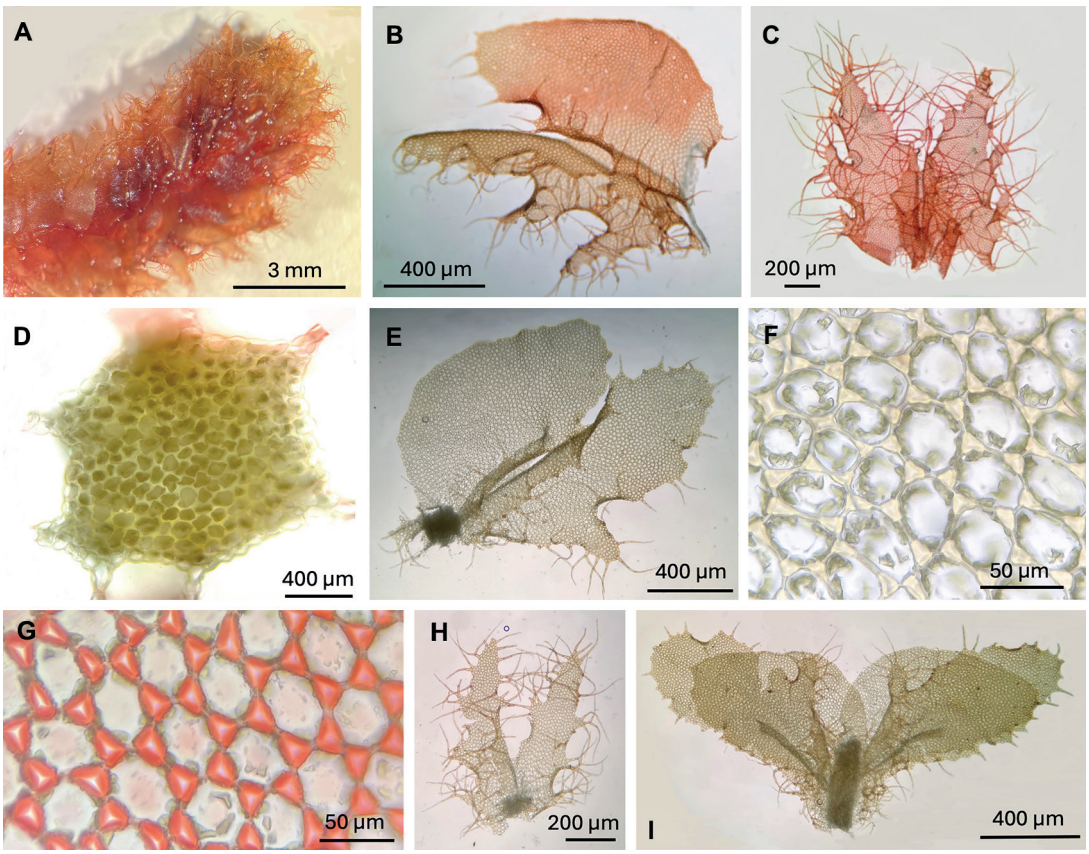


Fig. 7. *Schistochila sciurea* (**A**–**D** and **G** from *T. Koponen 35302*, **E**, **F**, **H** and **I** from *Kurz*, original material). — **A**: Habit. — **B**, **E** and **I**: Leaf variation showing broad and less lobed and ciliate dorsal lobes, and pinnate-lobed ventral lobes with ciliate margins, also dorsal and ventral wings. — **C** and **H**: Variation of underleaves. — **D**: Cross-section of stems with projections from a single-layered leaf and paraphyllia. — **F** and **G**: Collenchymatous leaf cells of plants from different environments, red pigmented from the location at higher elevation, green from well-shaded site.

onymisation of *S. yakushimensis* with *S. sciurea* (Katagiri *et al.* 2022). In line with this, based on both the original description and illustration of *S. minor* (Gao & Wu 2004) and our own examination of specimens from several different biogeographical regions, we agree with treating *S. minor* as a synonym of *S. sciurea*.

