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Schistochila gradsteinii sp. nov., a new species from New Caledonia related to *S. vitreocincta* (Schistochilaceae, Marchantiophyta), with a key to the local species and a description of the gynoeceum of *S. integerrima*

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ABSTRACT

Schistochila gradsteinii Thouvenot sp. nov., is added to the five *Schistochila* Dumort. species formerly known in New Caledonia. The new species is distinctive by the lack of underleaves, bilobed leaves entire margined, with larger ventral lobes oblong-lanceolate to oblong-ovate, apiculate, dorsal lobes oblong-ovate, inserted on the dorsal surface of ventral lobes, the free margins not reaching the ventral margins, leaf cells with seemingly 3-layered trigones, stems with a conspicuous epidermis. It shares with the endemic *S. vitreocincta* (Herzog) X.L.He & Glenny some features distinctive from the rest of the genus. In addition, the occurrence of *S. vitreocincta* is clarified, the gynoeceum of *S. integerrima* Steph. is newly described and a key to the New Caledonian species of *Schistochila* is provided.

RÉSUMÉ

Schistochila gradsteinii sp. nov., une nouvelle espèce néocalédonienne apparentée à *S. vitreocincta* (Schistochilaceae, Marchantiophyta), avec une clé des espèces locales et une description du gynoeceum de *S. integerrima*.

Schistochila gradsteinii Thouvenot sp. nov., est ajoutée aux cinq espèces de *Schistochila* Dumort. déjà connues de Nouvelle-Calédonie. La nouvelle espèce se distingue par l'absence d'amphigastre, des feuilles bilobées aux marges entières, avec des lobes ventraux plus grands, oblong-lancéolés ou oblong-ovales, apiculés, des lobes dorsaux oblong-ovales, insérés sur la surface dorsale des lobes ventraux, les marges libres n'atteignant pas les marges ventrales, cellules foliaires avec des trigones apparemment constitués de trois couches, des tiges avec un net épiderme. Elle partage avec l'endémique *S. vitreocincta* (Herzog) X.L.He & Glenny plusieurs caractères les distinguant du reste du genre. En supplément, l'occurrence de *S. vitreocincta* est affinée, le gynoeceum de *S. integerrima* Steph. est nouvellement décrit et une clé des espèces néocalédoniennes de *Schistochila* est donnée.

KEY WORDS

Schistochilaceae,
liverworts,
New Caledonia,
morphology,
Perssoniella,
new species.

MOTS CLÉS

Schistochilaceae,
hépatiques,
Nouvelle-Calédonie,
morphologie,
Perssoniella,
espèce nouvelle.

INTRODUCTION

The genus *Schistochila* Dumort. in New Caledonia includes five species (Thouvenot *et al.* 2011): two endemics, *S. caledonica* Steph. and *S. vitreocincta* (Herzog) X.L.He & Glenny as well as *S. integerrima* Steph., also present in Vanuatu, *S. sciurea* (Bees) Schiffn. (Asia, Melanesia) and the widely distributed *Schistochila aligera* (Nees & Blume) J.B.Jack & Steph. (Asia, Melanesia, Australasia). The family Schistochilaceae Buch includes currently a single genus but several other combinations were published before (for a review, see He *et al.* 2014) to accommodate the morphological diversity of these plants. Especially concerned in the New Caledonian context, are the following taxa. On the one hand, *Paraschistochila* R.M.Schust., created by Schuster (1963) to accommodate species lacking underleaves, was later on included in *Gottschea* Nees ex Mont. by Grolle & Zijlstra (1984). On the other hand, the monotypic genus *Perssoniella* Herzog was created by Herzog (1952) for the New Caledonian endemic *Perssoniella vitreocincta* Herzog. This species exhibits such outstanding features that Schuster (1963, 1964) introduced a new family, Perssoniellaceae R.M.Schust., and the new suborder Perssoniellinae R.M.Schust. These two genera were later transferred to *Schistochila* by He & Glenny (2010), but further publications (Sun *et al.* 2014; Engel & Glenny 2019) provide arguments for them to be kept as valid genera. In the phylogeny of Sun *et al.* (2014), *Perssoniella* is sister to *Gottschea* and “is on a very long branch from the base of the *Gottschea* clade”. But the estimated date of this divergence, 67 Mya, is inconsistent to the geological history of New Caledonia which was undergoing a long submersion until 37 Mya ago (Grandcolas *et al.* 2008).

