

## **A systematic revision of the genus *Lejeunea* Lib. (Marchantiophyta: Lejeuneaceae) in Malaysia**

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**Abstract** – A revision of the genus *Lejeunea* in Malaysia based on examination of about six hundred fresh collections and about four hundred herbarium specimens leads to the recognition of 30 species and 2 varieties. All species are keyed and illustrated, their morphological characters are described and discussed in detail, and distribution and habitat in Malaysia and world distribution are given. In addition, notes are presented on little-used or neglected morphological characters including superior central cells, oil bodies and vegetative propagules. Two species, *Taxilejeunea cuculliflora* Steph. [= *L. umbilicata* (Nees) Nees] and *Eulejeunea infestans* Steph. (= *L. papilionacea* Steph.) are new synonyms. Eight species are reported for the first time from Peninsular Malaysia [*L. alata* Gottsche, *L. cocoes* Mitt., *L. dimorpha* Kodama, *L. fleischeri* (Steph.) Mizut., *L. micholitzii* Mizut., *L. papilionacea* Steph., *L. tuberculosa* Steph., and *L. umbilicata* (Nees) Nees] and one species from East Malaysia, *i.e.* *L. compacta* (Steph.) Steph.

**distribution / *Lejeunea* / Lejeuneaceae / liverworts / Malaysia / morphology / taxonomy**

### **INTRODUCTION**

The genus *Lejeunea* with about three hundred currently accepted species is one of the largest genera of the family Lejeuneaceae (Marchantiophyta). The genus is a member of the tribe Lejeuneae (Schuster, 2001; Gradstein *et al.*, 2003) and represents a separate lineage (“clade D2”) in the molecular phylogenetic tree of the family (Wilson *et al.*, 2007). A modern, worldwide monograph or a revision for the Malesian region, or parts of it, does not exist and our current knowledge of the Malesian *Lejeunea* species is largely based on outdated treatments by Stephani (1915) and Eifrig (1937), on regional floristic studies (e.g., Mizutani & Piippo, 1986; Mizutani, 1975, 1977, 1986, 1987; Pócs *et al.*, 1994, 1995) and on checklists (Piippo *et al.*, 2002; Gradstein *et al.*, 2005; Lai *et al.*, 2008; Söderström *et al.*, 2010; Chuah-Petiot, 2011). Mizutani (1963, 1966, 1970, 1978) provided useful notes and preliminary keys to selected species of Malaysia, and Zhu & So (2001) in their comprehensive study of the epiphyllous liverworts of China described several species occurring in Malaysia. The latter authors also listed sixteen diagnostic features for the genus. A list of recent papers recording Asiatic species of *Lejeunea* is given in Table 1.

The genus *Lejeunea* as currently circumscribed is mainly characterized by: 1) hyaline papilla at the proximal side of the apical tooth of the lobule; 2) ocelli

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Table 1. *Lejeunea* species recorded from eastern and southeastern Asia

Country	Number of species recorded	Reference
China	42	So & Zhu (1998), Zhu & So (1999)
Java (Indonesia)	27	Söderström <i>et al.</i> (2010)
Taiwan	25	Wang <i>et al.</i> (2011)
Japan	23	Yamada & Iwatsuki (2006)
India	21	Singh (2001)
Thailand	10	Lai <i>et al.</i> (2008)
Hong Kong	10	So & Zhu (1996), Zhang & Corlett (2003)
Bhutan	9	Long & Grolle (1990)
Korea	9	Hong (1997), Yamada & Choe (1997)
Singapore	3	Püppo <i>et al.</i> (2002)
Peninsular Malaysia	11	Inoue (1967), Kitagawa (1971), Tixier (1980), Schäfer-Verwimp (2001), Lee <i>et al.</i> (2011b), Chuah-Petiot (2011)
East Malaysia	26	Eifrig (1937), Mizutani (1963, 1966, 1970, 1978), Lee <i>et al.</i> (2011a), Chuah-Petiot (2011)

usually absent; 3) lobules occasionally reduced and with one tooth (rarely 2); 4) small, granular or homogeneous oil bodies; 5) underleaves usually bifid (rarely entire), underleaf lobes upright; 6) epidermal cells thin-walled and larger than the medullary cells; 7) branches of the *Lejeunea*-type; and 8) gynoecea with lejeuneoid innovations. The circumscription of the genus has been considerably expanded in recent years due to the inclusion in *Lejeunea* of several groups which were previously treated as separate genera, e.g., *Hygrolejeunea* (Spruce) Schiffn. and *Taxilejeunea* (Spruce) Schiffn. (Mizutani, 1961, 1970, etc.), *Papillolejeunea* Pócs (Schuster, 1998), *Crossotolejeunea* (Spruce) Schiffn. and *Dactylolejeunea* R.M. Schust. (Reiner-Drehwald & Goda, 2000), *Echinocolea* R.M. Schust. (Ilkiu-Borges, 2005), *Amphilejeunea* R.M. Schust. and *Cryptogynolejeunea* R.M. Schust. (Reiner-Drehwald, 2005), *Otigoniolejeunea* (Spruce) Schiffn. (Reiner-Drehwald & Ilkiu-Borges, 2007), *Neopotamolejeunea* E. Reiner (Gradstein & Reiner-Drehwald, 2007), *Amblyolejeunea* Ast (Zhu & Cheng, 2008), *Inflatolejeunea* S. Arnell and *Macrolejeunea* (Spruce) Schiffn. (Reiner-Drehwald & Schäfer-Verwimp, 2008), *Cardiolejeunea* R.M. Schust. *et* Kachroo and *Stenolejeunea* R.M. Schust. (Söderström *et al.*, 2010) and *Cladolejeunea* Zwickel (Pócs, 2011). Several authors also included the genus *Microlejeunea* Steph. in *Lejeunea* (e.g., Mizutani 1961; Schuster 1980) but recent molecular work has supported the status of *Microlejeunea* as a separate genus (Dong *et al.*, 2013).

Several attempts have been made to classify the species of *Lejeunea* into subgenera and sections; these classifications were preliminary ones, however, and were not based on a comprehensive study of the whole genus. Schuster (1980) classified 20 species of *Lejeunea* in North America into six subgenera, with subgenus *Lejeunea* separated into seven sections; Reiner-Drehwald (1999) in her "Catalogue of the genus *Lejeunea* Lib. (Hepaticae) of Latin America", recognized 165 valid *Lejeunea* binomina in 12 subgenera; and Gradstein *et al.* (2001) recognized seven subgenera in tropical America. No comprehensive modern infrageneric classification for the genus exists.

