

# *Xylolejeunea*, a new genus of the Lejeuneaceae (Hepaticae) from the Neotropics, Madagascar and the Seychelles

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The genus *Trachylejeunea* (Spruce) Schiffn. is reviewed and its subgenus *Hygrolejeuneopsis* R.M. Schust. placed in synonymy of *Xylolejeunea* X.-L. He & Grolle *gen. nov.* (Lejeuneaceae, Hepaticae). Four species are recognized in *Xylolejeunea*: *X. aquarius* (Spruce) X.-L. He & Grolle *comb. nova*, *X. grolleana* (Pócs) X.-L. He & Grolle *comb. nova*, *X. muricella* X.-L. He & Grolle *sp. nova*, and *X. crenata* (Nees & Mont.) X.-L. He & Grolle *comb. nova*. Eight species names are proposed as new synonyms. A key to the species is provided. The genus is characterized by the following main features: (1) an almost longitudinal insertion line of the leaf lobe, (2) an ovate to falcate-ovate shape of the leaf lobe with an entire to finely denticulate margin, (3) two transverse rows of conspicuously enlarged and elongate cells at its base, of which the upper one constitutes the adjacently arranged ocelli, (4) a proximal position of the hyaline papilla relative to the slightly curved first lobule tooth, (5) a blunt, distinct or fairly distinct second lobule tooth, often with strongly thickened outer wall, (6) distant underleaves with an almost transverse insertion to the stem, (7) gynoecia with 1 short, pycnolejeuneoid innovation or without innovation, and (8) the equally sharply 5-keeled perianth with double, 1–4 cells wide, irregularly denticulate wings. The relationships between *Xylolejeunea* and allied genera are discussed. A description, an illustration, and a distribution map is presented for each species of *Xylolejeunea*.

Key words: Hepaticae, Lejeuneaceae, Lejeuneoideae, “peri-Afroamerican” element, *Trachylejeunea*, *Xylolejeunea gen. nov.*

## Introduction

In the course of revising *Trachylejeunea*, we have attempted to redefine its generic limits. As a result, many species previously assigned to *Trachylejeunea* should be transferred to other genera, among them a new one, which is treated in detail below and called *Xylolejeunea*. A taxonomic treatment of true *Trachylejeunea* (lectotype *T. acanthina*) and the excluded species will appear in a separate paper.

## History

In *Lejeunea* subg. *Trachylejeunea*, Spruce (1884) grouped together seven species of *Lejeuneae Schizostipae* primarily on the basis of the roughness of leaves and perianth, respectively. This roughness is due to very convex cell walls, or due to the presence of a large tubercle or wart on each cell (Evans 1903). Spruce (1884) realized that there are considerable differences among his species, and hence subdivided them into two groups, those with a single gynoeceal innovation and those without a gynoeceal innovation. Spruce stated that “a simple female branch is rarely found in the same subgenus as an innovant one, but there are cases where the two types of structure must necessarily stand side by side; where two species agree so nearly in every other respect that they cannot possibly be placed in different subgenera”. Spruce treated under subg. *Trachylejeunea* six species from the Neotropics, *Lejeunea acanthina*, *L. asperiflora*, *L. pellucidissima*, *L. pandurantha*, *L. aquarius*, and *L. immersa*, and, in addition, included also *Lejeunea papillata* from New Zealand. Later on the number of *Trachylejeunea* species rapidly increased in the works of Stephani (1889, 1890, 1896, 1899) and Schiffner (1893). In *Species Hepaticarum* (Stephani 1912–1917) the genus *Trachylejeunea* comprised 29 species, of which eight were described by him in that work.

*Trachylejeunea*, as well as the majority of the Sprucean subgenera, was formally raised to generic rank by Schiffner (1893) in his treatment of the Hepaticae. According to Art. 42.1 of the Tokyo Code (Greuter *et al.* 1994, 2000), however, *Trachylejeunea* (Spruce) Schiffn. 1893

was a younger homonym, because earlier the older name *Trachylejeunea* Steph. 1889 was unintentionally established by describing *T. elegantissima* Steph. (Bonner *et al.* 1961), a species belonging in the unrelated *Siphonolejeunea* Herzog 1942 (Grolle 1976). To keep the two well-established generic names *Trachylejeunea* (Spruce) Schiffn. and *Siphonolejeunea* Herzog, a conservation of *Trachylejeunea* (Spruce) Schiffn. 1893, against *Trachylejeunea* Stephani 1889, was proposed by Gradstein *et al.* (1982). The proposal was accepted and, hence, *Trachylejeunea* (Spruce) Schiffn. now is a *nomen conservandum*, see Greuter *et al.* (1994, 2000). Lectotype of *Trachylejeunea* (Spruce) Schiffn. is *T. acanthina* (Spruce) Schiffn., designated by Vanden Berghen (1948).

Subsequent to Stephani, studies on *Trachylejeunea* were carried out by several authors, mostly by contributing new species from various regions. In the West Indian islands three species, *T. dilatata* A. Evans (Evans 1908), *T. jamaicensis* Pearson (Pearson 1931), and *T. monophthalma* R.M. Schust. (Schuster 1970) have been described. In southeast Asia, Herzog (1930) described *Trachylejeunea chinensis* Herzog from China, and *T. malangensis* Herzog (Herzog 1931) and *T. schiffneri* Herzog (Herzog 1948) from Java. *Trachylejeunea kusaiensis* H. Inoue & H. A. Mill. from Caroline Island was described by Inoue and Miller (1965). Additions for South America were *T. buchtienii* Herzog (Herzog 1942) and *T. inflexa* var. *acuminata* Herzog (Herzog 1950), both from Bolivia. However, all these species names have been recently shown to fall into synonymy or to be wrongly placed (Schuster 1980a, He 1999, and X.-L. He & R. Grolle unpubl.)

Evans (1903) investigated *Trachylejeunea* of Puerto Rico and reported *T. aquarius* (Spruce) A. Evans. Evans emphasized that the roughness of leaf cells cannot alone confine the genus, and concluded that *Trachylejeunea* is not a very clearly defined group on the basis of the variation in leaf cells and branching patterns. Schuster (1963) established a new genus *Echinolejeunea* R.M. Schust. based on the New Zealandian species *Trachylejeunea papillata* (Mitt.) Steph. and transferred *T. schiffneri* to *Crossotolejeunea* (Spruce) Schiffn., which was later moved to *Stenolejeunea*

R.M. Schust. by Pócs *et al.* (1995). More species assigned to *Trachylejeunea* have recently been shown to belong to other genera (Mizutani 1972, Grolle 1979, 1984, 1989, Piippo 1986, Grolle & Reiner-Drehwald 1997, 1999, He 1999, Zhu & So 1999, X.-L. He & R. Grolle unpubl.). On the other hand, there are also species described in other genera of the Lejeuneaceae that have been removed to *Trachylejeunea*, such as *Prionolejeunea gossepapulosa* Steph. (Schuster 1970), *Lejeunea aneogyna* Spruce (Grolle 1979), and *Lejeunea crenata* Nees & Mont. (Schuster 1992). It appears that misunderstandings dating from its establishment as the subgenus *Trachylejeunea* have led to involvement of ten unallied genera: *Crossotolejeunea*, *Cyclolejeunea* A. Evans, *Echinolejeunea*, *Echinocolea* R.M. Schust., *Pycnolejeunea* (Spruce) Schiffn., *Cheilolejeunea* (Spruce) Schiffn., *Lejeunea* Lib., *Lepidolejeunea* R.M. Schust., *Siphonolejeunea* Herzog, and *Stenolejeunea*. Therefore, a thorough study on *Trachylejeunea* is, indeed, necessary in order to circumscribe the genus.

Schuster (1980a) divided *Trachylejeunea* into three subgenera. Subg. *Trachylejeunea* (type *T. acanthina*) is mainly characterized by a lack of subgynoecial innovation, spinose-dentate leaves, nontuberculate leaf cells, basal part of leaf lobe without ocelli, and two lobule teeth with a hyaline papilla in between. Subg. *Hygrolejeuneopsis* R.M. Schust. (type *T. aquarius*) consists of species with a subgynoecial innovation, edentate leaves, tuberculate leaf cells, 2–5 basal ocelli in the leaf lobe, and two lobule teeth with a hyaline papilla proximal to the first one. Subg. *Cheilolejeuneopsis* R.M. Schust. is similar to *Hygrolejeuneopsis*, but differs by its single lobule tooth and a single basal ocellus in the leaf lobe. Schuster (1980a) assigned two species in this subgenus, the type *T. monophthalma* and *T. gossepapulosa* (Steph.) R.M. Schust. However, the former species was shown to belong to *Pycnolejeunea* by He (1999) and the latter was transferred to *Lepidolejeunea* by Piippo (1986).

## Taxonomic treatment

Schuster's (1980a) establishment of the subg. *Trachylejeunea* and subg. *Hygrolejeuneopsis* of

*Trachylejeunea* was based mainly on the unique features of *T. acanthina*, in spite of the many differences between the two groups, as he stated. The present study, however, shows that the two subgenera remarkably differ in a series of features, which suggest that the subgenera are too distant to reconcile with a single generic type. These differentiating features can be observed in plant colour, texture, leaf cells, leaf lobule, underleaves, gynoecial innovation and perianth structures. In the subg. *Trachylejeunea*, the plants are usually dull-coloured and rigid, the leaf lobe usually has large, well-developed trigones as well as conspicuous intermediate thickenings, but rarely have ocelli present at the leaf base; the insertion line of the underleaf is arched, the gynoecia typically lack an innovation; and the keel of the perianth is devoid of wings. However, species in the subg. *Hygrolejeuneopsis* are commonly whitish-green or pale yellowish-green, and pellucid, the leaf lobe is virtually devoid of trigones except in *Trachylejeunea aquarius*, and the intermediate thickenings are lacking or rare; the ocelli usually number 2–5 per leaf lobe, they are adjacent, present in the base of the leaf lobe, except in *Trachylejeunea crenata*, which occasionally has scattered ocelli in the distal portion of leaf lobe; the two transverse rows of basal cells include ocelli, much enlarged and more elongate than the adjacent cells; the insertion line of the underleaf is usually transverse to the stem; the gynoecia have a single pycnolejeuneoid innovation or an innovation is lacking; and the keel of the perianth is double-winged. All these differentiating characters, as stated above, consistently distinguish subg. *Trachylejeunea* from subg. *Hygrolejeuneopsis*.

## *Xylolejeunea* X.-L. He & Grolle, *gen. nov.*

Derived from the Greek *xylon* = wood, because the plants often grow on rotten wood, prefixed to *-lejeunea*.