Here we describe a new species which share important features with *Schistochila vitreocincta* but, in the limits of the present work, we cannot add molecular arguments for generic reinstatement. So that, in the present paper we follow the broadly defined concept of *Schistochila* as used in the recent world checklist of liverworts (Söderström *et al.* 2016).

MATERIAL AND METHOD

During field work in 2019, we collected specimens of *Schistochila*. One among them turned out to be an undescribed species. The features of all the *Schistochila* specimens collected by the author since 2008 in New Caledonia were observed with light microscope and compared to the descriptions of the *Schistochila* genus around the world (De Notaris 1874; Hodgson 1942; Jones 1976; Schuster & Engel 1977, 1985; Inoue 1985; So 2003a, b; Juengprayoon *et al.* 2015). That has allowed us to demonstrate the unique combination of morphological characters of the new species. In addition, the range of *Schistochila vitreocincta* is summarised and fertile plants of *S. integerrima* allow us to describe its previously unknown gametangia.

Specimen gatherings were made with the following collecting permits of North Province (number 60912-2012, 60912-1275-2016, 609011-45-2019) and South Province Environment Departments (number 1238-2012, 794-2016, 2825-2019).

RESULTS

Family SCHISTOCHILACEAE H. Buch
Genus *Schistochila* Dumort.

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

Australian Systematic Botany 23: 237 (2010).

COMMENTS

Several expeditions in New Caledonia since 2008 increased our knowledge of the repartition of *S. vitreocincta* that Schuster (1964) described as limited to a few localities, in the vicinity of Montagne des Sources. In fact, the claim of this author that “the genus (*Perssoniella*) is seemingly restricted to the *Araucaria-Agathis* zone in the montane portions of southwestern New Caledonia” is partly true but *S. vitreocincta* is more frequent than then presumed. In this area, which corresponds to the southern ultramafic massif, this species grows on the barks of many large trunks of *Araucariaceae* species and was observed in elevations from 200 m to 1400 m.

Schistochila integerrima Steph.

Species Hepaticarum 6: 492 (1924).

SPECIMEN EXAMINED. — **New Caledonia**. North Province, Poindimié, Amoa valley, trail to Goro Até Mèkébo, on trunks in cloud forest, 724 m, 12.X.2019, *Thouvenot NC2825* (PC[PC0712101]).

COMMENTS

Among the *Schistochila* species lacking underleaves (formerly regarded as *Gottschea* Nees ex Mont.) and with entire margined leaves, *S. integerrima* is easily distinguished from species with subequal lobes and inflated keels (see below) by the insertion of the dorsal lobes on the dorsal face of the ventral ones. On the other hand, it is less easy to distinguish from *S. neesii* (Mont.) Lindb. (Mascareignes) or *S. nuda* Horik. (Asia) from which it differs only by larger leaves (leaves 5–6 mm long vs 3–4 mm long) and the total absence of teeth at the leaf apex which are unevenly present in the former species. As hypothesized by So (2003b), further studies involving molecular methods and more material would likely show these species and *S. integerrima* to be conspecific.

In the diagnosis, Stephani does not describe the gametangia of *S. integerrima* and So (2003b) states that the plant is known only in sterile condition. Here we provide a description of fertile shoots with unfertilized gynoeceia. Androeceia remain unknown.