Eifrig (1937) in his monograph of Asiatic *Taxilejeunea* (now = *Lejeunea*) was the first to record a species of *Lejeunea* from Malaysia, viz. *Taxilejeunea patersonii* from Mt. Kinabalu. This species was reduced to a synonym of *L. leratii* by Mizutani (1970). Mizutani (1963, 1966, 1970, 1978) reported 23 species from Mt. Kinabalu including three new species, viz. *L. contracta*, *L. kinabalensis* and *L. pectinella*. Two further new species have been described from Mt. Kinabalu, viz. *L. dimorpha* (Kodama, 1976) and *L. gradsteinii* (Lee *et al.*, 2011a). The first records of *Lejeunea* from Peninsular Malaya were by Inoue (1967) who reported 4 species from Cameron Highlands. Kitagawa (1971) recorded one species from Penang Hill and Tixier (1971) described the new species *L. pilifera* from Fraser's Hill, which was later renamed *L. patriciae* by Schäfer-Verwimp (2001). Tixier (1980) reported two further species of *Lejeunea* from Cameron Highlands and Lee *et al.* (2011b) added three species to the Peninsular Malaysian flora. A total of 29 species of *Lejeunea* have been reported from Malaysia, including 26 from Sabah and Sarawak and 11 from Peninsular Malaysia (Table 1).

In the present treatment, 30 species and 2 varieties of *Lejeunea* are recognized for Malaysia. All species are keyed and illustrated, their morphological characters are described and discussed in detail, and distribution and habitat in Malaysia and world distribution are given. In addition, notes are presented on little-used or neglected morphological characters including superior central cells, oil bodies and vegetative propagules.

## MATERIALS AND METHODS

This study is based on the examination of *ca* six hundred of fresh specimens as well as about four hundred herbarium specimens (including type specimens) kept in BM, BIOT, BO, BOHR, CAL, FH, G, GOET, HIRO, JE, NICH, NY, PC, SING, STR and TNS. All illustrations and measurements were taken from mature, well-developed plants. Staining or wetting agents were not used on the specimens. Branched shoots were studied preferentially because they are considered better developed than unbranched ones. Leaves were taken from the mid portions of the stem for measurement. Oil bodies were usually observed within one day after collecting of the material. The illustrations were prepared using a Leitz drawing tube. Author names are abbreviated according to Brummit and Powell (1992) and herbarium abbreviations follow *Index Herbariorum* (Holmgren *et al.*, 1990) Names of journals and books are abbreviated according to Crosby (1999). New state records in Malaysia are marked by an asterisk (\*).

Species are defined in this treatment as morphological entities separated from other species by at least two distinct characters (following Gradstein, 1975; Piippo, 1986; He, 1999). By this definition two species accepted here, viz. *L. mimula* and *L. leratii*, may not merit species rank because they are separated only by their different beak of the perianth. In this study these two taxa are maintained as species, however, due to the paucity of specimens examined. Further material should be studied for a better understanding of these two taxa. Subspecies (not recognized here) and varieties are defined by at least one diagnostic morphological character and, for subspecies, allopatric distribution. Thus, *L. exilis* var. *abnormis* is separated from var. *exilis* by its 5-keeled perianth (terete in var. *exilis*), being the only character separating the two.

## NOTES ON LITTLE-STUDIED MORPHOLOGICAL CHARACTERS

This section provides observations on anatomy of underleaf bases, oil bodies and vegetative propagules which have been little studied in the *Lejeunea* and are of considerable taxonomic importance.

### Anatomy of underleaf bases

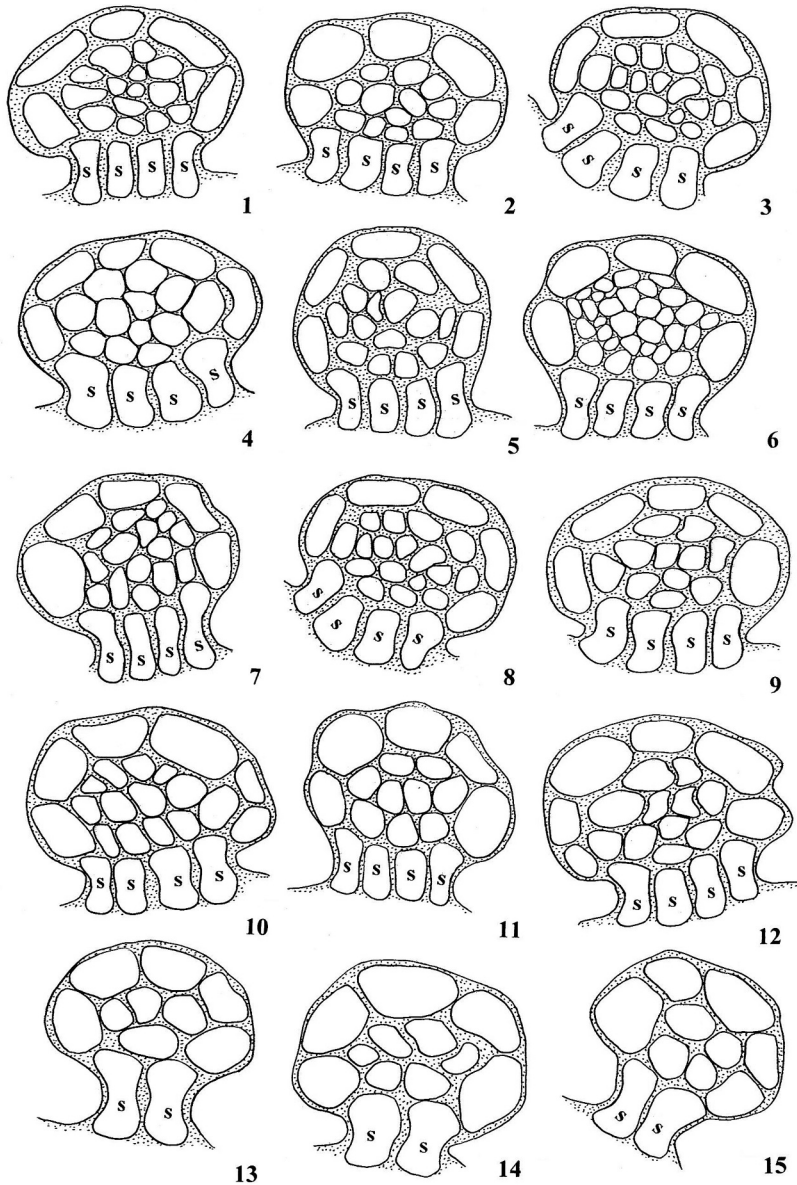
Underleaves of Lejeuneaceae are attached to the stem by superior central cells, inferior central cells and two large basal underleaf cells (Bischler, 1969; Winkler, 1970; Gradstein, 1975). The inferior central cells can be observed at the underleaf base whereas the superior central cells can be seen only in cross- or longitudinal sections. In cross-sections, the superior central cells are usually elongated or rectangular in shape as compared to adjacent cells while in longitudinal sections the superior central cell are large and U-shaped. The origin of the superior central cells remains uncertain (Gradstein, 1975); according to Winkler (1970) they belong to the underleaf. In some genera an intermediate layer of cells is found between the superior central cells and the primary rhizoid disc; accordingly, underleaf bases may be bistratose or tristratose (Winkler, 1970).