*Pycnolejeunea* (Spruce) Schiffn. *affinis*, *sed differt* (1) *foliorum lobo ovato, plerumque denticulato, basi duabus seriebus transversalibus cellularum satis amplificatarum et elongatum*, (2) *in earum serie distali 2–5 ocellis adjacentibus*, (3) *insertione foliorum lobi subrecta*, (4) *amphigas-*

*trii remotis et (5) carinis perianthii breviter bialatis.*

TYPE: *Xylolejeunea aquarius* (Spruce) X.-L. He & Grolle (≡ *Lejeunea aquarius* Spruce) — *Trachylejeunea* subg. *Hygrolejeuneopsis* R.M. Schust., Phytologia 45: 426. 1980. Type: *Trachylejeunea aquarius* (Spruce) A. Evans (≡ *Lejeunea aquarius* Spruce)

Plants autoicous (androecia not seen in *X. muricella*), small to relatively robust, up to 2.0 cm long and 1.0–1.5 mm wide, whitish or yellowish green, or brown in dry condition, forming appressed mats or mixed with other bryophytes, on rotten wood, bark of living trees, or rarely on rock. Vegetative branching of *Lejeunea*-type, growth habit irregularly pinnate, branches short to long, widely spreading. Stem 75–188 µm in diameter, stem cells rectangular or quadrate, on the ventral side 30–88 × 23–50 µm, in cross-section composed of 7–9 epidermal cells, surrounding 7–21 medullary cells; epidermal cells rectangular, 18–60 × 8–38 µm, cell walls thickened, medullary cells smaller than epidermal cells, rectangular or isodiametric, 11–38 × 8–25 µm; ventral merophytes of stem 2 cells wide. Leaves incubous, unequally bilobed, with a large dorsal lobe and a small ventral lobule, closely imbricate, when moist widely spreading; insertion line almost longitudinal except for a short distance near dorsal leaf base. Lobe convex, ovate or falcate-ovate, 0.32–0.70 mm long and 0.27–0.60 mm wide, dorsal margin broadly arched, ventral margin nearly straight or slightly arched, apex usually decurved, rounded, obtuse or acute, on leaves of slender branches usually acute, margin entire or finely denticulate. Lobe cells convex, smooth or papillate on dorsal surface, marginal cells quadrate to rectangular, 13–28 × 8–25 µm, median cells isodiametric or nearly so, or slightly elongate, 16–35 × 15–30 µm, basal cells typically composed of 2 almost transverse rows of conspicuously enlarged and elongate cells, the upper row usually consisting of 2–5 ocelli, 45–93 × 18–38 µm, adjacent cells in the lower row usually without one large oil body per cell, 40–75 × 10–28 µm, other normal basal cells 25–50 × 18–33 µm; trigones large and conspicuous, or lacking; intermediate thickenings rarely present or lacking; oil-bodies not seen. Lobule ovoid or triangular-ovoid, 0.11–0.20 mm long and 0.09–0.15 mm

wide, inflated, 0.2–0.4 of lobe length; lateral margin usually strongly inrolled, composed of (3–)4–5(–6) elongate marginal cells, apical margin composed of 3 marginal cells; keel arched, smooth to roughed with papillae or finely denticulate; apex semicircular, the first tooth 1-celled, short to relatively long, slightly curved outwards or rarely downwards, the second tooth distinct or nearly so, blunt, often with strongly thickened outer wall; the hyaline papilla positioned in a 1-cell wide notch between the two teeth, proximal to the first tooth; cells of lobule convex, slightly smaller than the cells of the lobe, smooth or papillate, trigones conspicuous or lacking. Underleaves small, distant, orbicular, narrowly or broadly orbicular, 0.12–0.24 mm long and 0.10–0.27 mm wide, 1.2–2.0 × stem width, bifid, lobed to 0.3–0.6 of their length, margin usually entire, often with a 1-celled, more or less distinct tooth on the outer margin, lobe triangular, obtuse or acute, sinus narrow, or V-shaped, rarely U-shaped. Rhizoid numerous at underleaf base. Asexual reproduction by caducous leaves (only seen in *X. crenata*).

Androecia (not seen in *X. muricella*) on short or elongate branches, terminal in position, inflated, spicate; bracts in 2–27 pairs, closely imbricate, margin entire or finely denticulate; bract cells smooth or papillate, ocelli lacking or present on bract lobes; bracteole similar to underleaf but smaller, 1–2 restricted to the base of male spike. Gynoecia (poorly seen in *X. muricella*) on short or elongate branches, innovation single with pycnolejeuneoid leaf sequence, or lacking. Female bracts in one pair, suberect, bract lobe obovate or oblong, 0.45–0.85 mm long and 0.20–0.45 mm wide, apex rounded, obtuse or subacute, margin usually finely denticulate; bract cells convex, smooth or papillate, ocelli lacking or present, adjacent or scattered in the lobe; bract lobule usually lingulate, 0.20–0.60 mm long and 0.14–0.18 mm wide, apex obtuse or acute, margin finely serrulate to denticulate in the upper part, without wings. Bracteole oblong, 0.38–0.80 mm long and 0.17–0.36 mm wide, bifid or nearly emarginate, apex 2-lobed to 0.1–0.2 of bracteole length, lobe apex acute or obtuse, overlapping or not, sinus narrow, margin entire to denticulate. Perianth obovate, covered partly to almost entirely by bracts and bracteole,

0.74–1.10 mm long and 0.36–0.80 mm wide, inflated, equally sharply 5-keeled, with double, 1–4 cells wide, irregularly denticulate wings, ventral keel extending to the middle of the perianth; perianth cells convex or papillate, quadrate to rectangular, ocelli lacking or occasionally scattered in upper portion of perianth, trigones lacking or rarely developed, intermediate thickenings rarely present; apex truncate or rounded; beak short. Sporophyte foot reduced, not entering stem; seta articulate, composed of 12 rows of outer cells and 4 rows of inner cells, capsule with cells of outer wall covered with nodulose thickenings, inner wall except the lower part covered by fenestrate sheets of thickenings. Elaters 22–34 per capsule, marginal elaters well developed, 175–283 × 10–18 µm, 5 or 6 in number in opposite valves, in case of 5 elaters one situated at the apex of valve and the other four are lateral; in case of 6 elaters all are lateral with three on each side of valve; upper end attached to valve margin. Inner elaters rudimentary, sometimes indistinct, 88–168 × 6–13 µm, usually 8–12 in number, when well developed 3 in each inner valve surface, one occurring on the central portion of the valve and the other two lateral, both ends attached to the inner surface. Spores (only seen in *X. crenata*) brown in dry condition, 20–30 × 10–18 µm, irregularly rectangular or irregularly shaped, arranged in decussate tetrads in unopened capsule; spore surface granulate.

We recognize four species of *Xylolejeunea*: *X. aquarius* (Spruce) X.-L. He & Grolle and *X. crenata* (Nees & Mont.) X.-L. He & Grolle from the Neotropics, *X. grolleana* (Pócs) X.-L. He & Grolle from Madagascar, and *X. muricella* X.-L. He & Grolle from the Seychelles.

#### Key to the species of *Xylolejeunea*

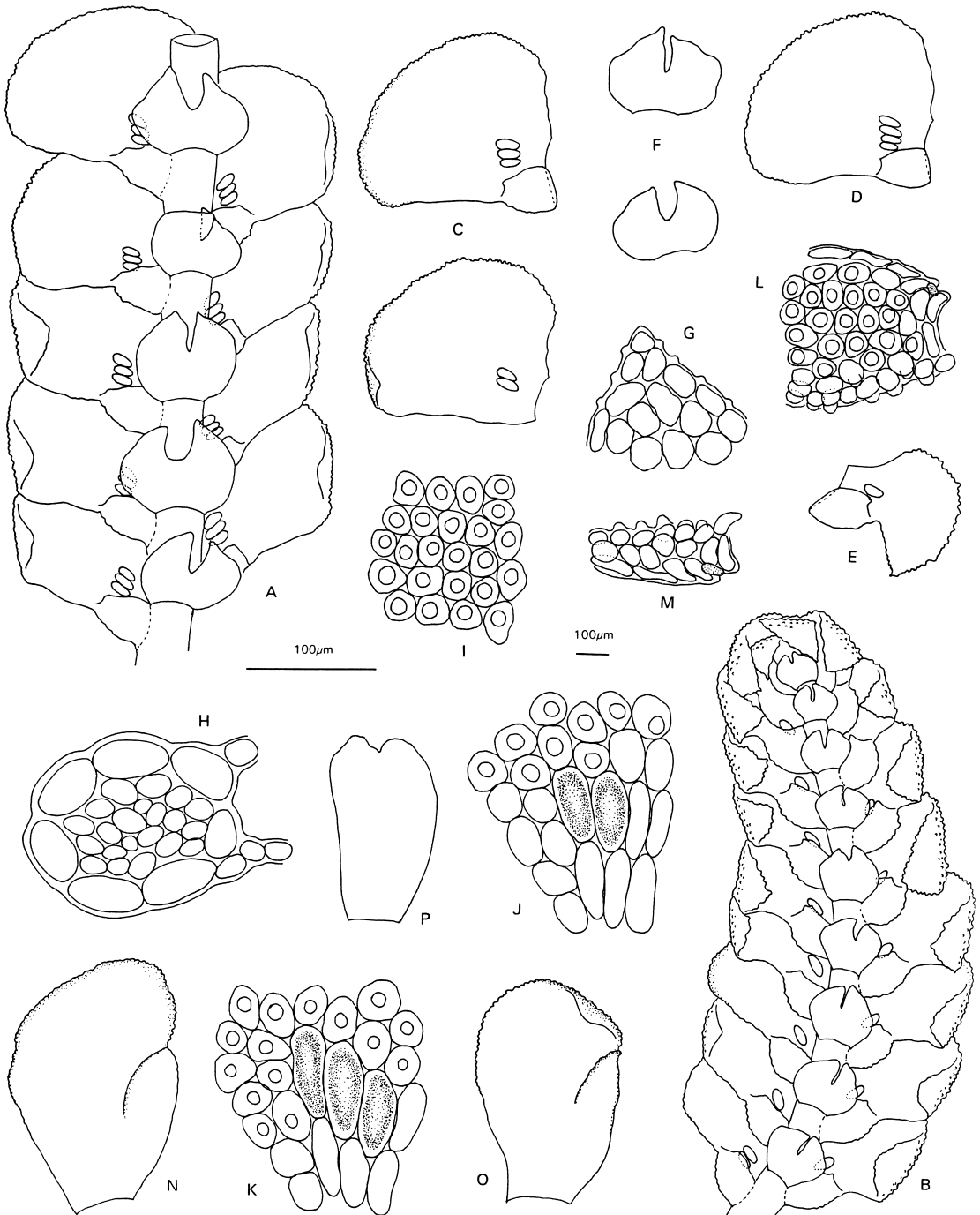
1. Leaf cells papillose; gynoecial innovation single, pycnolejeuneoid ..... 2
1. Leaf cells smooth; gynoecial innovation single, pycnolejeuneoid, or lacking ..... 4. *X. crenata*
2. Plants relatively robust, up to 1.5 mm wide; leaf cells with coarse, conspicuous trigones, each cell on dorsal leaf surface bearing a large, sphaerical or subsphaerical papilla ..... 1. *X. aquarius*
2. Plants small, up to 1.0 mm wide; leaf cells lack trigones, each cell on dorsal leaf surface bearing a

- large fingerlike or a small sphaerical papilla ..... 3
3. Leaf cells each with a large fingerlike papilla; lateral margin of lobule composed of 5 elongate marginal cells, the first tooth of lobule 1-celled, short, slightly outwards curved, keel of lobule smooth; underleaves usually narrowly ovate, longer than wide ..... 2. *X. grolleana*
3. Leaf cells with a small sphaerical papilla; lateral margin of lobule composed of 4 elongate marginal cells, the first tooth of lobule 1-celled, long, downwards curved, keel of lobule usually finely denticulate; underleaves usually orbicular ..... 3. *X. muricella*

#### *Xylolejeunea aquarius* (Spruce) X.-L. He & Grolle, *comb. nova* (Fig. 1)

*Lejeunea aquarius* Spruce, Trans. Bot. Soc. Edinburgh 15: 185. 1884. — *Trachylejeunea aquarius* (Spruce) A. Evans, Bull. Torrey Bot. Club 30: 561. 1903. — Type: Venezuela. Terr. Amazonas, Rio Negro, San Carlos, in lignis putridis, Spruce (lectotype, here designated: MANCH (L383)!, isolecto: G-17979!, JE!, MANCH!, YU!)