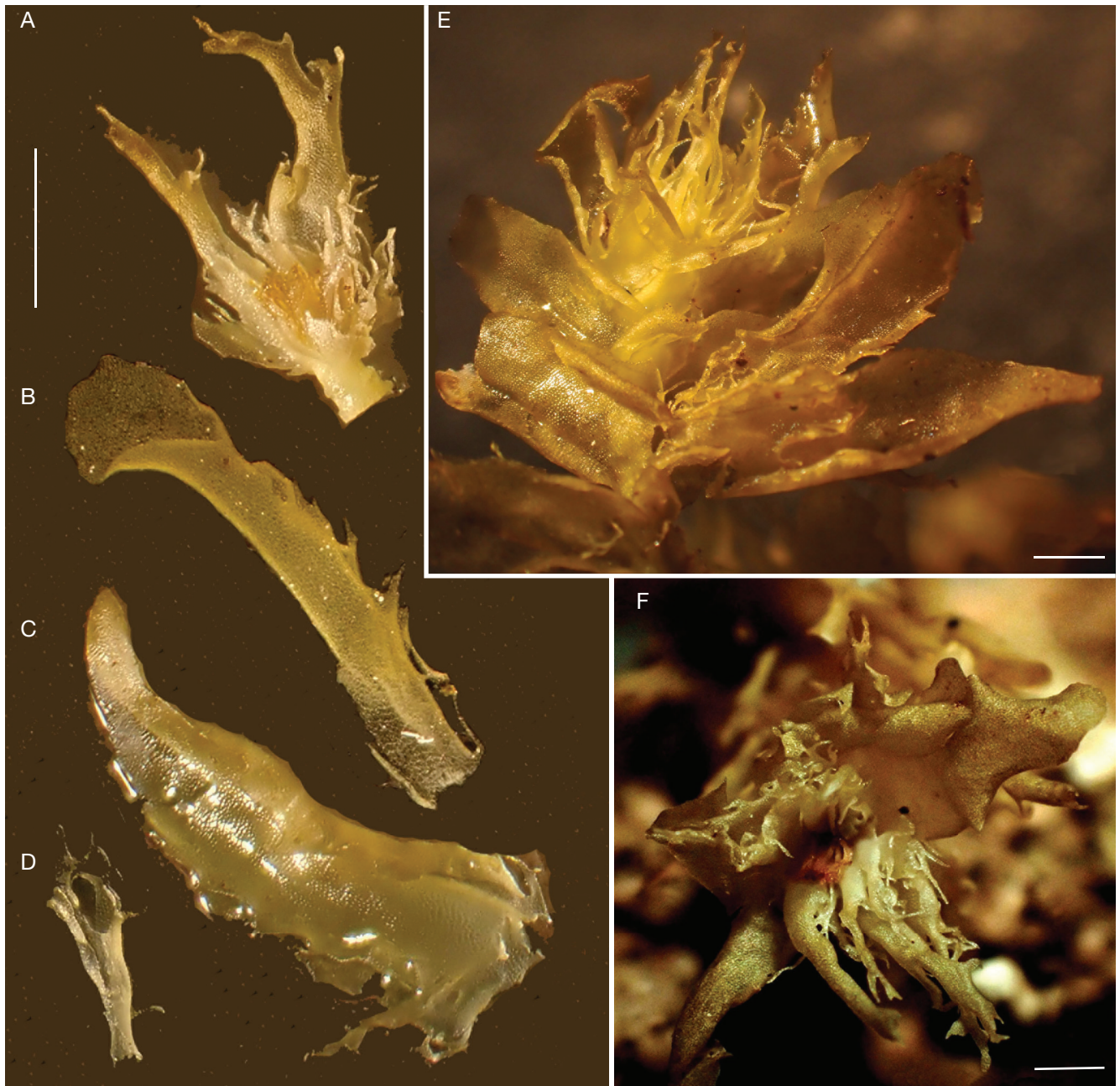


FIG. 1. — *Schistochila integerrima* Steph.: **A**, cluster of archegonia surrounded by scales, bract involucre and bracts (longitudinal section); **B**, **C**, bracts; **D**, bracteole; **E**, top of fertile shoot with gynoecium and fertile innovation; **F**, gynoecium (top view). From Thouvenot NC2825. Scale bars: 1 mm.