According to Bischler (1969) and Winkler (1970), genera of Lejeuneaceae subfam. Ptychanthoideae have four inferior central cells while those of subfam. Lejeuneoideae have two. These authors suggested that the number was constant at generic level and above. Piippo (1986) and He (1999), however, recorded the occurrence of 2, 4 or more superior central cells in species of *Lepidolejeunea* resp. *Pcynolejeunea* (both Lejeuneoideae). In this study, stem cross-sections revealed the presence of two or four superior central cells in the Malaysian species of *Lejeunea* (Figs 1-15). All species had bistratose underleaf bases. Thus, the presence of more than two superior central cells in the subfamily Lejeunoideae and within a single genus, was confirmed. Two superior central cells were found in *L. anisophylla*, *L. apiculata*, *L. cocoes*, *L. exilis*, *L. papilionacea*, *L. patriciae* and *L. tamaspocsii*; all other species had four superior central cells. The number of superior central cells appeared to be constant at species level and a morphological cluster analysis divided the Malaysian species into two groups based on this character (Lee *et al.*, submitted).

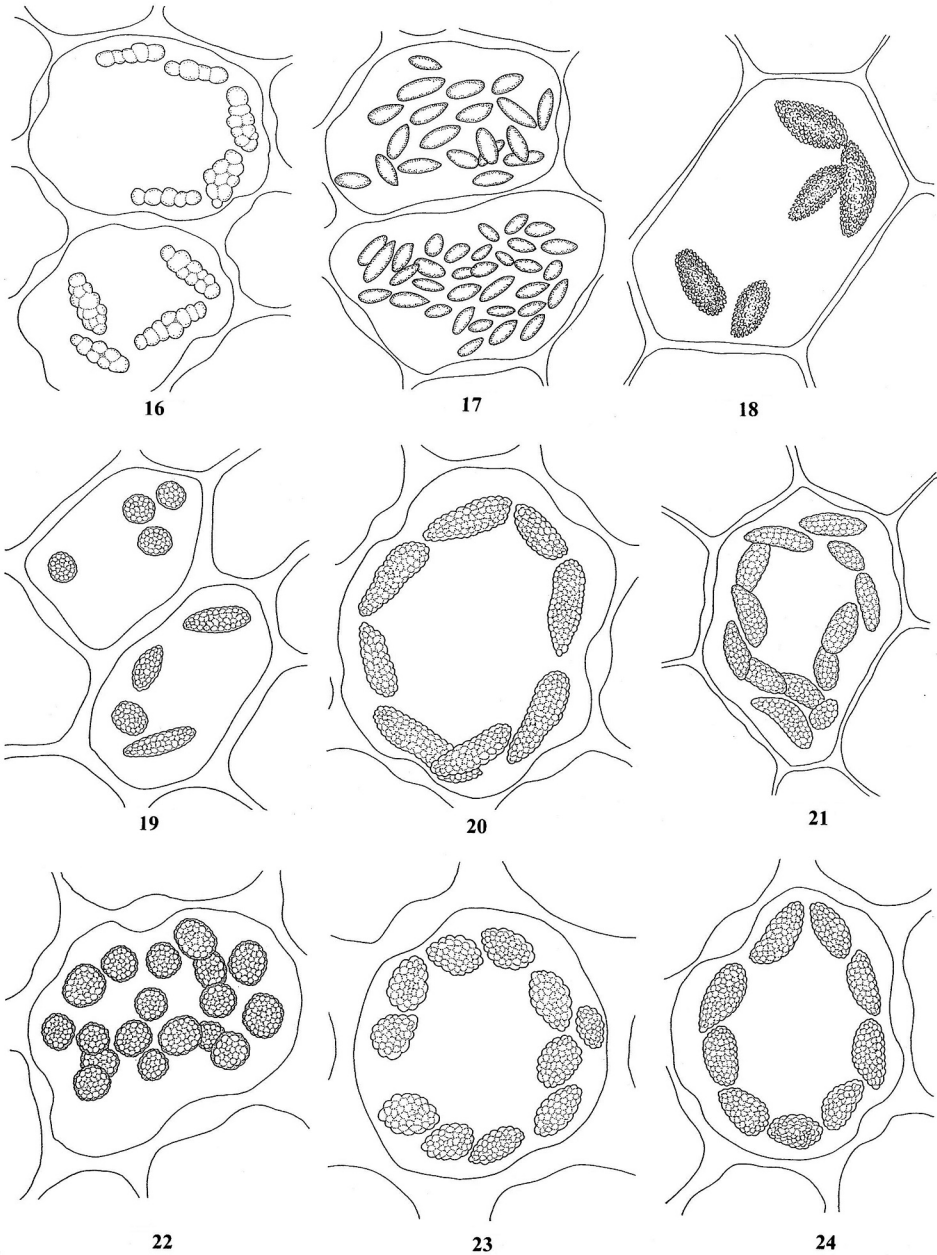
### Oil bodies

The morphological characteristics of liverwort oil bodies have been shown to be taxonomically significant (Schuster, 1966; Gradstein, 1978, etc.). Observations of oil bodies must be made on living material; due to the rapid disintegration of oil bodies after drying, observations on rewetted material may be unreliable. For example, finely segmented *Jungermannia*-type oil bodies may become more or less homogeneous upon disintegration (Gradstein *et al.*, 1977). The latter authors recognized four oil bodies types in Lejeuneaceae: *Massula*-type (oil bodies homogeneous, numerous and small), *Bazzania*-type (oil bodies homogeneous, few and large), *Calypogeia*-type (oil bodies coarsely segmented, like a "grape-cluster") and *Jungermannia*-type (oil bodies finely segmented). Additional types were described by Schuster (1980) and Kis & Pócs (1997).

In this study, oil bodies have been observed in thirteen species. Four oil body types were observed (Figs 16-24):



Figs 1-15. Stems in cross-section of *Lejeunea* species, showing superior central cells (s). **1.** *L. pectinella* from G.E. Lee 2009; **2.** *L. gradsteinii* from G.E. Lee 1886; **3.** *L. albescens* from G.E. Lee 1744; **4.** *L. sordida* from A. Damanhuri 11-1; **5.** *L. flava* from G.E. Lee 1572; **6.** *L. eifrigii* from G.E. Lee 2297; **7.** *L. dimorpha* from A. Damanhuri 11-370; **8.** *L. umbilicata* from G.E. Lee 1424; **9.** *L. utriculata* from G.E. Lee 1902; **10.** *L. micholitzii* from G.E. Lee 2077; **11.** *L. discreta* from G.E. Lee 1423; **12.** *L. patersonii* from A. Damanhuri 11-465; **13.** *L. patriciae* from G.E. Lee 1205; **14.** *L. anisophylla* from G.E. Lee 2145; **15.** *L. tamaspocsii* from G.E. Lee 1423.



Figs 16-24. Oil bodies of *Lejeunea* species. **16.** glistening-botryoidal (*Calypogeia*-type), *L. sordida*; **17.** glistening-homogeneous (*Massula*-type); *L. dimorpha*; **18.** opaque-papillose (rough *Jungermannia*-type), *L. eifrigii*; **19-24.** somewhat glistening to faintly opaque-granular (fine *Jungermannia*-type); **19.** *L. discreta*; **20.** *L. mimula*; **21.** *L. micholitzii*; **22.** *L. patriciae*; **23.** *L. umbilicata*; **24.** *L. kinabalensis*.