Autoicous. Plants small to relatively robust, up to 2.0 cm long and 1.5 mm wide, whitish or yellowish-green, or brown in dry condition, forming appressed mats or mixed with other bryophytes, on rotten wood. Vegetative branching of *Lejeunea*-type, growth habit irregularly pinnate, branch usually abundant, short to long, widely spreading; stem 150–180 µm in diameter, stem cells rectangular or quadrate, on the ventral side 55–88 × 40–50 µm, in cross-section composed of 7–8 epidermal cells, surrounding 19–21 medullary cells, epidermal cells rectangular, 33–60 × 20–38 µm, cell wall thickened, medullary cells smaller than epidermal cells, isodiametric to rectangular, 13–25 × 10–15 µm; ventral merophytes of stem 2 cells wide. Leaves closely imbricate, when moist widely spreading, insertion line almost longitudinal except for a short distance near dorsal leaf base; leaf lobe convex, often decurved at the apex, ovate or falcate-ovate, 0.45–0.65 mm long and 0.42–0.60 mm wide, margin entire or slightly denticulate, each marginal cell tipped by a large, spherical or subspherical papilla, dorsal margin broadly arched, ventral margin slightly arched or nearly straight, apex rounded, obtuse to acute, on leaves of slender branches usually acute; leaf cells strongly convex, each cell on dorsal surface except leaf base bearing a large, spherical or



**Fig. 1.** *Xylolejeunea aquarius* (Spruce) X.-L. He & Grolle. (from Bisse & Lippold 11165/a, JE). — **A:** Habit. — **B:** Branch. — **C–E:** Leaves. — **F:** Underleaves. — **G:** Lobe apex of underleaf. — **H:** Cross-section of stem. — **I:** Cells from middle portion of leaf. — **J** and **K:** Cells from basal portion of leaf. — **L:** Leaf lobule with hyaline papilla. — **M:** Lateral margin cells and hyaline papilla of lobule from inner side. — **N** and **O:** Female bracts. — **P:** Female bracteole. — Use the shorter 100  $\mu\text{m}$  scale for **A–F** and **N–P**, and the longer 100  $\mu\text{m}$  scale for **G–M**.

subspherical papilla, marginal cells rectangular or quadrate,  $13\text{--}20 \times 10\text{--}18 \mu\text{m}$ , median cells isodiametric or nearly so,  $23\text{--}33 \times 20\text{--}25 \mu\text{m}$ , basal cells typically composed of 2 transverse rows of conspicuously enlarged and elongate cells, the upper row consists of 2–4 ocelli in number,  $63\text{--}88 \times 28\text{--}38 \mu\text{m}$ , adjacent, the lower one usually without ocelli,  $43\text{--}70 \times 15\text{--}25 \mu\text{m}$ , other normal basal cells slightly elongate,  $28\text{--}35 \times 20\text{--}25 \mu\text{m}$ ; trigones usually large, conspicuous, rarely confluent, intermediate thickenings rarely present; oil-bodies not seen. Lobule ovoid,  $0.15\text{--}0.20 \text{ mm}$  long and  $0.12\text{--}0.14 \text{ mm}$  wide, strongly inflated, ca. 0.3 of lobe length; lateral margin usually strongly inrolled, composed of 4 elongate marginal cells, apical margin composed of 3 marginal cells, keel arched, often roughened from papillae; apex semicircular, the first tooth 1-celled, slightly curved outwards, the second tooth distinct or nearly so, blunt, often with strongly thickened outer wall; the hyaline papilla positioned in a 1-cell wide notch between teeth, proximal first tooth; lobule cells convex, papillate, trigones conspicuous. Underleaves distant, broadly orbicular,  $0.20\text{--}0.28 \text{ mm}$  long and  $0.27\text{--}0.36 \text{ mm}$  wide,  $2.0 \times$  stem width, bifid, lobed to 0.5–0.6 of their length, lobe triangular, acute, sinus narrow, margin entire, or often with local thickenings by marginal cells. Rhizoids numerous at underleaf base. Asexual reproduction not seen. Androecia on short or elongate branches, terminal in position, inflated, spicate, male bracts in 2–14 pairs, margin finely denticulate, each marginal cell tipped by a large papilla, ocelli lacking; male bracteole 1, restricted to the base of the spike; margin entire. Gynoecia on short branches, innovation single, with a pycnolejeuneoid leaf sequence, female bracts in one pair, suberect, bract lobe obovate,  $0.55\text{--}0.82 \text{ mm}$  long and  $0.35\text{--}0.45 \text{ mm}$  wide, apex rounded to obtuse, margin usually finely denticulate in upper and middle portion; bract cells convex, each cell on the dorsal bract surface bearing a large, spherical or subspherical papilla, ocelli lacking; bract lobule lingulate,  $0.45\text{--}0.58 \text{ mm}$  long and  $0.12\text{--}0.18 \text{ mm}$  wide, apex obtuse to acute, margin slightly denticulate in upper portion, without wings. Bracteole oblong,  $0.54\text{--}0.57 \text{ mm}$  long and  $0.32\text{--}0.35 \text{ mm}$

wide, apex slightly bifid or nearly emarginate, lobe obtuse, margin slightly and irregularly denticulate in upper portion, sinus narrow. Perianth obovate, covered less than half by bracts and bracteole, ca.  $1.10 \times 0.60 \text{ mm}$ , equally sharply 5-keeled, with double, 1–4 cells wide, irregularly denticulate wings; ventral keel usually extending to the middle of perianth, rarely to the lower part; perianth cells in the upper portion papillate, in the lower portion convex; apex truncate; beak short. Seta articulate, consists of 12 rows of outer cells and 4 rows of inner cells, outer wall of capsule covered with orange brown nodular thickenings, inner wall except the lower part covered by fenestrate sheets of thickenings. Elaters 30–34 per capsule, marginal elaters 22, 5 or 6 on each valve,  $213\text{--}283 \times 10\text{--}13 \mu\text{m}$ , upper end attached to valve margin; inner elaters usually 8–12, when well-developed, 3 in each valve, one occurring on the central portion of the inner valve surface and the other two are lateral,  $133\text{--}168 \times 9\text{--}13 \mu\text{m}$ , both ends attached to inner valve surface. Spores not seen.

*Xylolejeunea aquarius* is a very distinctive species. It can be well distinguished from other members of the genus by the relatively robust size, the large, spherical papillae on dorsal leaf surface, and the conspicuous trigones in leaf lobe cells.

The unique leaf base structure, which serves as an important generic character, has been interpreted differently. When describing *Trachylejeunea aquarius*, Schuster (1992) stated that a group of as many 6–8 basal cells, in two tiers, appears to constitute the ocelli, as in *Trachylejeunea crenata*. Therefore, he questioned Evans' (1903) report of the same species having 2–5 ocelli (Evans 1903). Pócs (1999) also mentioned that two rows of ocelli formed a basal vitta in *Trachylejeunea grolleana*. However, in the present study we observed that only the upper one of the two transverse rows of the remarkably enlarged and elongate basal cells contains single and large oil-bodies, consequently the ocelli number is fewer. The same observation can be seen in the illustrations of *T. aquarius* by Evans (1903: plate 22, fig.17), where he showed three ocelli in the leaf lobe and their position. In *Xylolejeunea crenata*, we did find an extreme

case of a single ocellus occurring in the lower portion of the two specialized cell rows, when many ocelli are scattered in the distal portion of leaf lobe. Furthermore, these two peculiar cell rows are not treated as vitta in this paper, since the cell walls are not any thicker than in the adjacent cells.

**DISTRIBUTION AND HABITAT:** Cuba (Oriente), Puerto Rico, Venezuela and Brazil (Fig. 6). *Xylolejeunea aquarius* usually grows on rotten logs or tree trunks near streams, in humid lowland and montane rainforests.

**SPECIMENS EXAMINED:** — Am 3: **Cuba**. Oriente, Prov. Guantánamo, Baracoa, El Yunque, on old log, 1903 *Underwood & Earle 1183/a* (JE); Prov. Holguín, Moa, La Melba falda este de la Sierra de Moa 800–1000 m, pluviosilva mit *Micropterygium trachyphyllum*, 1968 *Bisse & Lippold 11165/a* (JE), 11209/a (JE), camino desde Moa hacia La Melba, 1969 *Lippold 12199* (JE), 12271/a (JE), Cuchillas de Moa, 2 km al Norte de La Melba, cerca las cascadas Dos Comadres, bosque siempreverde sobre rocas de serpentina, alt. 400 m, sobre corteza podrida, 1980, *Pócs & Reyes 9170/AM* (JE), 9170/EJ (JE), siempreverde, alt. 400–500 m, sobre madera pod., 1980 *Reyes 9173/F* (JE), pluviosilva montana con musgos, en la ladera NE del Pico El Toldo, 900–1000 m, sobre madera podrida, 1980 *Pócs 9176/BD* (JE). **Puerto Rico**. North slope of the Luquillo Mts., auf morschem Holz, *Heller 4745* (JE). — Am 4: **Venezuela**. See the type collections cited above. — Am 5: **Brazil**. Estado Amazonas, Rio Negro, *Spruce* (MANCH), Camanáos, 1928 *Lützelburg 22154/a* (JE).