DESCRIPTION OF A FEMALE BRANCH (Fig. 1)

A series of underleaves present on fertile shoots just below the gynoecia, the underleaves all deeply and unevenly bilobate with acute lobes, the outermost underleaves divided half-way to the base with margins indistinctly toothed, the innermost underleaves more deeply divided, the lobes tube-like and lacinate. Fertile innovations frequent so that gynoecia are usually in several levels situated one above the other, separated by a few normal leaves with underleaves present or absent; leaves just below the gynoecium progressively modified into bracts, the outermost ciliate only at the base, the innermost leaves 3.5–4.5 mm long, heavily lacinate, connate at base,

linked together in a fringed involucre surrounding linear to furcate scales and many archegonia, ventral lobes canaliculate to involute with margins undulate and apices rounded, dorsal lobes linear, involute.

Schistochila gradsteinii Thouvenot sp. nov. (Figs 2; 3A, B)

DIAGNOSIS. — Stems with a one-layered cortex of thin-walled cells and unevenly thickened medullar cells; leaves conduplicate, the ventral lobes larger, oblong-lanceolate, acuminate, tapering to acute

or apiculate apices, margins entire, the dorsal lobes inserted on the dorsal surface of the ventral lobes in a slightly curved line, the free margins not reaching the ventral lobe margins; leaf cells uniform with large three-layered trigones as in *Schistochila vitreocincta*; underleaves lacking.

TYPE. — **New Caledonia**. North Province, Hienghène, Ouaième rocks, coordinates UTM 58K: 0485 E, 7717 N, 22 Sept. 2019, *Thouvenot NC2807* (holotype PC[PC0712100]; isotype in author's private herbarium).

ETYMOLOGY. — This species is dedicated to Professor Stephani Robbert Gradstein, eminent specialist of the tropical liverwort flora, especially of the Lejeuneaceae. The author would like to express his gratitude for the invaluable support and friendly encouragement that Professor Gradstein provided him thorough his researches.

DISTRIBUTION. — Endemic to New Caledonia.

HABITAT. — Known only from the type, in North Province of New Caledonia, growing on the trunk of small trees in cloud forest, at 950 m elevation.

DESCRIPTION

Dioicous (?).

Plants

Light yellow green to light brownish; shoots simple, creeping and attached by dense rhizoids along almost the whole length of the plant, canaliculate with the leaves curved upward.

Stems

0.55 mm wide, 18 cells across, with an obvious epidermis made of 1-layered thin-walled cells 25–37 µm in diameter, hyaline, surrounding medullary cells (28) 40 (50) µm in diameter, unevenly thickened, walls variously multi-stratified, whitish, the corners thicker but without well-defined trigones.

Leaves

Distichous, spreading at angles 90–120°, entire, without a border of hyaline cells, ventral lobes usually 5.50 mm long, 2.25 mm wide, oblong-lanceolate to oblong-ovate, apices from acuminate-acute to obtuse-apiculate, ending in a file of up to six uniseriate quadrate cells, dorsal lobes distinctly smaller and narrower, 3.75 mm long, 1.75 mm wide, inserted on the dorsal surfaces of the ventral lobes in a slightly curved line, the free margins not reaching the ventral lobe margins, oblong-ovate, apices truncate to rounded, not or hardly exceeding the insertion line; leaves fragile, apices often broken and margins eroded so that broken cells in the border release cell contents enclosed in thin membrane in the form of ephemeral stellate chips.

Underleaves

Lacking.

Leaf cells

Similar in both lobes, without a border of differentiated hyaline cells, cells more or less uniform, rounded, 30–35 µm in diameter, walls thin, at angles with seemingly 3-layered thickenings (Fig. 2J, M) as in *Schistochila vitreocincta*, the internal

layers consisting of small, rounded trigones, surrounded by large circular areolae, eventually confluent, colourless, the external layers made of a thin membrane and agglutinated cell contents.

Gynoeceia

Terminal, 7.5 mm long, bracts laciniate, bracteoles bifid, at most up to the base, lobes sublinear canaliculate to tubular, perianth narrowly tubular, 4-plicate, plicae widely rounded, split at least half of the total length, four lobes secondarily divided and laciniate; androeceia not seen.