**1. Glistening-botryoidal oil bodies** (*Calypogeia*-type): *L. anisophylla*, *L. albescens*, *L. sordida*. Oil bodies appear like a cluster of grapes; they are rather coarsely segmented into large granules ( $> 2 \mu\text{m}$ ), few, less than 5 per cell, faintly rough externally (Fig. 16). Disintegration of the oil body occurs by breakup into smaller granules.

**2. Opaque-papillose oil bodies** (rough *Jungermannia*-type): *L. eifrigii*. Oil bodies are finely segmented into small granules ( $< 2 \mu\text{m}$ ), few, less than 8 per cell (usually 3-5), rough externally (Fig. 18). The disintegration process was not observed.

**3. Somewhat glistening to faintly opaque-papillose oil bodies** (fine *Jungermannia*-type): *L. discreta*, *L. flava*, *L. kinabalensis*, *L. micholitzii*, *L. mimula*, *L. patriciae*, *L. tuberculosa*, *L. umbilicata*. The oil bodies are finely segmented into small granules ( $< 2 \mu\text{m}$ ), usually more than 5 per cell, to 10-18 (-24), somewhat rough externally (Figs. 19-24). Two types of disintegration were observed: 1) Merging of granules into a large granule, the size of the oil body remaining unchanged or becoming slightly smaller. This type of breakup is seen in smaller-sized, spherical oil bodies. 2) Merging of granules followed by decay of the membrane and breakup of the oil body into numerous small granules. This type of disintegration is seen in large, ellipsoid oil bodies. Cells with both small and large oil bodies may show both types of disintegration.

**4. Glistening-homogeneous oil bodies** (*Massula*-type): *L. dimorpha*. The oil bodies are smooth externally, rarely faintly segmented into indistinct granules; they are small and numerous, usually *ca* 30 per cell (Fig. 17). Disintegration occurs by breakup into numerous small oil droplets.

## Vegetative propagation

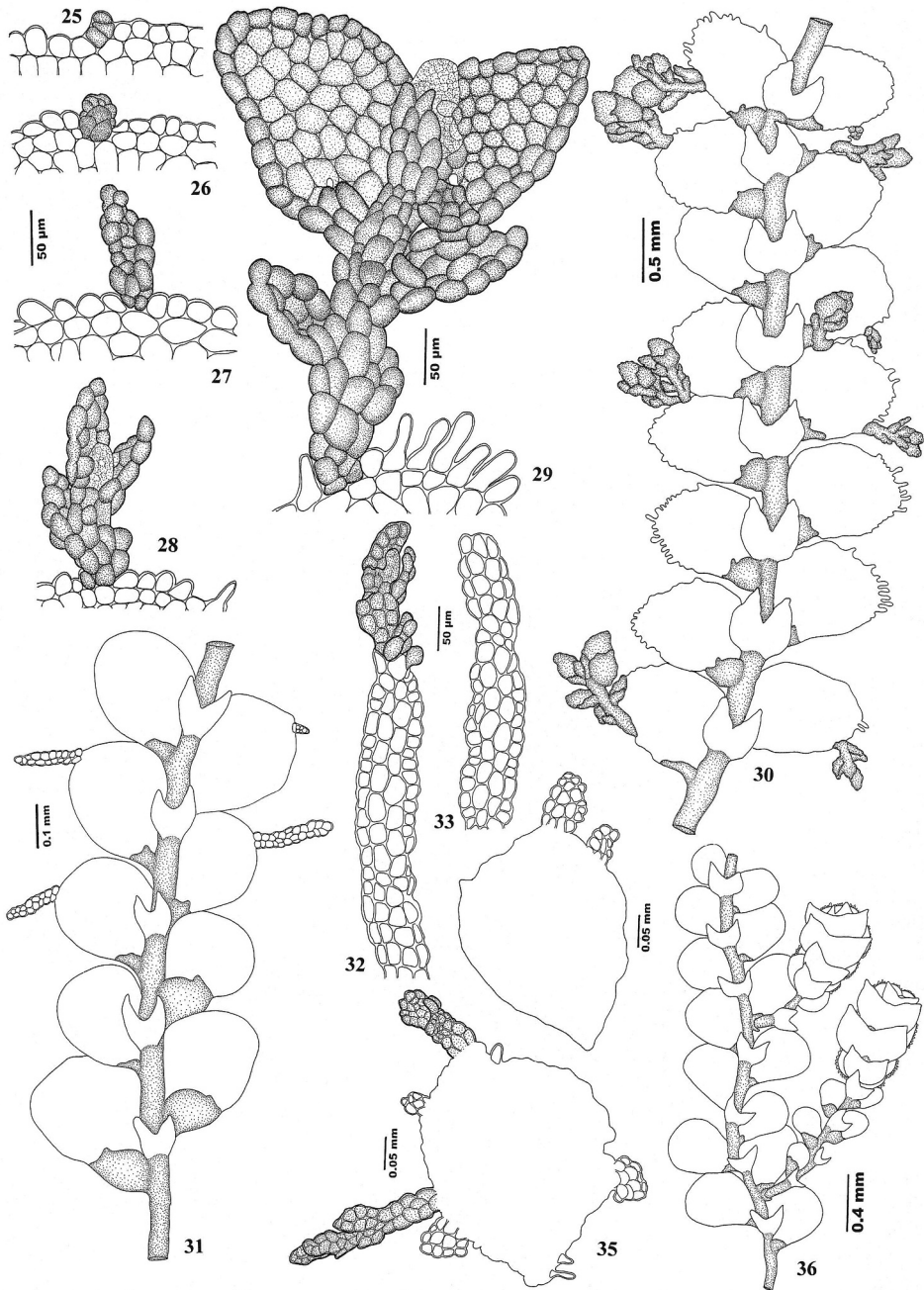
In Malaysian *Lejeunea*, vegetative propagation was observed in seven species, viz. *L. cocoes*, *L. dimorpha*, *L. exilis*, *L. patriciae*, *L. sordida*, *L. tuberculosa* and *L. umbilicata*. Four different types of vegetative reproduction were observed (Figs 25-36):

**1. Regenerants** (Figs 25-30); in *L. patriciae*, *L. sordida*, *L. tuberculosa* and *L. umbilicata*. Young plantlets arise from marginal cells of unmodified, non-caducous leaves, get detached and grow into new plants.

**2. Ribbon-like propagules** (Fig. 31); in *L. cocoes* and *L. exilis*. Regeneration is similar to the previous type except for the ribbon-like structure of the regenerants, being 2-4 cells wide and 3-5 (9-23) cells long. *Lejeunea exilis* and *L. cocoes* showed this type of regeneration. This type of vegetative propagation has previously been described from *Lejeunea* by Pócs *et al.* (1995), Reiner-Drehwald & Goda (2000), Zhu & So (2001) and Zhu & Grolle (2003).