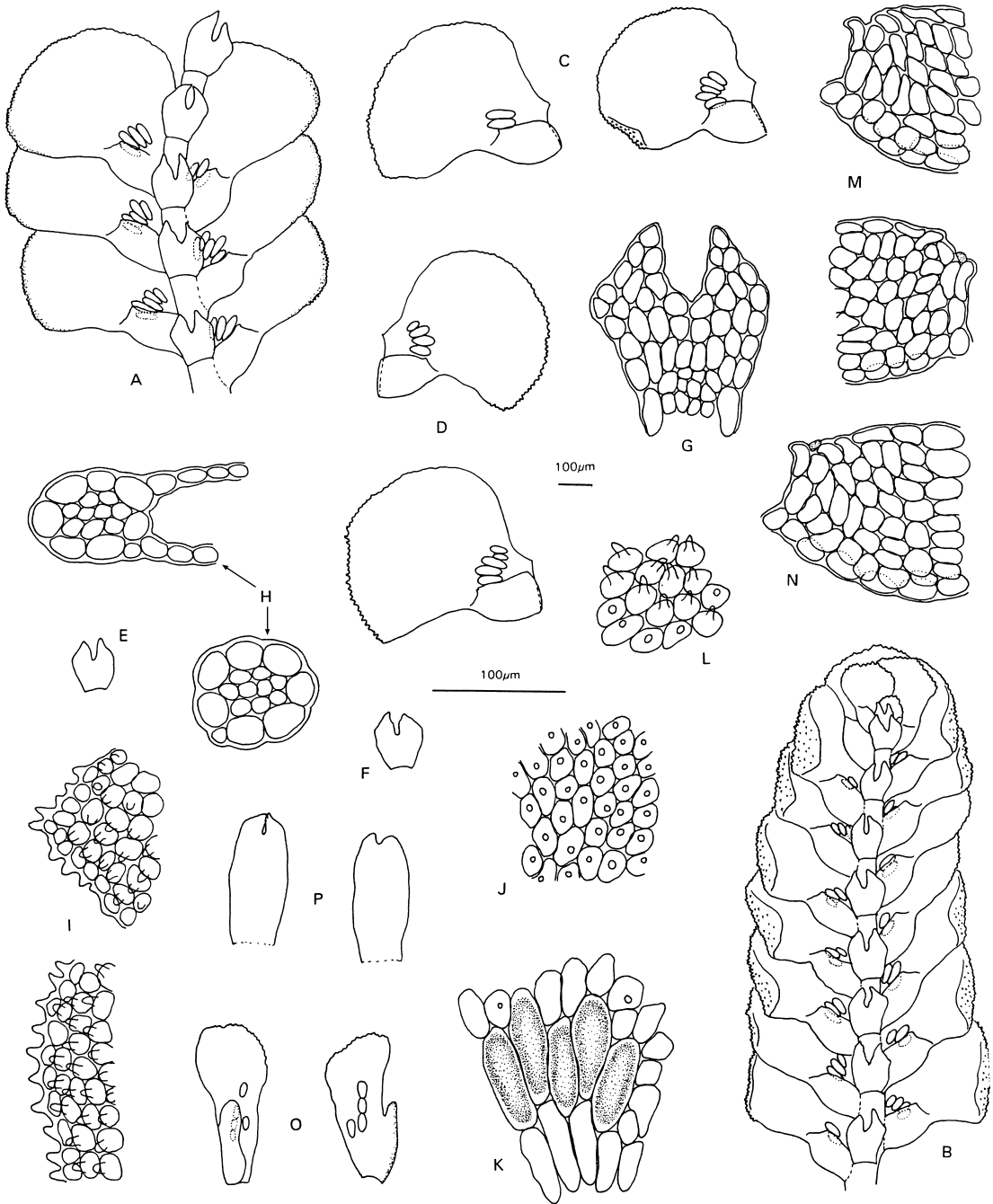
***Xylolejeunea grolleana* (Pócs) X.-L. He & Grolle, *comb. nova* (Fig. 2)**

*Trachylejeunea grolleana* Pócs, Haussknechtia Beiheft 9: 285. 1999. — Type: Madagascar. Toamasina Prov., Mananara-Nord Biosphere Reserve and National Park. Very wet types of lowland rainforest on the E slopes of Mahavoho hill along Mahavoho river, with many tree ferns, palms and *Pandanus* ssp. At 220 m alt., 16°27'S, 49°46.9–47.5'E, on decaying logs, 17.VIII.1998 *T. Pócs & A. Szabó 9878/CY* (holotype EGR, isotypes GOET!, H!, JE!). The same locality and habitat, on decaying wood at 240 m alt, 16.VIII.1998 *T. Pócs & A. Szabó 9878/CP* (isoparatype H!).

Autoicous. Plants small, up to 1.5 cm long and 1.0 mm wide, green, whitish or yellowish-green, or brown in dry condition, closely creep-

ing or forming appressed mats, on rotten wood. Vegetative branching of *Lejeunea*-type, growth habit irregularly pinnate, branches short to long; stem 75–100 µm in diameter, stem cells rectangular, on the ventral side 30–50 × 23–28 µm, in cross-section composed of 7–8 epidermal cells, surrounding 9–15 medullary cells, medullary cells smaller than epidermal cells, quadrate to isodiametric, 12–18 × 10–18 µm; ventral merophytes of stem 2 cells wide. Leaves closely imbricate, when moist widely spreading, insertion line almost longitudinal except for a short distant near dorsal base; leaf lobe strongly convex, and decurved at the apex, ovate or falcate-ovate, 0.40–0.55 mm long and 0.32–0.48 mm wide, margin entire or finely denticulate, apex obtuse to broadly acute, on leaves of slender branches usually acute; leaf cells convex, each cell on dorsal surface except near the base bearing a large, fingerlike papilla, marginal cells quadrate or rectangular, 13–18 × 8–13 µm, median cells isodiametric to slightly elongate, 20–33 × 15–20 µm, basal cells typically composed of 2 transverse rows of enlarged and elongate cells, the upper row consists of 2–5 ocelli, 53–95 × 18–35 µm, adjacent, the lower one usually without ocelli, 40–75 × 10–20 µm, other normal basal cells usually elongate, 35–50 × 18–26 µm; trigones lacking, intermediate thickenings lacking; oil-bodies not seen. Lobule ovoid, 0.11–0.19 mm long and 0.09–0.14 mm wide, inflated, 0.3–0.4 of lobe length; lateral margin usually inrolled, composed of 5 elongate marginal cells, apical margin composed of 3 marginal cells, keel arched, smooth; apex semicircular, the first tooth usually curved outwards, 1-celled, the second tooth 1-celled, distinct or nearly so, blunt, often with a strongly thickened outer wall, the hyaline papilla positioned in a 1-cell wide notch between teeth, proximal to first tooth; lobule cells slightly convex, without papilla. Underleaves distant, narrowly ovate, ovate or rarely orbicular, usually longer than wide, 0.12–0.18 mm long and 0.10–0.15 mm wide, 1.2–2.0 × stem width, bifid, lobed to 0.3–0.6 of their length, often with a 1-celled, more or less distinct tooth on the outer margin, lobe triangu-





**Fig. 2.** *Xylolejeunea grolleana* (Pócs) X.-L. He & Grolle (from isotype, H). — **A:** Habit. — **B:** Branch. — **C** and **D:** Leaves. — **E–G:** Underleaves. — **H:** Cross-sections of stem. — **I:** Cells from apical leaf margin. — **J:** Cells from middle portion of leaf. — **K:** Cells from basal portion of leaf, with 5 ocelli. — **L:** Leaf cells, showing finger-like papillae. — **M:** Partial leaf lobules. — **N:** Leaf lobule with hyaline papilla. — **O:** Female bracts. — **P:** Female bracteoles. — Use the shorter 100  $\mu\text{m}$  scale for **A–F** and **O–P**, and the longer 100  $\mu\text{m}$  scale for **G–N**.

lar, acute, usually 3–4 cells wide at their base, sinus usually V-shaped or rarely U-shaped, margin entire. Rhizoids numerous at underleaf base. Asexual reproduction not seen. Androecia on short or elongate branches, terminal in position, inflated, spicate, male bracts in 4–10 pairs, with hypostatic lobules, lobe usually ocellate, ocelli 2–3; bracteole 1–2, restricted to the base of the spike; margin entire. Gynoecia on short or elongate branches, innovation single, leaf sequence pycnolejeuneoid. Female bracts in one pair, suberect, bract lobe oblong, 0.45–0.57 mm long and 0.20–0.22 mm wide, apex rounded or obtuse, margin usually finely denticulate, ocelli 2–5 per leaf lobe, adjacent or isolated in the middle portion of lobe; bract lobule usually lingulate, ca. 0.5 of lobe length, without wings. Bracteole oblong, 0.38–0.42 mm long and 0.17–0.20 mm wide, apex slightly bifid, lobe acute or obtuse, overlapping or not, margin entire. Perianth obovate, covered less than half by bracts and bracteole, 0.75–0.95 mm long and 0.35–0.46 mm wide, equally sharply 5-keeled, with double, 1–4 cells wide, irregularly, slightly denticulate wings; ventral keel extending to the middle of perianth length; perianth cells in the upper portion tuberculate with large papillae, in the lower portion slightly convex, without papilla; trigones lacking; apex rounded; beak short. Seta articulate, consists of 12 rows of outer cells and 4 rows of inner cells, outer wall of capsule covered with orange brown nodulose thickenings, inner wall except lower portion covered by fenestrate sheets of thickenings. Elaters 30–34 per capsule, marginal elaters 22, 5 or 6 on each valve, 183–250 × 10–13 µm, upper end attached to valve margin; inner elaters rudimentary, sometimes indistinct, 8–12, when well-developed, 3 in each valve, one occurring on the central portion of the valve surface and the other two lateral, 88–138 × 6–8 µm, both ends attached to valve inner surface. Spores not seen.

*Xylolejeunea grolleana* is an easily recognizable species on the basis of its small leaf lobe with two transverse rows of considerably enlarged and elongate cells and ocelli at the base, and high, fingerlike papillae on the dorsal leaf surface. Other diagnostic characters are rather a small size, ovate or falcate-ovate leaf lobe with entire to finely denticulate margin, smooth keel

of the lobule, and usually narrowly ovate underleaves. As in *X. aquarius*, we found that double-winged keels of the perianth occur also in *X. grolleana*, therefore it is regarded as one of the generic characters. Moreover, further observations on the wall structure and the arrangement and number of the elaters of the capsule are reported in the present study.

*Xylolejeunea grolleana* is similar to another African species, *X. muricella* in its small size, but the latter differs in having small, sphaerical papillae on the dorsal surface of the leaf lobe, conspicuously denticulate leaf margin, 3–4 lateral marginal cells of lobule, and orbicular underleaves.

DISTRIBUTION AND HABITAT: Known only from Madagascar (Fig. 6). *Xylolejeunea grolleana* occurs in very humid lowland rain forests at low elevation, 220–260 m. It grows on decaying wood, occasionally with *Arachniopsis diacantha* (Mont.) M. Howe, *Telaranea nematodes* (Gottsche ex Austin) M. Howe, and species of *Aneura*, *Riccardia*, *Callicostella*, *Leucoloma*, Geocalycaceae, Calymperaceae and Sematophyllaceae. It was also found on a newly fallen tree trunk at 15 m height in the canopy (Pócs 1999).