COMMENTS

Schistochila gradsteinii sp. nov. is easily distinguished from the other *Schistochila* species lacking underleaves by the combination of the following characters: 1) ventral leaf lobes acuminate to obtuse-apiculate, the apices usually piliferous; 2) dorsal lobe insertion curved, apices rounded, free margins not reaching the ventral lobe margins; 3) both lobes with margins entire; 4) ventral side of stems matted with rhizoids along almost their whole length; 5) leaf cells with large three-layered trigones; and 6) stem structure with an epidermis of thin walled cells and medullary cells unevenly thick walled.

The new species resembles *S. vitreocincta* in distichous leaves with entire margins, the huge 3-layered trigones, the thin-walled epidermis cells and the absence of underleaves, but differs from that species in the dorsal leaf lobes being distinctly smaller than the ventral lobes (slightly larger than ventral lobes in *S. vitreocincta*) and the leaves without a hyaline border (with a broad hyaline border in *S. vitreocincta*). In its characters the new species seems morphologically intermediate between *S. vitreocincta* and other members of the genus *Schistochila*, especially those of the genus *Gottschea* which is phylogenetically close to *S. vitreocincta* (He & Glenney 2010; Sun *et al.* 2014). It resembles also the entire margined *S. integerrima*, but in this species the ventral lobes have rounded apices and the dorsal lobe free margins exceed the ventral ones. Furthermore, the leaf cell trigones are of simple structure and the stem cellular pattern is very different, with the outer cells thick walled, smaller but little different from the underlying cells.

The transverse section of the stems in all other *Schistochila* species observed (*S. aligera*, *S. caledonica*, *S. integerrima* and *S. sciurea*) is consistent with the description of this structure in the publications on *Schistochila*, with relatively homogeneous cells, of subequal sizes, and wall thickness gradually decreasing from the moderately thick cortical to the thin innermost cells. In contrast, *S. vitreocincta* has an epidermis of thin-walled cells (a hyaloderm) and significantly thicker medullary cells, with multi-layered walls. The new species has the same pattern, but the pattern is less conspicuous since the medullary cell walls are unevenly thick-walled and irregularly multi-layered. Interestingly, *S. integerrima* shows a tendency to have a differentiated epidermis made of a layer of cells smaller than the innermost cells, that is thick walled, and the medullary cells are unevenly thickened, but the differentiation is subtle (Fig. 3).