**3. Cladia** (Fig. 36); only seen in *L. dimorpha*, apparently restricted to these epiphyllous plants. The leaves of the cladia (= specialized caducous branches) differ from ordinary ones by having numerous marginal rhizoids; moreover, the underleaves of the cladia are very large and the stems are very fragile. In collections of *L. dimorpha* cladia occur frequently, being closely attached to the surface of the living leaf by the marginal rhizoids while the large underleaves are widely spreading from the stem. The caducous specialized branches usually have 3-5(-10) pairs of leaf lobes and 3(-7) underleaves. Vegetative propagation happens when the specialized branches break off from the stem.

**4. Caducous leaves with ribbon-like propagules and regenerants** (Figs 32-35); also seen in *L. cocoes*. The caducous leaves are only found on main



Figs 25-36. Vegetative propagules of *Lejeunea* species. 25-30. Regenerants (various stage of development), *L. patriciae*; 31. Ribbon-like propagules, *L. cocoes*; 32-35. Caducous leaves with ribbon-like and plantlet regenerants, *L. cocoes*; 36. Cladia or specialized caducous branches, *L. dimorpha*.



stems, not on branches. The caducous leaves are so fragile even the slightest touch of a fine-tipped forceps will cause it to drop off from the stem. Each caducous leaf may produce 2(-6) regenerants. Similar caducous leaves have been reported by Reiner-Drehwald (2000), Reiner-Drehwald & Ilkiu-Borges (2007) and Reiner-Drehwald & Schäfer-Verwimp (2008) in various Neotropical species and by Pócs (2010) in *L. kuerschneriana* Pócs from Africa

### TAXONOMIC TREATMENT

*Lejeunea* Lib., *Ann. Gén. Sci. Phys. Bruxelles* 6: 372 (1820),

“*Lejeunia*” corr. Hampe (1837), *nom. et orth. cons.*

TYPE: *L. libertiae* E.B. Bonner et H. Mill. (= *L. cavifolia* (Ehrh.) Lindb.).

**Plants** autoicous or dioicous, minute to medium-sized (0.5-2.0 mm wide with leaves), delicate to somewhat robust, growing in loose mats and patches or occasionally tightly appressed to the substrates, sometimes pendulous, *somewhat glossy light green to yellowish green or whitish green* to pure or pale (somewhat dull) green when fresh, turning somewhat brownish when dry. **Stems** with *hyalodermis*, delicate, soft-textured, irregularly branched, *branches of Lejeunea-type or Radula-type* (only innovations), the branches short or long, leafy or sexual, *collar with three lobes*, small to large, microphyllous branches lacking in Asiatic plants; *ventral merophyte usually 2 cells wide* (4-10 cells wide in some neotropical species); stem 4-10 cells high in cross-section, *usually with 7 epidermal cells and 5-50 medullary cells, all stem cells more or less thin-walled, epidermal cells distinctly larger than the medullary cells; superior central cells 2 or 4.* **Leaves** attached to the stem along a *J-shaped line of insertion*, about 10-15 lobe cells long, incubous, complicate-bilobed, imbricate to distant, flat to convex, leaf position somewhat similar in dry or moist conditions except for recurvation somewhat stronger in dry condition, erect-spreading to spreading. **Leaf lobes** ovate, ovate-triangular, ovate-rectangular or ovate-orbicular; apex mostly broadly to narrowly rounded, apiculate in a few species, sometimes with a few rhizoids; margins entire or denticulate (toothed in some species), ventral margin mostly making a blunt angle of 120-180° with the keel when flattened (90-100° in some species). **Leaf lobules** ovate, ovate-oblong or ovate-triangular, *inflated, often reduced*; free margins flat or incurved partially to fully; apical tooth erect to suberect, *small, obtuse to oblong, never sharp acuminate; hyaline papilla at the proximal side of the apical tooth*; marginal cell below the apical tooth mostly of the same size as the apical tooth, sometimes large (= disc cell) in robust plants. **Leaf cells** with thin hyaline to somewhat yellowish walls, *rather uniform*, gradually becoming smaller towards the leaf margin and larger and sometimes elongate towards the leaf base; *ocelli lacking* (present in the neotropical *L. huctumalcensis*); trigones indistinct to well-developed; intermediate thickenings frequently present or occasionally absent, sometimes with 2 (3) intermediate thickenings between adjacent trigones; cuticle smooth to rough. **Oil bodies** present in cells of leaves, underleaves, stem epidermis, female and male leaves including perianth, varying from very numerous, 30-50 per cell, minute and homogeneous, to 3-10 per cell, small and segmented, *never very large and only 1-2 per cell.* **Underleaves** suborbicular to reniform, bilobed to unlobed, imbricate to distant, 2-7 times wider than the stem; lobes 4-20 cells wide, lanceolate to very shallowly triangular, usually oblique,

straight to somewhat divergent; margins entire to strongly crenulate; bases cuneate, straight to shallowly curved or cordate to more or less auriculate; two large basal underleaf cells present or lacking; rhizoids hyaline to brownish, in loose fascicles at the base of the underleaves; secondary rhizoidal disc usually lacking, sometimes present in epiphyllous plants. **Androecia** mostly on short or long lateral branches, occasionally terminal on branches or main shoots, bracts in 3-10 pairs, winged or without wing, closely imbricate, always smaller than the normal leaves and with strongly inflated and larger lobules, *the lobules hypostatic*, margins entire or crenulate, male bracteoles slightly bilobed to unlobed, somewhat similar to the normal underleaves, often slightly smaller, restricted to the base of the androecial shoot (in all Malaysian species) or present throughout the androecial shoot. **Gynoecia** on short or long lateral branches, rarely on the main stem, with 1-2 *lejeuneoid innovations* which are sterile or fertile, gynoecia 1-5 in a lateral row; bracts and bracteoles in 2 series. Female bracts loosely arranged to somewhat crowded, usually erect-spreading when moist and occasionally enveloping the perianth, bilobed and usually smaller than the normal leaves or almost of the same size; bract lobes oblong to obovate, margins entire to strongly crenulate; bract lobules lanceolate to obovate, apex truncate to acuminate, rarely with marginal rhizoids, sinus with a hyaline papilla at the lateral side. Female bracteoles ovate to obovate, frequently connate at base with one or both bracts, longer than the underleaves and almost as long as the bract lobes, plane, rarely recurved, gradually or rarely abruptly narrowed to the base; margin entire to crenulate to somewhat toothed; lobes distant to overlapping. Perianths inflated to a little compressed dorsiventrally, with 0-5 prominent keels, the dorsal keel occasionally indistinct; keels smooth to mammillose, sometimes extended above as auricles, sometimes 2-winged; apex rounded to truncate, *beak present or lacking*, when present 2-10 cells long, sometimes trumpet- or funnel-shaped. **Sporophyte:** *seta short, articulate, hyaline, made up of 12 outer and 4 inner cell rows*; capsule splitting into 4 valves, cells thin-walled, colorless; elaters hyaline or pale brown, with thickened walls, without spiral bands of thickenings, attached to the upper margin of each capsule valve; spores elongate, in decussate tetrads, surfaces with rosettes and spines. **Vegetative propagation** by means of young plantlet or ribbon-like regenerants, caducous specialized branches or caducous leaves, *never by discoid gemmae*.