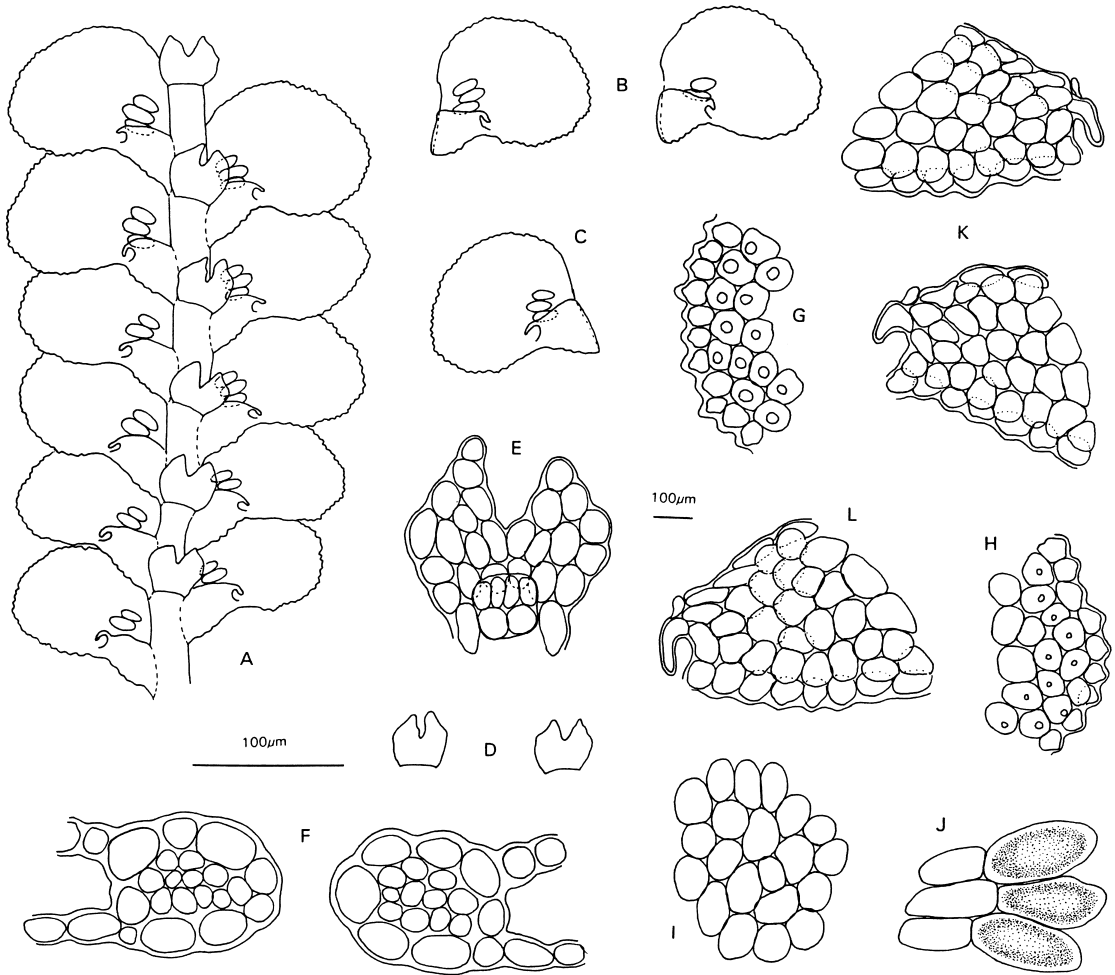
SPECIMEN EXAMINED: See the type collections cited above.

***Xylolejeunea muricella* X.-L. He & Grolle, sp. nova (Fig. 3)**

*Xylolejeunea grolleana* (Pócs) X.-L. He & Grolle *similis*, sed differt (1) quaeque cellula foliorum lobi papilla parva sphaericala obsita, (2) margine laterali foliorum lobuli 4 cellulis marginalibus elongatis exstructis, (3) dente primario foliorum lobuli longo decurvato, (4) carina foliorum lobuli minute denticulata et (5) amphigastriis plerumque orbiculatis.

TYPE: Seychelles. Mahe Island. Lower part of Moustache River. On shaded rocks, mixed with *Bazzania approximata* Onraedt, alt. 40 m, 27.XI.1973 A. H. Norrett 17902 (holotype BM!, isotypes JE!, NICH!).

Plants small, up to 1.0 cm long and 0.7–1.0 mm wide, whitish, yellowish green or brown in dry condition, loosely creeping, on shaded rock. Vegetative branching of *Lejeunea*-type, growth



**Fig. 3.** *Xylolejeunea muricella* X.-L. He & Grolle (from holotype, BM). — **A:** Habit. — **B** and **C:** Leaves. — **D** and **E:** Underleaves. — **F:** Cross-sections of stem. — **G** and **H:** Cells from apical leaf margin. — **I:** Cells from middle portion of leaf. — **J:** Cells from basal portion of leaf. — **K:** Leaf lobules with hyaline papillae. — Use the shorter 100  $\mu\text{m}$  scale for **A–D** and the longer 100  $\mu\text{m}$  scale for **E–K**.

habit irregularly pinnate, branches few; stem 100–125  $\mu\text{m}$  in diameter, stem cells quadrate to rectangular, on the ventral side 35–73  $\times$  25–35  $\mu\text{m}$ , in cross-section composed of 7–9 epidermal cells, surrounding 7–12 medullary cells, epidermal cells rectangular, thickened, 18–38  $\times$  8–23  $\mu\text{m}$ , medullary cells isodiametric, 11–30  $\times$  10–25  $\mu\text{m}$ ; ventral merophytes of stem 2 cells wide. Leaves imbricate, when moist widely spreading, insertion line almost longitudinal except for a short distance near dorsal base; leaf lobe convex, ovate or falcate-ovate, 0.32–0.50 mm long and 0.27–0.43 mm wide, margin usually con-

spicuously denticulate, dorsal margin broadly arched, ventral margin gently arched, apex rounded; leaf cells convex, marginal cells quadrate or rectangular, 13–23  $\times$  10–15  $\mu\text{m}$ , median cells isodiametric or slightly elongate, 16–35  $\times$  15–30  $\mu\text{m}$ , basal cells typically composed of 2 transverse rows of conspicuously enlarged and elongate cells, the upper row consists of 2–4 ocelli, 45–83  $\times$  23–35  $\mu\text{m}$ , adjacent, the lower one without ocelli, 40–65  $\times$  19–28  $\mu\text{m}$ , other normal basal cells rounded to elongate, 25–45  $\times$  20–25  $\mu\text{m}$ ; trigones lacking, intermediate thickenings lacking; oil-bodies not seen. Lobule ovoid or

triangular-ovoid, 0.14–0.17 mm long and 0.13–0.15 mm wide, slightly inflated, ca. 0.4 of lobe length; lateral margin slightly inrolled, composed of 3–4 elongate marginal cells, apical margin composed of 3 marginal cells; apex semicircular, the first tooth 1-celled, rather long, downwards curved, the second tooth 1-celled, distinct or nearly so, blunt, often with strongly thickened outer wall, the hyaline papilla in a 1-cell wide notch between the two teeth, proximal to the first tooth. Underleaves small, distant, usually orbicular, 0.14–0.16 mm long and wide, 1.4–1.6 of stem width, bifid, lobed to 0.4–0.5 of their length, lobe triangular, obtuse to acute, sinus narrow to V-shaped, margin entire. Rhizoids numerous at underleaf base. Asexual reproduction not seen. Androecia not seen. Gynoecia on the top of main shoots, innovation single, with pycnolejeuneoid leaf sequence. Sporophyte not seen.

The almost longitudinal leaf insertion line, the imbricate leaf lobe with denticulate margin and unique leaf base features, the lobule morphology, the remote underleaves, and the pycnolejeuneoid innovation indicate the generic position of this species. *Xylolejeunea muricella* is characterized by its rather small size, conspicuously denticulate leaf margin, dorsal leaf lobe with small, sphaerical papillae, two transverse rows of considerably enlarged and elongate cells, with 2–4 ocelli in the upper row at the leaf base, a long, downward-curved lobule tooth, and small, distant underleaves. The differences between *Xylolejeunea muricella* and *X. grolleana* are discussed under the latter species.

The available material of *Xylolejeunea muricella* is unfortunately insufficient. Some characters of the gametophyte, including those of the perianth, could not be studied and we have not seen the sporophyte. Therefore, more collections of this species are needed in order to confirm the species status.

**DISTRIBUTION AND HABITAT:** Known only from the Seychelles (Fig. 6). *Xylolejeunea muricella* has been found on shaded rocks in lowland rainforests.

**SPECIMEN EXAMINED:** See the type collection cited above.

***Xylolejeunea crenata* (Nees & Mont.) X.-L. He & Grolle, *comb. nova* (Figs. 4–5)**

*Lejeunea crenata* Nees & Mont. in Mont., Ann. Sci. Nat. Bot., ser. 2, 9: 48. 1838. — *Crossotolejeunea crenata* (Nees & Mont.) Lacout., Rev. Bryol. 35: 109. 1908. — *Trachylejeunea crenata* (Nees & Mont.) R.M. Schust., J. Hattori Bot. Lab. 72: 253. 1992. — Type: French Guiana. “Cayenne, leg. Bory, Nees no.” 155 (lectotype, here designated, PC-Mont.), isoelectotypes G-18406!, S!, W ex Herb. Lindenb. 6305!)

*Lejeunea weigelii* Lindenb. in Gottsche, Lindenb. & Nees, Syn. Hep.: 341. 1845, *syn. nov.* — Type: Surinam. *Weigelt* (lectotype, here designated, W ex Herb. Lindenb. 6304!, isoelectotypes G 18412!, BM ex Herb. Hampe!)

*Lejeunea tenuistipula* Lindenb. & Gottsche in Gottsche, Lindenb. & Nees, Syn. Hep.: 757. 1847, *syn. nov.* — *Crossotolejeunea tenuistipula* (Lindenb. & Gottsche) Steph., Spec. Hep. 5: 234. 1913. — *Trachylejeunea tenuistipula* (Lindenb. & Gottsche) Steph., Spec. Hep. 5: 311. 1913. — Type: Mexico. Estado Oataca, Tepinapa, 600 m, VI. 1842 *Liebman 315/b* (lectotype, here designated, C!), isoelectotypes G 10103!, W ex Herb. Lindenb. 6379!)

*Lejeunea lignicola* Ångstr., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 33(7): 85. “1876” 1877, *syn. nov.* — *Cyclelejeunea lignicola* (Ångstr.) Steph., Spec. Hep. 5: 189. 1913. — *Crossotolejeunea lignicola* (Ångstr.) Steph., Spec. Hep. 5: 231. 1913. — Type: Brazil. Caldas, Regnell (holotype S!, isotype G 18427!)