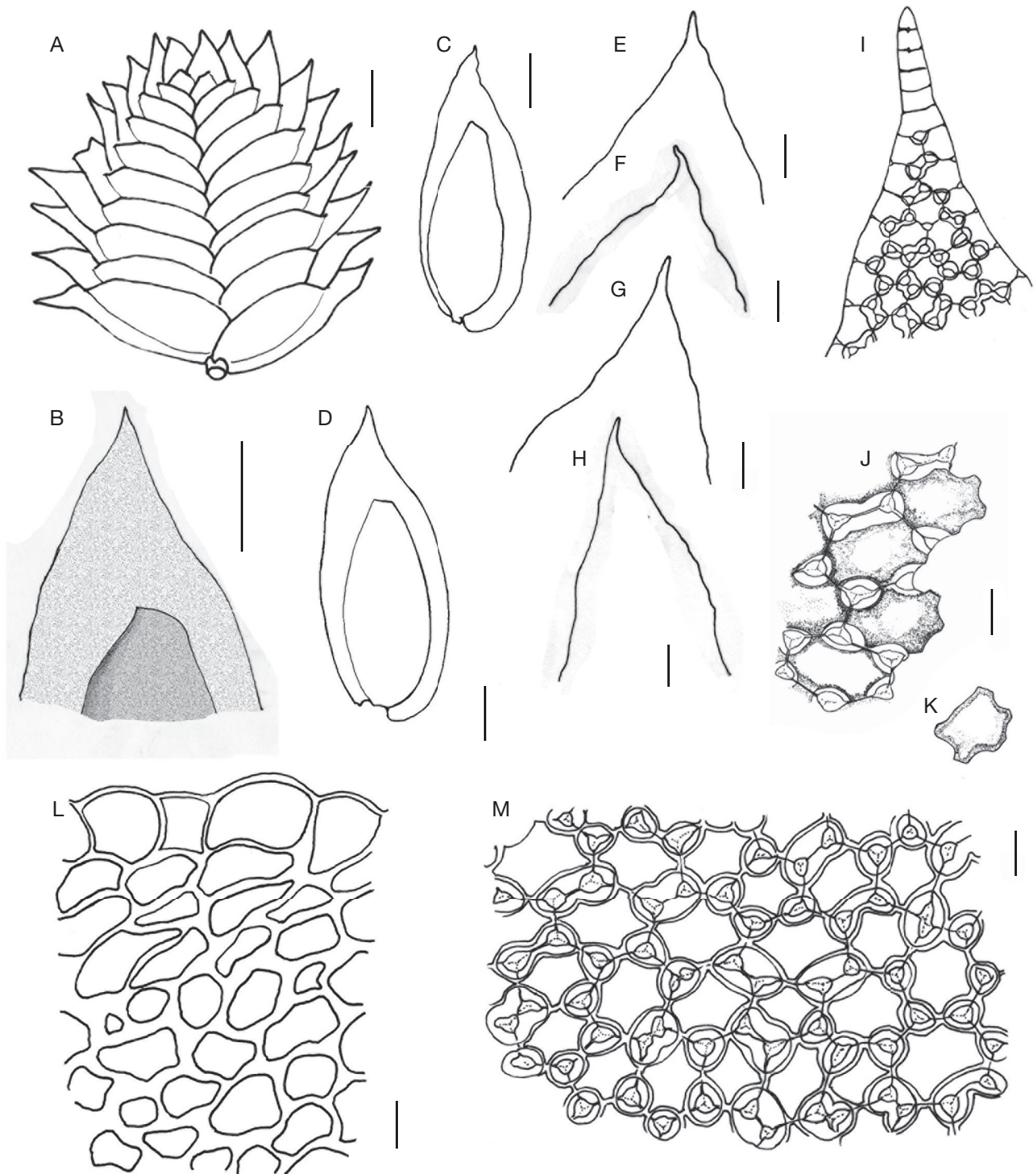


FIG. 2. – *Schistochila gradsteinii* Thouvenot sp. nov.: **A**, habit in dorsal view of the apical portion of a shoot; **B**, apices of both lobes in dorsal view; **C**, **D**, leaves in dorsal view; **E–H**, ventral lobe apices in outline; **I**, detail of ventral lobe apex; **J**, cells on the border of a broken leaf with a released propagule (**K**); **L**, portion of the transverse section of a stem showing epidermis and medullar cells; **M**, leaf cells. All from the holotype. Scale bars: A–D, 1 mm; E–I, 10 μ m; J–M, 20 μ m.

The unusual structure of the leaf cells of *Schistochila gradsteinii* sp. nov., also observed in *Bazzania kokawana* N.Kitagawa & T.Kodama and *S. vitreocincta* might provide endogenous gemmae which are released in the environment when the fragile leaves broke, as stressed by Kitagawa (1983), taken up

by Schuster & Engel (1985). In *S. vitreocincta*, according to Kitagawa (1983), the innermost layer is the true trigone, the median layer is an empty space and the outermost layer is the wall of a “daughter cell”. When cell walls break out, the cell contents enclosed by the membrane bordering the giant