The distinguishing features of species and varieties in this treatment are mainly based on sexuality, perianth, leaf lobule, underleaf, characters of leaf cells and vegetative propagules (see also Lee *et al.*, 2011c).

## Sexuality

This is a very straight-forward character and varies very little. Determination of sexuality may sometimes be difficult, however, and a few species are autoicous and dioicous. For the species of *Lejeunea* in Malaysia, it is often quite easy to determine their sexuality, however, as the autoicous plants are usually fertile with abundant androecia and gynoecia. For example, in the autoicous *L. anisophylla* 37 out of 57 specimens examined had perianths and in *L. papilionacea* 31 out of 43. In some cases, it is difficult to separate species when sterile, e.g., *L. cocoes* and *L. anisophylla* which are very similar and differ mainly in sexuality. Many authors (e.g., Spruce, Evans, Schuster, Jones) had treated sexuality as an important taxonomic character for separating species or subspecies of Lejeuneaceae. Nevertheless, Gradstein (1975) limited sexuality to evidence supporting other morphological characters in the separation of the species of

*Acrolejeunea*. In this study, sexuality is never used as the sole diagnostic taxonomic character but only in combination with other characters.

### **Perianth**

Perianths are important taxonomic features for separating species of *Lejeunea* in Malaysia. In this study, this character has been one of the first to consider as it proved to be the least variable character within species of the genus. Particularly important are the shape of perianth, the beak, the keels, the cells of the keel (smooth or mammillose), the presence or absence of wings and cilia, the position of perianth (emerged or submerged between bracts), and possibly opaque appearance. Some character states have limited distribution among species, e.g. funnel-shaped beaks occurs only in *L. mimula*, submerged perianths with a long beak and 2-3 teeth on ventral keels are restricted to *L. pectinella*, auriculate perianths to *L. papilionacea*, and winged perianth to *L. dipterota*, *L. patersonii* and *L. tamaspocsii*, and therefore valuable for species identification.

### **Leaf lobule**

The shape of the leaf lobule is an important character together with the recurvation of the free margin and the presence or absence of a large, rectangular “disc cell” below the apical tooth. The shape of the lobules is rather consistent in many of the species. Species such as *L. discreta* and *L. mizutanii* have large and ovate-oblong lobules, while a small, ovate-triangular leaf lobule with a large disc cell separates *L. lumbricoides* from *L. stephaniana*, *L. discreta*, *L. mizutanii*, *L. fleischeri* and *L. utriculata*.

### **Underleaves**

The shape, arrangement and margin of the underleaves has proved to be useful to separate some of the species, e.g., large, reniform underleaves with truncate apex in *L. mimula*, small, strongly crenulate and distant underleaves in *L. tamaspocsii* and dimorphic underleaves in *L. exilis*.

### **Leaf cells**

Presence of well-developed trigones and intermediate thickenings can be used to separate some of the species, such as between *L. stephaniana* and *L. fleischeri*. Several species are distinguished by the number of intermediate thickenings between adjacent trigones such as *L. micholitzii*, *L. patriciae* and *L. dimorpha*, in which 2(-3) intermediate thickenings occur between adjacent trigones particularly in the basal leaf cells. Mizutani (1970) mentioned nodulous intermediate thickenings as a character, e.g., in *L. pectinella*. In this study, however, it was not possible to distinguish between nodulous and not-nodulous intermediate thickenings, therefore this character has been excluded in this treatment.

### **Vegetative propagation**

Some species are distinguished by their characteristic vegetative propagules, e.g., plantlet regenerants in *L. patriciae*, ribbon-like regenerants in *L. exilis*, caducous leaves and ribbon-like regenerants in *L. cocoes*, and specialized caducous branches in *L. dimorpha*.

## KEY TO THE SPECIES OF *LEJEUNEA* IN MALAYSIA

(by G.E. Lee and S.R. Gradstein)

1. All or some leaf apices with short marginal rhizoids . . . . . 2
1. Leaf apices never with short marginal rhizoids . . . . . 3
2. Marginal rhizoids restricted to specialized caducous branches; underleaves on caducous branches much larger than on the main stem. Exclusively epiphyllous . . . . . *L. dimorpha*
2. Marginal rhizoids occurring on ordinary stems and branches; specialized caducous branches with large underleaves absent. On bark, rotten logs and living leaves. . . . . *L. patriciae*
3. Leaf apices apiculate . . . . . 4
3. Leaf apices rounded to obtuse, never apiculate . . . . . 6
4. Underleaves large, 4-5 × wider than the stem, entirely covering the leaf lobules; leaf apices recurved . . . . . *L. microloba*
4. Underleaves smaller, ca 2 × wider than the stem, not entirely covering the leaf lobules; leaf apices flat. . . . . 5
5. Leaf apices long apiculate, ending in a row of (2-)3-4 cells; underleaves deeply bifid to 2/3 of length, with narrow lanceolate lobes; perianth keels irregularly dentate. . . . . *L. apiculata*
5. Leaf apices short apiculate, ending in a row of 1-2 cells; underleaves less deeply bifid (to 1/2 of length), with broader lobes; perianth keels mammillose, not dentate. . . . . *L. eifrigii*
6. Underleaves dimorphic, undivided and bilobed; plants very small, less than 0.8 mm wide; leaves remote, obliquely spreading . . . . . *L. exilis*
6. Underleaves not dimorphic, undivided or bilobed, not both; plants small or large; leaves usually widely spreading (rarely obliquely spreading) . . . . . 7
7. Underleaves unlobed, truncate to weakly retuse; perianth with a funnel-shaped beak . . . . . *L. mimula*
7. Underleaves bilobed; perianth without funnel-shaped beak . . . . . 8
8. Underleaves large, 3-7 × stem width, entirely covering the leaf lobules (lobule not visible in ventral view) . . . . . 9
8. Underleaves small or large, but not entirely covering the leaf lobule (at least apex of lobule visible in ventral view). . . . . 15
9. Leaf margins distinctly crenulate by projecting cells; leaf lobules without large disc cell . . . . . 10
9. Leaf margins entire or slightly crenulate; leaf lobules without or with a large disc cell along the free margin distal to the apex (present in *L. compacta* and *L. dipterota*) . . . . . 11
10. Underleaves shallowly bifid, to 1/6-1/4 of underleaf length, sinus between underleaf lobes wide; perianth without keels and without beak . . . *L. albescens*
10. Underleaves more deeply bifid, to 1/2 of underleaf length, sinus between underleaf lobes narrow; perianth with 5 keels and with a short beak . . . . . *L. kinabalensis*
11. Leaf apices recurved . . . . . 12
11. Leaf apices flat . . . . . 13
12. Leaf apices broadly rounded; leaf cells with well-developed trigones and intermediate thickenings; leaf lobules with a large disc cell; perianth beak sometimes trumpet-shaped. . . . . *L. compacta*