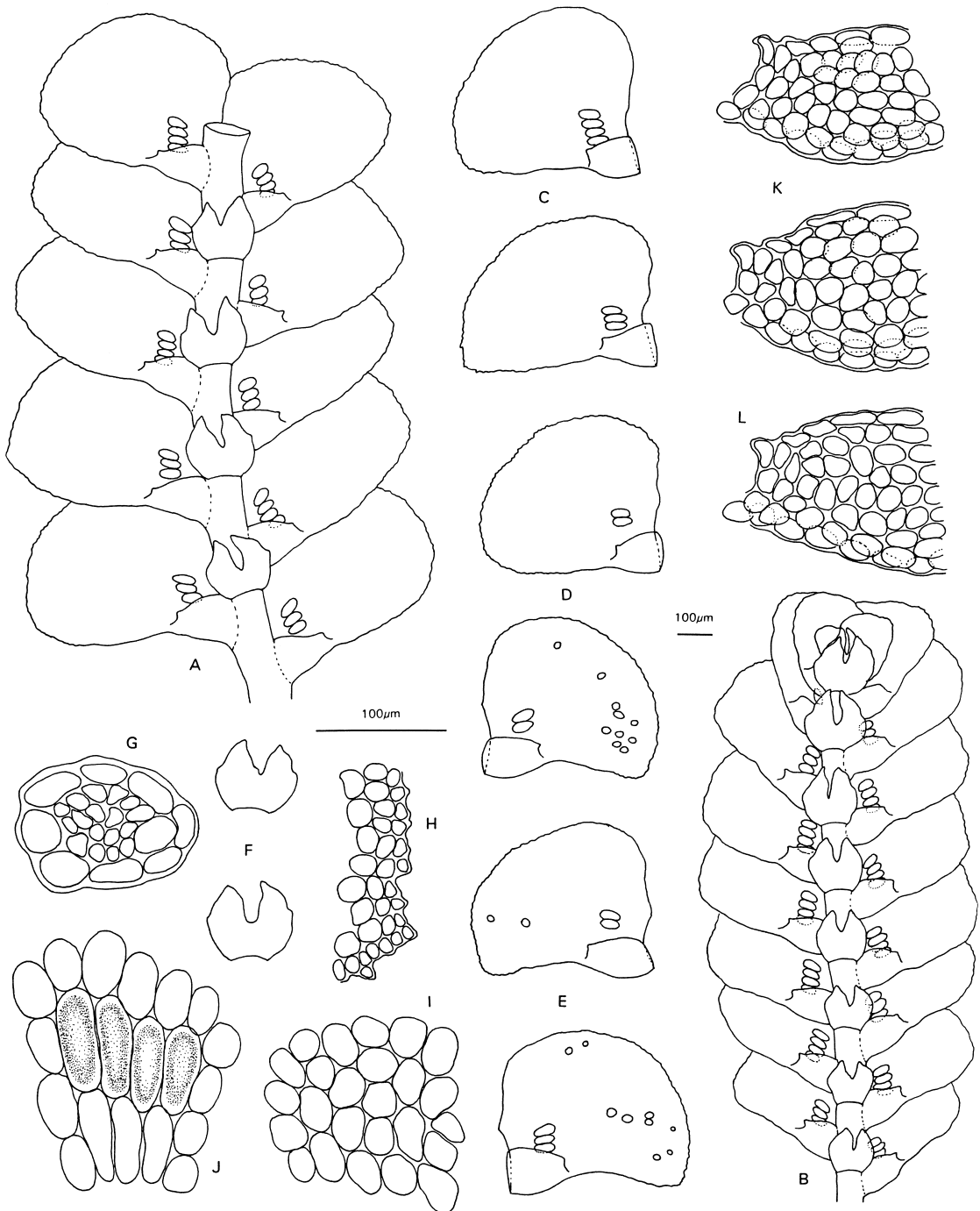
*Lejeunea pandurantha* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 184. 1884, *syn. nov.* — *Trachylejeunea pandurantha* (Spruce) Steph., Spec. Hep. 5: 304. 1913. — Type: Brazil. “In fl. Negro, Uaupés, etc. sylvis, supra truncos putridos, frequens”, *Spruce* (lectotype, here designated, MANCH!, syntypes B!, G 009628!, G 18030!, G 18031!, JE!, M!, W!, YU!)

*Lejeunea pellucidissima* Spruce, Trans. Proc. Bot. Soc. Edinburgh 15: 184. 1884, *syn. nov.* — *Trachylejeunea pellucidissima* (Spruce) Steph., Spec., Hep. 5: 309. 1913. — Type: Venezuela. Terr. Amazonas, San Carlos del Rio Negro, *Spruce* (lectotype, here designated, MANCH (L-398)!, syntypes BM ex K!, G 18043!, G 18044!, G 18045!, MANCH!, NY!, YU!)

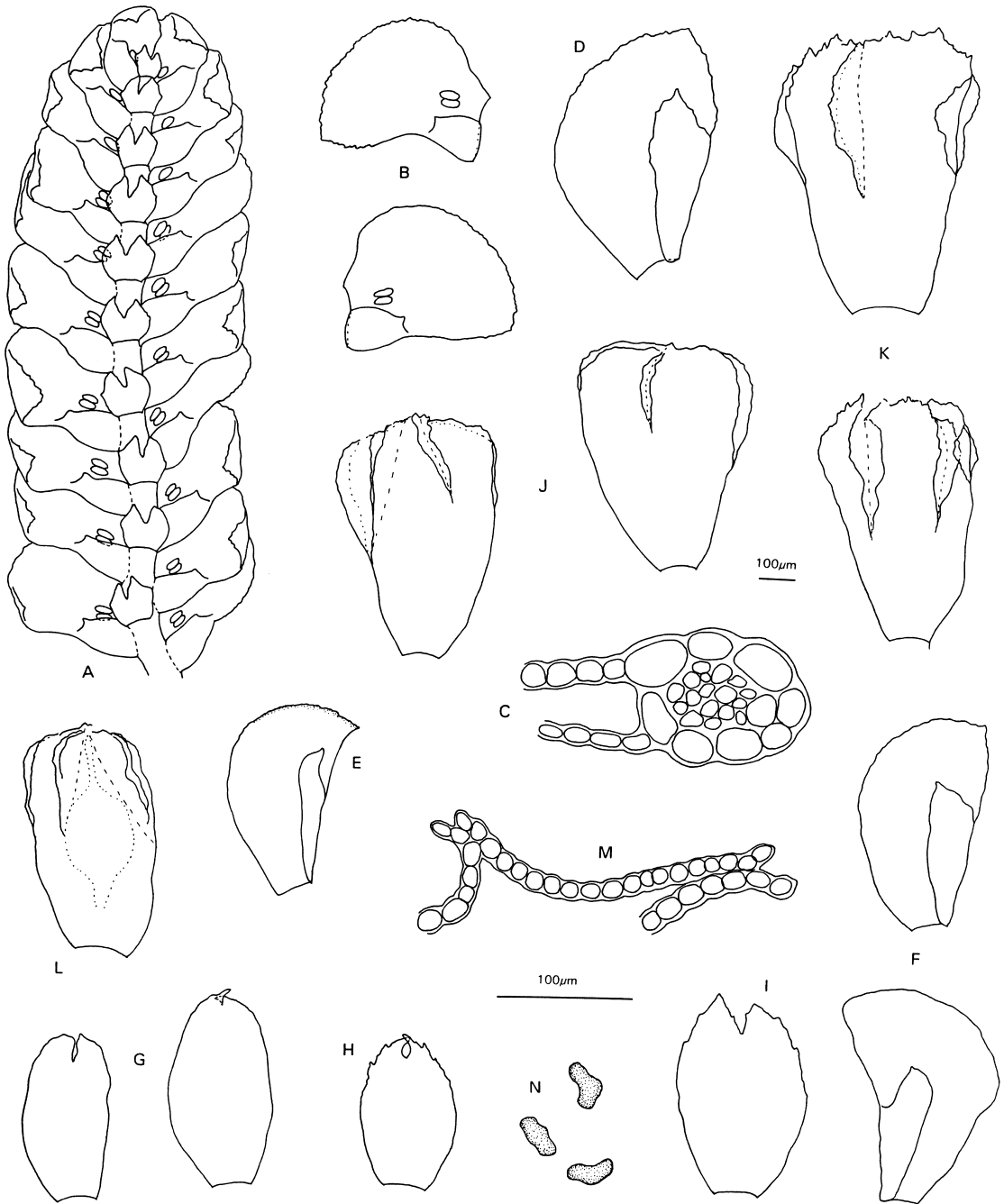
*Trachylejeunea spruceana* Steph., Hedwigia 35: 138. 1896, *syn. nov.* — Type: Guadeloupe. *L’Herminier* (isotype JE!)

*Prionolejeunea erosodentata* Steph., Spec. Hep. 6: 388. 1923, *syn. nov.* — Type: Surinam. Paramaribo, *Kegel* (holotype G!)

*Trachylejeunea buchtienii* Herzog, Beih. Bot. Centralbl. 61 B: 577. 1942, *syn. nov.* — Type: Bolivia. “San Carlos bei Mapiiri, 850 m, leg. O. Buchtien, XI. 15, no. 286 ex p.” (Per typographical error cited as no. 256 ex p. in the protologue) (holotype JE!, isotype B!)



**Fig. 4.** *Xylolejeunea crenata* (Nees & Mont.) X.-L. He & Grolle (**A, B** from *Bekker 1192/b*, U 545120B, **C, G–J** from *Bekker 1083b*, U 545070B, **D, E** from *Cornelissen & ter Steege C165*, U 509177B, **F** from *Bekker 1209*, U 543076B, **K, L** from *Cremers 7031*, U 543069B). — **A**: Habit. — **B**: Branch. — **C–E**: Leaves. — **F**: Underleaves. — **G**: Cross-section of stem. — **H**: Cells from apical leaf margin. — **I**: Cells from middle portion of leaf. — **J**: Cells from basal portion of leaf, with 4 ocelli. — **K** and **L**: Leaf lobules. — Use the shorter 100  $\mu\text{m}$  scale for **A–F**, and the longer 100  $\mu\text{m}$  scale for **G–L**.



**Fig. 5.** *Xylolejeunea crenata* (Nees & Mont.) X.-L. He & Grolle (**A–C** from *Cremers* 7031, U 543069B, **D, H, I** and **K** from *Bekker* 1768b, U 545111B, **E, G, J** and **L–N** from *Vital et al.* 3782, U 500551B, **F** from *Bekker* 1775, U 543064B). — **A**: Branch. — **B**: Leaves. — **C**: Cross-section of stem. — **D–F**: Female bracts. — **G–I**: Female bracteoles. — **J–L**: Perianths. — **M**: Partial cross-section of perianth, showing double wings. — **N**: Spores. — Use the shorter 100  $\mu\text{m}$  scale for **A, B,** and **D–L,** and the longer 100  $\mu\text{m}$  scale for **C, M,** and **N.**