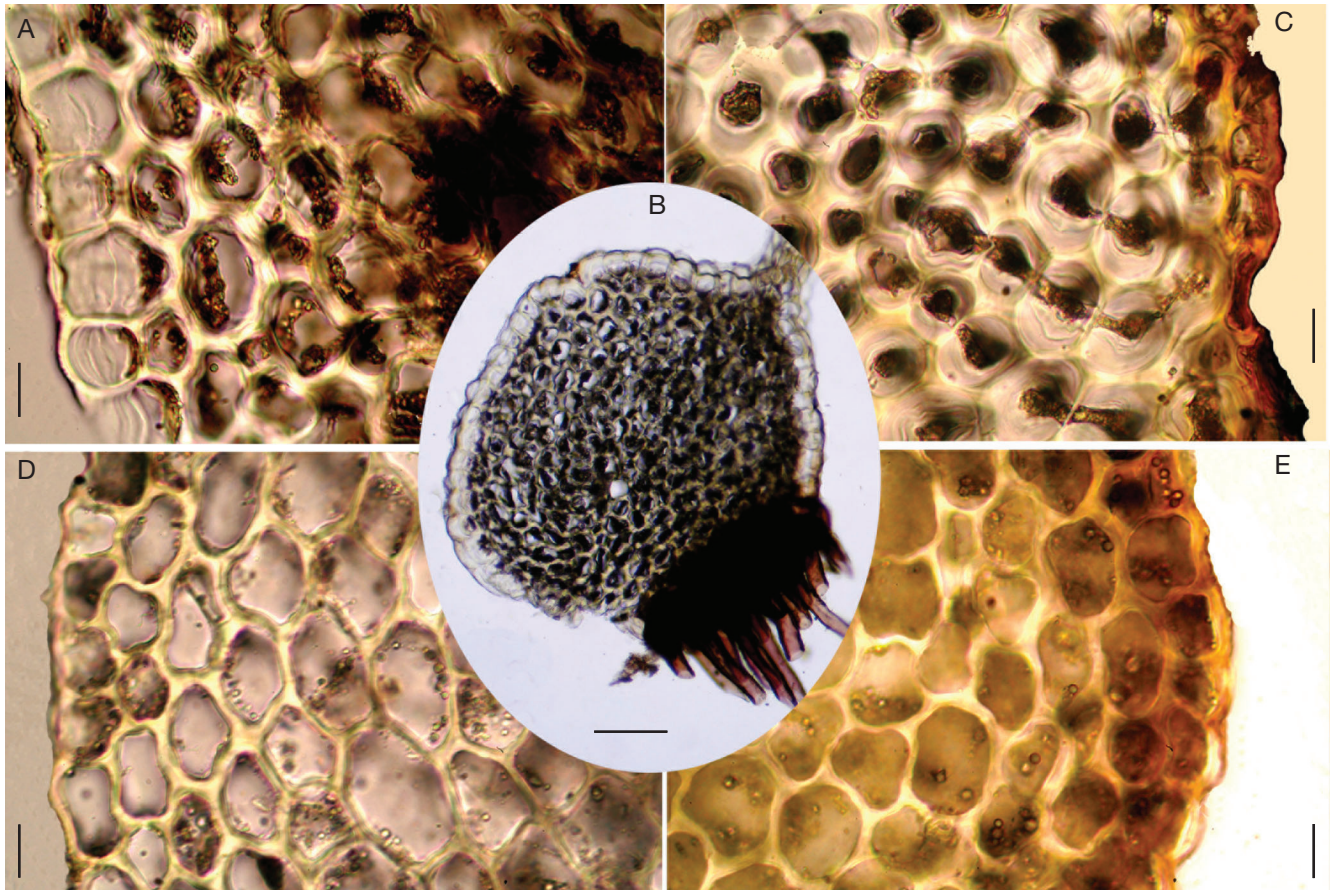


FIG. 3. – Transverse sections of stems of: **A, B**, *Schistochila gradsteinii* Thouvenot sp. nov.; **C**, *S. vitreocincta* (Herzog) X.L.He et Glenny; **D**, *S. aligera* (Nees et Blume) J.B.Jack et Steph. **E**, *S. integerrima* Steph. A, B from the holotype, C from Thouvenot NC1732, D from Thouvenot NC671, E from Thouvenot NC2825. Scale bars. A, C-E: 20 µm, B, 100 µm.