12. Leaf apices narrowly rounded; leaf cells without trigones and without intermediate thickenings; leaf lobules without large disc cell; perianth beak short cylindrical, not trumpet-shaped. . . . . *L. contracta*
13. Leaf lobules with a large disc cell; perianth with undulate, 2-winged keels. . . . .  
 . . . . . *L. dipterota*
13. Leaf lobules without large disc cell; perianth keels not undulate and without wings . . . . . 4
14. Underleaves longer than wide; autoicous . . . . . *L. flava*
14. Underleaves wider than long; dioicous. . . . . *L. sordida*
15. Leaf apices always recurved when dry; leaf lobe usually more than 0.6 mm long . . . 16
15. Leaf apices flat, rarely recurved when dry; leaf lobe usually less than 0.6 mm long (to 0.8 mm long in *L. micholitzii* and 0.9 mm long in *L. gradsteinii*) . . . 23
16. Leaf lobules very small, 0.1-0.2 mm long; perianth without keels and without beak. . . . . *L. umbilicata*
16. Leaf lobules when well-developed larger, 0.3-0.5 mm long; perianth with keels and beak . . . . . 17
17. Leaves obliquely spreading, at an angle of 30°-40° to the stem; leaf cells without trigones and intermediate thickenings; leaf lobules without large disc cell. . . . . *L. stephania*
17. Leaves widely spreading, at an angle of 60°-90° to the stem; leaf cells with well-developed trigones and intermediate thickenings; leaf lobules with a large disc cell along the free margin distal to the apex . . . . . 18
18. Leaf lobules with flat free margin . . . . . *L. mizutanii*
18. Leaf lobules with fully or partially incurved free margin . . . . . 19
19. Leaf lobes ovate, apex narrowly rounded; perianth beak 2-3 cells long, trumpet-shape . . . . . *L. discreta*
19. Leaf lobes ovate-orbicular, apex broadly rounded, perianth beak 5-10 cells long, cylindrical . . . . . 20
20. Underleaves distant, distinctly longer than wide; underleaf bases cordate, sometimes with auricles; stem cross-section with 40-50 medullary cells . . . . .  
 . . . . . *L. lumbricoides*
20. Underleaves imbricate to contiguous, wider than long or orbicular; underleaf bases shallowly curved, without auricles; stem cross-section with 10-20(-30) medullary cells . . . . . 21
21. Underleaves 3-4 × stem width, covering less than half of leaf lobules . . . *L. utriculata*
21. Underleaves larger, 5-6 × stem width, covering more than half of leaf lobules . . . 22
22. Underleaves reniform; perianth not emergent beyond the bracts, perianth keels ± toothed, beak 8-10 cells long. . . . . *L. pectinella*
22. Underleaves ovate-orbicular; perianth emergent beyond the bracts, keels smooth, beak 5-6 cells long . . . . . *L. fleischeri*
23. Underleaves attached to the stem by 2 superior central cells . . . . . 24
23. Underleaves attached to the stem by 4 superior central cells . . . . . 27
24. Leaves distant, obliquely spreading, at an angle 40°-50° to the stem, sometimes caducous; dioicous. . . . . *L. cocoas*
24. Leaves imbricate to contiguous, widely spreading, at an angle 60°-80° to the stem, never caducous; autoicous . . . . . 25
25. Leaf apex narrowly rounded; leaves asymmetrical, with strongly arched dorsal margin and straight or slightly curved ventral margin; perianth keels strongly mammillose and 2-winged . . . . . *L. tamaspocsii*
25. Leaf apex broadly rounded; leaves subsymmetrical, with arched dorsal and ventral margin; perianth keels smooth or slightly mammillose, not winged . . . . . 26

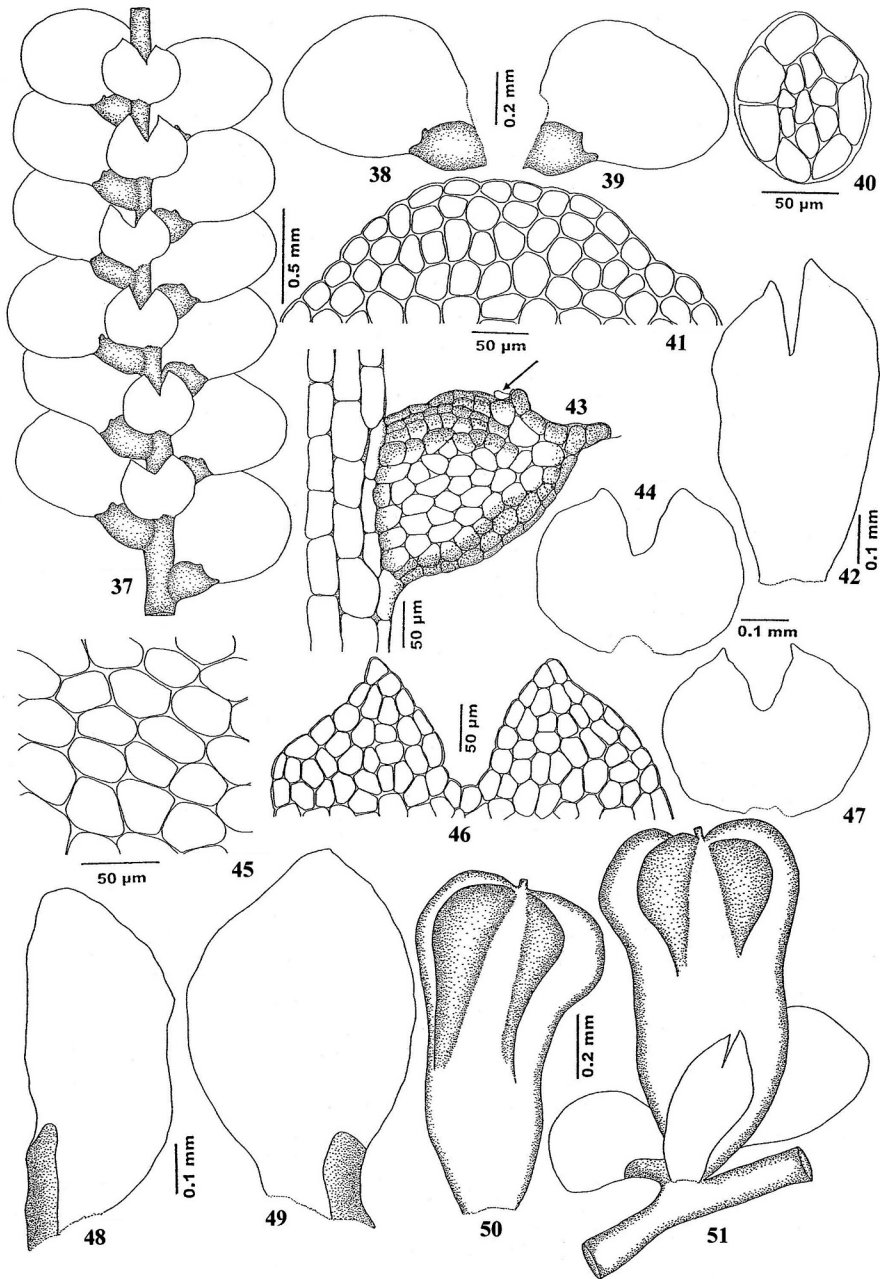
26. Leaves bordered by 2-3 rows of quadrate to rectangular cells; underleaves lobes wider, sometimes with a blunt angle on the outer margins; leaf cells with well-developed trigones and intermediate thickenings; perianth keels expanded above into auricles and sometimes with a 1-2 celled wing . . . . .  
 . . . . . *L. papilionacea*
26. Leaves not bordered, leaf margin cells  $\pm$  similar to inner cells; underleaves lobes narrowly lanceolate, without blunt angle on outer margins; leaf cells without distinct trigones and without intermediate thickenings; perianth keels not expanded into auricles, without wing . . . . . *L. anisophylla*
27. Leaf and underleaf margins distinctly crenulate by projecting cells; perianth keels strongly mammillose and sometimes 2-winged . . . . . *L. patersonii*
27. Leaf and underleaf margins entire; perianth keels smooth or slightly mammillose, not winged . . . . . 28
28. Underleaves wider than long . . . . . 29
28. Underleaves longer than wide to as long as wide . . . . . 30
29. Leaf cells with conspicuous intermediate thickenings; perianth obovoid; dioicous . . . . . *L. micholitzii*
29. Leaf cells without intermediate thickenings; perianth clavate; autoicous . . . . .  
 . . . . . *L. alata*
30. Underleaf lobes to 2/3 of underleaf length; leaf lobules with two teeth, free margin flat . . . . . *L. gradsteinii*
30. Underleaf lobes to 1/2 of underleaf length; leaf lobules with one teeth, free margin incurved. . . . . *L. tuberculosa*