Autoicous. Plants small to relatively robust, up to 2.0 cm long and 1.3 mm wide, whitish or yellowish-green, or brown in dry condition, forming appressed mats or mixed with other bryophytes, on fallen decaying tree trunks. Vegetative branching of *Lejeunea*-type, growth habit irregularly pinnate, branches short to long; stem 88–188  $\mu\text{m}$  in diameter, stem cells rectangular or quadrate, on the ventral side 40–65  $\times$  33–40  $\mu\text{m}$ , in cross-section composed of 7–9 epidermal cells surrounding 10–20 medullary cells, epidermal cells rectangular, 28–43  $\times$  18–30  $\mu\text{m}$ , cell walls thickened, medullary cells isodiametric or rectangular, 10–38  $\times$  8–25  $\mu\text{m}$ ; ventral merophytes of stem 2 cells wide. Leaves closely imbricate, when moist widely spreading, insertion line almost longitudinal except for a short distance near dorsal leaf base; leaf lobe convex, ovate or falcate-ovate, 0.40–0.70 mm long and 0.37–0.55 mm wide, margin often entire or finely denticulate, dorsal margin broadly arched, ventral margin nearly straight or slightly arched, apex rounded, obtuse or acute; leaf cells convex, marginal cells radially rectangular or quadrate, becoming finely denticulate, submarginal cells usually larger than marginal cells, often isodiametric, 16–28  $\times$  15–25  $\mu\text{m}$ ; median cells isodiametric or nearly so, sometimes more or less 6-angled, 28–35  $\times$  22–28  $\mu\text{m}$ , ocelli usually lacking, rarely scattered in the distal portion of leaf lobe; basal cells typically composed of 2 transverse rows of conspicuously enlarged and elongate cells, the upper row consists of ocelli 2–4(–5) in number, 73–93  $\times$  30–38  $\mu\text{m}$ , adjacent, the lower row usually without ocelli, 50–65  $\times$  15–28  $\mu\text{m}$ , other normal basal cells rounded to elongate, 30–45  $\times$  30–33  $\mu\text{m}$ ; trigones lacking or rarely present, intermediate thickenings lacking; oil-bodies not seen. Lobule ovoid, 0.16–0.20 mm long and 0.11–0.15 mm wide, strongly inflated, 0.2–0.3 of lobe length; lateral margin usually strongly inrolled, composed of 4(–6) elongate marginal cells, apical margin composed of 3 marginal cells, keel arched, more or less roughened from projecting cells; apex semi-circular, the first tooth slightly curved outwards, 1-celled, the second tooth blunt, distinct or near-

ly so, often with strongly thickened outer wall; hyaline papilla positioned in a 1-cell wide notch between teeth, proximal to first tooth. Underleaves distant, occasionally contiguous on slender branches, orbicular or broadly orbicular, 0.21–0.24 mm long and 0.20–0.27 mm wide, ca. 2.0  $\times$  stem width, bifid, lobed to 0.5(–0.6) of their length, lobe triangular, acute or obtuse, sinus narrow, margin entire, often on both sides with a 1-celled, more or less distinct tooth on the outer margin; insertion line to stem almost transverse. Rhizoids numerous at underleaf base. Asexual reproduction by caducous leaves. Androecia on short specialized branches, terminal in position, inflated, spicate, male bracts in 2–27 pairs, ocelli absent or occasionally present on bract lobe; male bracteole 1, restricted to the base of the spike; margin entire. Gynoecia on short branches, innovation single or lacking, leaf sequence pycnolejenuoid when innovations present. Female bracts in one pair, suberect, bract lobe obovate, 0.60–0.85 mm long and 0.35–0.45 mm wide, apex rounded, obtuse or subacute, margin finely denticulate, ocelli usually absent, sometimes present in the middle of lobe, adjacent or sparsely scattered; bract lobule lingulate, 0.47–0.60 mm long and 0.14–0.16 mm wide, apex obtuse or acute, margin finely serrulate or denticulate in upper part, without wing; bracteole oblong, 0.50–0.80 mm long and 0.25–0.36 mm wide, bifid, apex 2-lobed to 0.1–0.2 of bracteole length, lobe apex acute or obtuse, overlapping or not, sinus narrow; margin denticulate. Perianth obovate, half to almost entirely covered by bracts and bracteole, 0.74–1.0 mm long and 0.48–0.80 mm wide, inflated, equally sharply 5-keeled, with double, 1–4 cells wide, irregularly denticulate wings; ventral keel usually extending to the middle of perianth length; perianth cells convex, quadrate to rectangular, trigones lacking or rarely developed, intermediate thickenings rarely present, ocelli absent or occasionally scattered in upper part of perianth; apex truncate; beak short. Seta articulate, consists of 12 rows of outer cells and 4 rows of inner cells, cells of outer wall of capsule thickened, often with nodulose thickenings, in-

ner wall except the lower part covered by fenestrate sheets of thickenings. Elaters 22–34 per capsule, marginal elaters 22, 5 or 6 on each valve,  $175\text{--}250 \times 10\text{--}18 \mu\text{m}$ , upper end attached to valve margin, inner elaters rudimentary, sometimes indistinct, when well-developed, 3 in each valve, one occurring on the central portion of the valve surface and the other two are lateral,  $120\text{--}143 \times 8\text{--}10 \mu\text{m}$ , both ends attached to the inner valve surface. Spores brown in dry condition, irregularly rectangular,  $20\text{--}30 \times 10\text{--}18 \mu\text{m}$ , spore surface granulate.

*Trachylejeunea crenata* and *T. pandurantha* have often been reported from the Neotropics, but their relationships were rarely discussed, maybe because the boundary between the two taxa seemed rather clear. Generally *T. pandurantha* has been separated from *T. crenata* by lack of innovations, a rounded leaf apex, and perianth without a double keel. However, after studying a numerous specimens we found out that *T. crenata* is a very variable species. Its gynoecia can be without innovation or with a pycnolejeuneoid innovation, and the apex of leaf lobe often varies from acute to rounded in the same shoot. In all specimens we have studied the perianth keels are double, 1–4 cells wide. But it is not easy to see the double keels, especially when they are just 1–2 cells wide. This may explain why *T. pandurantha* has been differently defined. Furthermore, the other morphological features show no difference between the two taxa and therefore we treat *T. pandurantha* as a synonym of *Xylolejeunea crenata*.

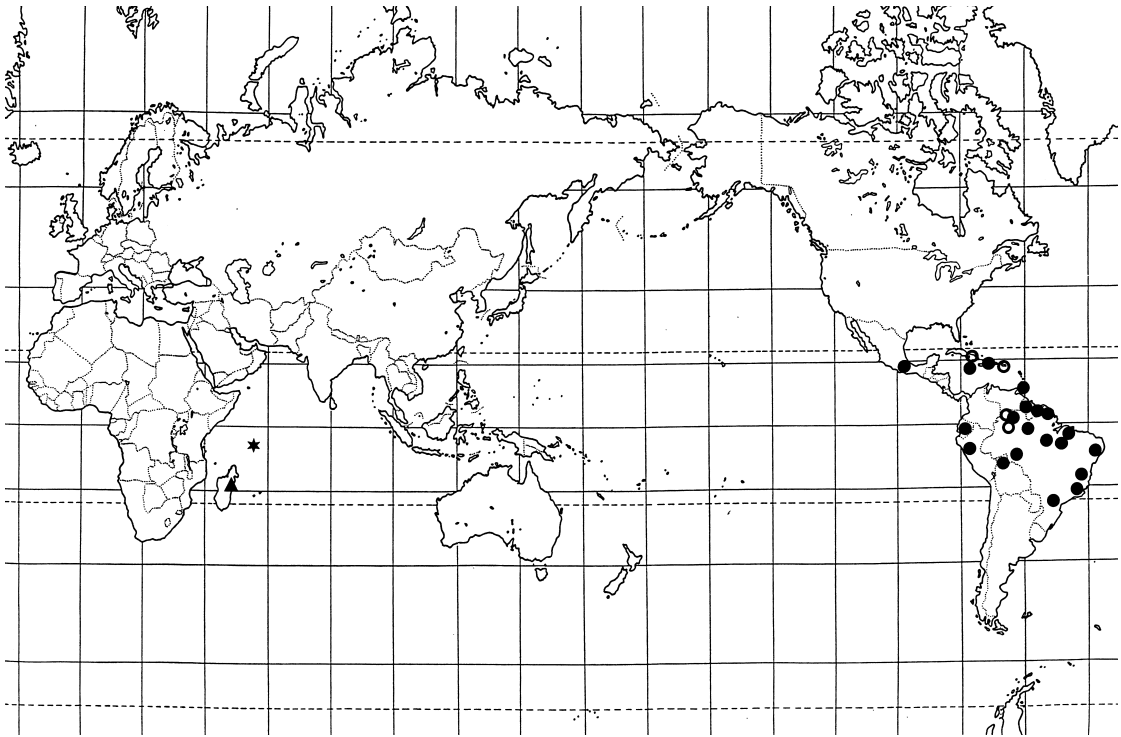
*Xylolejeunea crenata* also varies in size, leaf margin and leaf cells. The plants are small to relatively robust and the leaf margin ranges from entire to finely denticulate. Trigones in leaf lobes are usually lacking but occasionally developed. Ocelli are typically restricted to the upper one of two rows of remarkably enlarged and elongate basal cells, but occasionally ocelli exist also scattered in the distal portion of leaf lobe. In this case a single ocellus, as well, may occur in the lower one of the two peculiar cell rows at the leaf base.

**DISTRIBUTION AND HABITAT:** Mexico, Barbados, Dominica, Guadeloupe, Jamaica, Martinique, Trinidad, Bolivia, Ecuador, Peru, Venezuela, Brazil, French Guiana, Guyana, Suriname

(Fig. 6). *Xylolejeunea crenata* is a widely distributed species of the Neotropics. It occurs in different habitats, but typically grows on rotten logs in humid, virgin lowland rainforests. It grows also in more open savannah forests.

**SPECIMENS EXAMINED:** — Am 2: **Mexico.** See type material of *Lejeunea tenuistipula*. — Am 3: **Barbados.** (JE-H1752). **Dominican Republic.** On decaying tree, 1895 *Elliott 973* (JE). **Guadeloupe.** *L'Herminier* (JE). **Jamaica.** *Wilson 714* (JE). **Martinique.** Bois entre le Lorrain et les Deux-Choux, 690 m, sur les arbres et le bois pourissant, 1900 *Duss 247/b* (JE). **Trinidad & Tobago.** Aripo Savanna, 1920 *Britton et al. 337* (JE), Mt. Tocuche, auf morschem Holz, 1920 *Britton et al. 1480/b* (JE); long stretch via Valencia, on dead wood, 1928 *Broadway 6796/b* (JE). — Am 4: **Bolivia.** See type material of *Trachylejeunea buchtienii*; Beni, ca. 10–15 km NW of Guayaramerín along the road to Cachuella Esperanza, roadside and adjacent forest, on rotted log, 1978 *Reese 13106* (JE), Vicinity of Guayaramerín, dense, mature forest on sandy soil, gentle slope to a swampy stream bottom, on rotted log, 1978 *Reese 12740* (JE). **Ecuador.** “Andes Quitenses, San Gabriel, in cortice putrescente”, *Spruce* (JE-H1591). **Peru.** Dept. San Martín, Prov. Lamas, 200m, 1984 *Bryotrop (Frahm et al.) 1778* (JE), 2005 (JE), 2007 (JE). **Venezuela.** Amazonas, Dpto. Rio Negro, Neblina base camp, along Rio Mawarimuma, ca. 140 m,  $00^{\circ}50'N$ ,  $66^{\circ}10'W$ , along stream in the south west side of island, white sand banks, 1984 *Sastre-De Jesús 274/b* (JE), *Sastre 310* (JE). — Am 5: **Brazil.** Amazonas State, Manaus, Reserva Campina, along the road Manaus-Caracará, km 60, on fallen tree trunk, in Amazonian forest, 1974 *Vital, Griffin & Yano DV-3782* (U 500551B); Reserva Egler, km 65, Estrada Manaus-Itacoatiara, on downed moist log, in humid terra firme forest, 1974 *Griffin, Vital & Yano 486* (JE), along the Rio Negro between Manaus and São Gabriel, along the Rio Marié, at Manauná, primary forest with large rocks over white sand,  $00^{\circ}40'S$ ,  $66^{\circ}45'W$ , on wet vertical rocks, 1979 *Buck 2416* (U 482633B), Rondônia,  $11^{\circ}S$ ,  $64^{\circ}W$ , ridges of Serra dos Pacaás, 400 m, on rotten log, 1978 *Reese 13336* (JE); Estado Pará, Município de Ourem, in swampy forest, on tree trunk, 1974 *Vital 2962* (JE), Belém, Reserva do Mocambo, mata de terra firme, lugar muito úmido, sobre tronco caído, 1983 *Lisboa & Bahia 592* (U 540805B); Proc. Município de Turiacu, Maranhão State, growing on base of a rotten trunk, in a humid virgin forest, ca. 8 km NW of Maranhãozinho village, 1974 *Vital 2957* (U 493707B), Estado Maranhão, Município de Turiacu, in humid virgin forest, on base of rotten trunk, 1974 *Vital 2957* (JE); Estado Pernambuco, Rio Formoso, *Pôrto 198* (JE), Reserva Biologica de Salinho, on decayed wood, 1985 *Pôrto 554* (JE); prov. Minas Geraes, Caldas, *Regnell* (JE-H1680); Rio de Janeiro, *Regnell 58* (JE); Prov. São Paulo, Santos auf morschem Holz, 1875 *Mosén 85* (JE), Prov. São Paulo, 1000 m, ad arbores in silvaticis prope Barra Mansa in districtu