Schistochila sciurea mostly occurs in hyper-humid mountain forests as an epiphyte on tree trunks. It was first described from Java, Indonesia (Nees 1830), and was subsequently collected from other parts of the archipelago including Ambon (Schiffner 1893), Sumatra and Sulawesi (Buch 1939), as well as from Fiji (Jack & Stephani 1894, Schiffner 1898), Malaysia (Sarawak) and Sri Lanka (Buch 1939). Later, the species was also collected from New Guinea in both West Irian and Papua New Guinea (Grolle & Piippo 1984, Piippo 1984, So 2003b) and from the Solomon Islands (Grolle & Piippo 1984). In New Caledonia, *S. sciurea* has been reported from the South Province, with a few records from Mt. Ouin (ca. 1100 m a.s.l.) in mountain forests and Mt. Victoria (1000–1100 m a.s.l.) in cloud forests (Hürlimann 1998).

Schistochila sciurea has been shown to have a sister relationship with the New Zealand endemic *S. glaucescens*, and they, together with the Chile endemic *S. sciophila*, form a monophyletic lineage, the clade Sciophilae (Fig. 1, modified from Sun *et al.* 2014: fig. 2), which is sister to the rest of the genus. Each of the three species is on a long phylogenetic branch. A fourth species, *S. kunkelii*, known only from the

Juan Fernández Islands, likely also belongs to this group based on its similar morphology and ecology (Schuster 1971, Schuster & Engel 1977, 1985, Sun *et al.* 2014).

Schistochila sciurea is the sole species of the Sciophilae clade that occurs in parts of the Pacific Islands and Southeast Asia, possibly indicating that New Caledonia may have maintained this early-diverging lineage of the genus and allowed further radiations northward to New Guinea and Southeast Asia. However, there is also the possibility that the species arrived in New Caledonia through recent dispersal from nearby islands, such as Fiji or the Solomon Islands, or from some presently submerged land area.

All species of the Sciophilae clade have a highly complex leaf structure. The plants are very soft-textured and pellucid, prostrate and have a hairy appearance owing to the presence of dense furcate cilia on the margins of the leaves, underleaves and leaf wings (*S. sciurea* and *S. kunkelii*) and/or lamellae (*S. sciophila, S. sciurea* and *S. glaucescens*), as well as branched ciliiform processes on the leaf surface (*S. glaucescens, S. kunkelii* and *S. sciophila*). The development of these complex leaf structures may represent an adaptation to the relatively stable environments in which the species grow, i.e. in wet and deeply shaded mossy forests, either as epiphytes (*S. sciurea)* or as understorey species on moss-covered logs, peaty humus, rocks or soil.

Distribution. China, Fiji, Indonesia, Laos (Bakalin *et al.* 2025), Malaysia, Myanmar (Söderström *et al.* 2025), New Caledonia, Papua New Guinea, the Philippines, Singapore, Solomon Islands (Grolle & Piippo 1984), Sri Lanka, Thailand, Vietnam (Buch 1939, Piippo 1984, Hürlimann 1998, So 2003a, b, Ohnishi & Deguchi 2003, Gao & Wu 2004, Shu *et al.* 2017, Katagiri *et al.* 2022).

Specimens examined. **Indonesia**. Java, herb. Nees, Mt. Salak, alt. 6500', leg. *W. S. Kurz s.n.* (H-SOL2784007, possible type material). **Malaysia**. Borneo, Sarawak, *O. Beccari s.n.* (H-SOL2784012). **Papua New Guinea.** Morobe Prov., *T. Koponen 33807* (H3191983); West Sepik Prov., *T. Koponen 35302* (H3191988), *35305* (H3191989). **Solomon Islands.** Kolombangara, *D. H. Norris & G. L. Roberts 49670* (H3228471).