trigones are released into the surrounding area like stellate chips with truncate arms. In *Schistochila gradsteinii* sp. nov., each cell in the young leaves has the same pattern which gradually deteriorates in the oldest cells. The cell contents are enclosed in a membrane that looks like the endogenous gemma of *S. vitreocincta*. But, unlike in *S. vitreocincta* and *Bazzania kokawana*, whose cells contain numerous dark oil-bodies and whose membrane of the released daughter cell is thick, making it able “to endure unfavorable environmental conditions” (Kitagawa 1983), in *S. gradsteinii* sp. nov., the oil bodies are not persistent and the “daughter cells” are thin-walled, so that they are fragile and we could not find any evidence of the ability of the cells produced by *S. gradsteinii* sp. nov. to persist and propagate in the environment. Therefore, experimentation with more available material is required in order to test the ability of such cells to act as propagules.

CONCLUSION

The morphological common ground between *Schistochila gradsteinii* sp. nov. and *S. vitreocincta* argues to bring them together in a reinstated genus *Perssoniella*. The origin of an

endemic bryophyte genus such as *Perssoniella* remains a puzzling question considering the geological history of New Caledonia. Geological evidence for 20 Mya long submersion during Paleocene and Eocene calling into question the conservation of the Gondwanan heritage, the present New Caledonia flora is likely due to recolonization not earlier than 37 Mya ago (Grandcolas *et al.* 2008). But “recent phylogenies give somewhat conflicting evidence as to the continuous presence of a landmass in the New Caledonian area, but the flora is likely to have both an old Cretaceous element with a continuous presence there, and a younger element resulting from transoceanic dispersal (Heads, 2008; Espeland and Murienne, 2011)” (Sun *et al.* 2014). The old age of *Perssoniella vitreocincta*, evaluated at 67 Mya by molecular clock, and the discovery of a new species very close are at the heart of the matter, as well as the small genera *Brevianthus* J.J.Engel & R.M.Schust. and *Goebeliella* Steph.

The discovery of this related new species provides further insight regarding classification and endemism status of the former genus *Perssoniella*. Some of its distinctive characters (complanate habit, lack of underleaves) are attributed to evolution associated with epiphytism (He & Glenny 2010), but the unusual trigone structure is not (D. Glenny pers.

KEY TO THE NEW CALEDONIAN SPECIES OF *SCHISTOCHILA* DUMORT.

1. Leaf cells with huge trigones, seemingly three-layered; stem epidermis distinctive, with thin-walled cells, medullar cells more or less evenly thick walled; leaf margins entire, underleaves lacking..... 2
- Leaf cells with simple trigones, large to inconspicuous, stem cells more or less homogeneous, cortical cells less differentiated with wall cells moderately thick becoming progressively thinner toward central medulla; leaf margins entire or toothed to lacinate, underleaves present or lacking on sterile shoots..... 3
2. Dorsal leaf lobes slightly larger than ventral lobes, both lobes short rectangular-oblong. Leaves with a broad hyaline border; stem medullar cells very thick walled, the walls thicker than the lumina..... *Schistochila vitreocincta* (Herzog) X.L.He & Glenny
- Dorsal leaf lobes conspicuously smaller than ventral lobes which are oblong-lanceolate, acuminate to obtuse apiculate. Leaves without hyaline border; stem medullar cells unevenly thickened, the walls thinner than the lumina *Schistochila gradsteinii* sp. nov.
3. Underleaves lacking in sterile shoots..... 4
- Underleaves present in sterile shoots..... 5
4. Ventral lobe apex entire *Schistochila integerrima* Steph.
- Ventral lobe apex toothed-ciliate *Schistochila aligera* (Nees & Blume) J.B. Jack & Steph.
5. Underleaves and leaf lobe with additional ciliate lobes..... *Schistochila sciurea* (Nees) Schiffn.
- Underleaves and leaf lobes without additional lobes *Schistochila caledonica* Steph.

comm.). Further phylogenetic studies including *Schistochila gradsteinii* sp. nov. are necessary and could lead to formally recognizing a number of genera in the Schistochilaceae family, *Perssoniella* being one of them.

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