**Fig. 6.** Distribution of *Xylolejeunea aquarius* (Spruce) X.-L. He & Grolle (○), *X. grolleana* (Pócs) X.-L. He & Grolle (▲), *X. muricella* X.-L. He & Grolle (\*), and *X. crenata* (Nees & Mont.) X.-L. He & Grolle (●).

urbis Itapeirica, 1901 *Schiffner 1828* (JE), 20 m flumen “Rio Branco” prope Santos in silva ad truncos putridos, 1901 *Schiffner 1962* (JE), São Paulo State, Município de Canaëia, at northern part of the Ilha do Cardoso, on rotten fallen log, in a restinga vegetation, 1977 *Vital 6842* (JE), Ilha do Cardoso, on decaying log, in forest at the western slope of the Cardoso mountain, 1983 *Vital 11.315* (JE), Estado São Paulo, Bertioga, ca. 1.5 km from the sea, on rotten trunk in a humid forest, 1974 *Vital 4735* (JE). **French Guiana.** ENE de Saül, camp no 2, 8.5 km Nord de Saut Mais, epiphyte sur arbre en sous bois, 1980 *Cremers 6246* (JE, U 545119B), NW de St Georges de l’Cyapock, epiphyte en forêt en pied de la montagne des Trois Pitons, 1981 *Cremers 7031* (JE, U 543069B); Kourou, Mt. Des Singes, mixed rainforest along “sentier botanique”, on rotting log over rivulet, 1986 *Gradstein 6262* (U 494202B); Piste de Risquetout a 12 km de la route du Tour de l’Ile, epiphyte sur arbre en sous bois, 1979 *Cremers 6026* (JE, U 543070B); Route de Cayenne à St Laurent, PK 185, 10 km après l’embranchement de Mana, au Sud près d’un saut, sur arbre, 1979 *Cremers 5977* (JE), 5978 (JE), 5980 (JE, U 543081B). **Guyana.** Mabura Hill, 180 km SSE of Georgetown, alt. 0–50 m, 5°20’N and 58°40’W, near Yaya Creek in mixed lowland rain forest, on decaying log, 1985 *Cornelissen & ter Steege C145* (U 509156B), *C146* (U 509162B), in dry, evergreen forest on white sand, dominated by *Eperua*

spp., on decaying log near a creek, 1985 *Cornelissen & ter Steege C155* (U 509178B); upper Mazaruni District, Jawalla, at confluence of Kukui river and Mazaruni river, ca. 25 m tall virgin forest, on dead wood, alt. 500 m, 5°40’N and 60°29’W, 1985 *Gradstein 4840* (U 456439B), east bank of Waruma river, 4 km S of confluence with Kako river, ca. 25 m tall, virgin riverine forest, on rotten log, 1985 *Gradstein 5016* (U 456256B), *5021* (JE, U 456505B); right bank of the Mazaruni river, 1.25 miles below its junction with the Kamarang river, along trail 0–1.25 miles E from the river, 60°34’W, 5°52’N, alt. 1 550–2 100 ft, in deep secondary forest, on fallen logs by trail, 1985 *Robinson 85-0071* (U 463896B). **Suriname.** Tibiti savanne, Savanna forest on third line, on dead tree, 1949 *Lanjouw & Lindeman 1945B* (U 514763B); Tosso-mountain between Tosso-creek and Saracreek, virgin forest, on decaying log, 1950 *J. & P. A. Florschütz 314A* (U 514765B); area of Kabalebo Dam project, distr. Nickerie, near camp road km 23, 5N 57W qu. SW, line on westborder of river Kabalebo, slope forest with wallaba, on bark of cut down tree of *Eperua falcata*, open space, alt. 0–150 m, 1981 *Bekker 1334* (JE, U 543059B), line NW from road km 39.5, p. 5N 58W qu. SE, alt. 0–50 m, savannah forest, on a rotting log, open space, 1981 *Bekker 1209* (U 543076B), *1210* (U 545998B), *1211* (U 545067B), *1233b* (U 545102B), *1234b* (U 545103B), *1240* (U 545101B), *1241* (U 545100B), *1280a* (U

543072B), 1289 (U 545087B), 1299b (U 545088B), 1302 (U 543077B), 1303 (U 543074B), 1304a (U 543075B), 1306a (U 545089B), line W from road km 34, p. 5N 58W qu. SE, alt. 0–100 m, rainforest, on a rotting log, 1981 *Bekker 1082* (JE, U 545072B), 1083b (U 545070B), 1087 (U 545073B), 1088 (U 545071B), 1089 (U 545096B), 1096 (U 545077B), 1110 (U 543062B), 1114 (U 543063B), 1115 (U 545076B), 1189b (U 545079B), 1190 (U 545081B), 1192b (U 545120B), 1194 (U 545124B), 1200 (U 543071B), 1202a (U 545112B), 1204 (U 543078B), 5219A (U 545110B), near camp road km 212, 4N 58W qu SE, alt. 0–50 m, rainforest, on a rotting log, 1981 *Bekker 1746* (U 545091B), 1775 (U 543064), 1768b (U 543066B), road km 96.2, 5N 58W qu SE, alt. 0–50 m, on a rotting log near a creek in xeromorphic high forest of *Dimorphandra conjugata*, 1981 *Bekker 1511a* (U 545099B), 1525b (U 545092B), 1539 (U 545082B), 1540c (U 545107B), 1519 (U 545078B), line E from road km 80, p. 5N 58W qu SE, on a rotting log, in rainforest with *Eperua falcata*, 1981 *Bekker 1368* (U 545090B), 1383a (U 545104B), 1390 (U 545098B), 1406 (U 545065B), 1418b (U 545116B), 1420 (U 545114B), 1423a (U 545083B), 1545 (U 545094B), 1546 (U 545093B).

## Distribution

Two species of *Xylolejeunea*, *X. aquarius* and *X. crenata* have rather wide geographic ranges in tropical America, while the other two species, *X. grolleana* and *X. muricella*, are only recorded from Madagascar and the Seychelles, respectively (Fig. 6). A similar pattern of disjunction can be found also in other bryophyte groups, for example, in *Adelothecium* Mitt., *Symbiezidium* Trevis. and *Bryopteris* (Nees) Lindenb. These taxa have been referred to as “peri-Afroamerican” element, which comprises tropical American plants occurring also in the Indian Ocean islands but which are absent in continental Africa (Stearn 1971). This peculiar disjunction type in bryophytes was discussed by Gradstein *et al.* (1983), Gradstein and van Beek (1985), Reese (1985), and Pócs (1999). It is postulated that at least some of these genera evolved before the break-up of the Afro-American part of Gondwanaland. At the time of the break-up, the species were able to survive in the coastal areas, where the climate remained relatively stable, but they went extinct in the interior of the land mass, where harsh climate changes took place.

As stated by Pócs (1999), *Xylolejeunea* (as subg. *Hygrolejeuneopsis* of *Trachylejeunea*) is

probably an ancient group of Lejeuneaceae. Since the break-up the land masses, further speciation took place and resulted in morphological diversity in the genus. On the other hand, the possibility of the disjunction by more recent long-distance dispersal seems unlikely, because the species of *Xylolejeunea* grow in the understorey of dense lowland rain forests, a habitat that does not favour long-distance dispersal. Although asexual reproduction by caducous leaves occurs in *Xylolejeunea*, these vegetative diaspores disperse more locally.

## Generic relationships

*Xylolejeunea* is most easily separated from related genera by the following features: (1) an almost longitudinal insertion line of leaf lobe; (2) an ovate to falcate-ovate leaf lobe, with an entire to finely denticulate margin; (3) two transverse rows of conspicuously enlarged and elongate cells at the leaf base, of which the upper ones are adjacently arranged ocelli; (4) a proximal position of hyaline papilla in relation to the slightly curved first lobule tooth; (5) a blunt, distinct or nearly distinct second lobule tooth, often with a strongly thickened outer wall; (6) distant underleaves with an almost transverse insertion to the stem; (7) gynoecia with 1 short, pycnolejeuneoid innovation or without innovation; and (8) a sharply 5-keeled perianth with double, 1–4 cells wide, irregularly denticulate wings. Of these characters, (3) and (8) will serve to separate the genus immediately from *Cheilolejeunea*, which is probably closely allied to the species of *Trachylejeunea* in strict sense (X.-L. He & R. Grolle unpubl.).

The roughness of the leaf cells, presence of ocelli at the base of leaf lobe, sharply 5-keeled perianth, and pycnolejeuneoid innovation suggest that *Xylolejeunea* is close to *Pycnolejeunea*. However, species of *Pycnolejeunea* have a J-shaped insertion of leaf lobe to the stem, typically an ovate leaf lobe, an entire margin of leaf lobe, imbricate underleaves, not remarkably enlarged or elongate basal cells, and no double perianth wings. Ecologically, species of *Xylolejeunea* usually occur on decaying logs in perhumid floors of virgin lowland rainforests. Thus,

the habitats are completely different from those of *Pycnolejeunea*, the species of which are sun epiphytes, growing on canopies of tall emergent trees of lowland or lower montane rainforests, or in secondary vegetation and plantations (He 1999).

The genus *Cyclolejeunea* may resemble *Xylolejeunea* by the denticulate margin of leaf lobe, convex leaf cells, basal ocelli and pycnolejeuneoid innovation. However, the former differs by producing disciform gemmae on the margin of leaf lobe, having denticulate underleaves, a flattened perianth with lateral keels expanded into low auricles, and a typically epiphyllous growth form.

In the Lejeuneoideae, species growing on rotten wood in the understorey of humid rainforests are also present in *Crossotolejeunea*, *Prionolejeunea* and *Echinocolea*. All of those genera consist of rather small and pellucid plants, resembling *Xylolejeunea*. However, they differ from *Xylolejeunea* in the usually crenulate margin of leaf lobe, lack of ocelli, and a 1-toothed leaf lobule. Further differentiating characters of *Crossotolejeunea* are the plane leaf cells and 1–2 lejeuneoid innovations. *Prionolejeunea* has a flattened perianth with 2 sharply dentate-laciniate auricles. *Echinocolea* has mammillose leaf cells and a lejeuneoid innovation.

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