Key to the species of *Schistochila* of New Caledonia

1. Stem epidermal cells hyaline, thin-walled; medullary cells with strongly thickened walls, cell lumen reduced and cell content condensed, appearing darkly pigmented; trigones of leaf cells conspicuous, irregularly triangular to rectangular, separated by thin-walled pits or confluent 2
1. Stem epidermal and medullary cells thin to slightly thickened; trigones of leaf cells moderately sized, typically triangular, separated by thin-walled pits 4
2. Leaves oblong-ovate with lobes subequal in size, dorsal lobe slightly larger than ventral lobe; leaf margins distinctive, forming a border of 4–5 rows of hyaline cells, margins entire, apex rounded ..... *S. vitreocincta*
2. Leaves oblong-lanceolate with dorsal lobe smaller than ventral lobe, ca. 0.7–0.8 of ventral lobe length; leaf margins entire or toothed, without a border of hyaline cells 3
3. Leaf margins irregularly toothed, teeth 1–2 cells long, distal portion of the ventral lobe conspicuously incised-lobulate, apex acutely triangular to acuminate, terminating in an elongated, thickened cell that is often hyaline ..... *S. angulata*
3. Leaf margins entire, apices of ventral lobes acuminate-acute to obtuse-apiculate, ending in a row of up to six uniseriate and quadrate cells ..... *S. gradsteinii*
4. Dorsal leaf lobes typically larger and broader than ventral lobes, two parallel wings present along midline of leaves, margins of leaves and wings bearing dense cilia which are often furcate and then refurcate ..... *S. sciurea*
4. Dorsal leaf lobes smaller and narrower than ventral lobes or of the same size, wing single, leaf margins toothed or entire 5
5. Leaf margins dentate with 1-celled, occasionally a few broad-based (2–3 cells) teeth, thick-walled, terminating in a sharp projection; apex of ventral lobe acuminate to narrowly rounded; underleaves small, bilobed to one-third to half of their length, distantly scattered on stem, margins armed with sparse 1–few-celled teeth ..... *S. caledonica*
5. Leaf margins dentate or entire, underleaves present only on fertile shoots, absent on sterile shoots 6
6. Shoots robust, up to 15 cm long and 2 cm wide; ventral lobes narrowly ovate or lanceolate and taper to apex, bearing a few coarse marginal teeth at distal half, otherwise entire; apex rounded to acuminate, ending in a 1–3-celled tooth; underleaves absent on sterile shoots that bear paraphyllia ..... *S. aligera*
6. Shoots small to medium sized, 2–4 cm long, 5–6 mm wide; ventral lobe oblong-elliptic with a rounded apex; underleaves absent on sterile shoots, paraphyllia lacking ..... *S. integerrima*

Conclusion

Of the four major lineages currently recognised within *Schistochila*, three are represented in New

Caledonia. *Schistochila angulata*, described in the present paper, and its recently discovered relative *S. gradsteinii* highlight the importance of New Caledonia for the diversity of the genus. The liverwort flora of New Caledonia has generally been considered to have stronger connections to Indomalaya than to Australasia, whereas *Schistochila* exhibits a diverse and dynamic biogeographical history, as exemplified by the New Caledonian representatives. New Caledonia supports both ancient and relatively young lineages, with *S. angulata*, *S. gradsteinii* and *S. vitreocincta* having probably evolved and diversified within the region. Other lineages, currently represented by *S. aligera*, *S. caledonica* and *S. integerrima*, have reached the island at later times via long-distance dispersal. These patterns should be analysed further using molecular data. All New Caledonian species of *Schistochila* are predominantly epiphytic and are confined to humid mountain forests, with environmental conditions closely resembling those of the temperate forests in the Southern Hemisphere. Our examination of the three New Caledonian endemics provides new insight into how these minute plants have adapted to stressful environments, an intriguing topic for liverworts and bryophytes in general.

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