**1. *Lejeunea alata* Gottsche, in Gottsche et al., Syn. Hepat. 406 (1845) Figs 36-57**

= *Taxilejeunea mitracalyx* Eifrig, *Ann. Bryol.* 9: 94 (1937)  $\equiv$  *Lejeunea mitracalyx* (Eifrig) Mizut., *J. Hattori Bot. Lab.* 33: 244 (1970). TYPE: Indonesia. "Sumatra occid, in mte. Singalang, 1400-1600 m, in reg. inferiore in silva primaeva, epiphylla, Iter Indic. 1893/94", *Schiffner 2889* (holotype: JE!), syn. *vide* Grolle (1977).

For further synonyms see Grolle (1977).

**Plants** autoicous, relatively large, 1.2-1.6 mm wide, usually light green to pale green when fresh to light brown when dry, irregularly and densely branched, sometimes bipinnately branched, branches erect-spreading to spreading, collar with three small lobes. **Stem** 0.10-0.14 mm in diameter, about 5 cells high in cross-section; epidermal cells 7, 25-40  $\mu$ m wide, medullary cells 8-17, 10-20  $\mu$ m wide. **Leaves** contiguous to imbricate, often somewhat crisped and slightly recurved when dry, erect-spreading and plane when moist. **Leaf lobes** 0.60-0.65 mm long, 0.45-0.50 mm wide (when flattened), ovate; leaf apex broadly rounded, flat; leaf margin entire to slightly crenulate; the ventral margin forming an angle of 140°-150° with the keel when flattened; insertion line 12-13 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually quadrate to hexagonal, irregularly quadrate to rectangular towards the leaf margin; apical cells 13-15  $\mu$ m long and 10-13  $\mu$ m wide, median cells 30-38  $\mu$ m long and 25-30  $\mu$ m wide, basal cells 50-55  $\mu$ m long and 25-30  $\mu$ m wide; cell walls hyaline, with well-developed trigones and without intermediate thickenings. Cuticle smooth. Oil bodies not seen. **Leaf lobules** often reduced, 0.1-0.3 mm long, (0.08) 0.1-0.2 mm wide, to 1/3 the length of the lobe, at an angle of 60°-70° to the stem, ovate, inflated along the keel; apex obliquely truncate; keel straight to curved; free margin flat; apical tooth 25-30  $\mu$ m long, oblong, somewhat erect, apex



Figs 37-51. *Lejeunea alata* Gottsche. 37. Part of plant in ventral view; 38, 39. Leaves; 40. Cross-section of stem; 41. Apical cells of leaf lobe; 42. Female bracteole; 43. Stem portion and leaf lobule (hyaline papilla shown by arrow); 44, 47. Underleaves; 45. Median cells of leaf lobe; 46. Apical cells of underleaf; 48, 49. Female bracts; 50. Perianth; 51. Perianth with bracts and bracteole. 37-43, 44, 46, 47 drawn from G.E. Lee 1199 (UKMB); 45, 48-51 from G.E. Lee 1198 (UKMB).

obtuse; margin between tooth and sinus 3-4 cells long, large disc cell lacking, cell below the apical tooth 15-30  $\mu\text{m}$  long and 14-18  $\mu\text{m}$  wide. **Underleaves** 0.2-0.3 mm long, 0.25-0.35 mm wide, to 3 times wider than the stem, distant, suborbicular (slightly wider than long); covering 1/2-3/4 of the leaf lobules; bilobed, lobes to 1/2 of underleaf length, about 10 cells wide, triangular; sinus narrow to broad, acute to obtuse, U-shaped to V-shaped; underleaf margin entire; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.4-0.5 mm long, 0.2-0.3 mm wide with bracts, usually on the main shoots, sometimes terminal on short or long lateral branches. Male bracts in 3-5 pairs, crenulate without wing, apex obtuse, keels inflated. Male bracteole 0-1, smaller than underleaf, margin entire. Antheridia not seen. **Gynoecia** on short pinnate branches or on long branches, female bracts loosely arranged, with one innovation, 2-4 gynoecia in a lateral row due to repeatedly fertile innovations. Female bracts smaller than the leaf, erect-spreading when moist, not enveloping the perianth. Lobes 0.45-0.50 mm long, 0.25-0.30 mm wide, ovate to somewhat oblong, apex obtuse, margin entire. Lobules 0.15-0.22 mm long, 0.05-0.10 mm wide, usually reduced, 1/6-1/4 the width and 1/4-1/3 the length of the lobe, oblong to ovate, apex obtuse, keels straight, smooth, 0.15-0.18 mm long. Female bracteoles 0.3-0.4 mm long, 0.2-0.3 mm wide, 1/3 of the perianth length, obovate with tips acute, lobes to 1/3 of female bracteole length, sinus narrow to broad, acute to obtuse, margin entire. Perianths 0.8-1.0 mm long, 0.4-0.6 mm wide, emergent to 1/2-2/3 of the perianth length, clavate, with 5 sharp keels, the keels extended above as auricles, 0.10-0.15 mm wide; beak 2 cells long; cells of the perianth at the keels sometimes mammillose; stalk-like elongation sometimes present, 0.3-0.4 mm long. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined.** **MALAYSIA. Pahang:** Genting Highlands, along stream, ca 1200 m, 1996, *N. Ohnishi 2826* (HIRO); road to Gunung Ulu Kali, 1650 m, 2009, *G.E. Lee 1197, 1198, 1199* (UKMB); Goh Tong Jaya, near waterfall, 845 m, 2011, *G.E. Lee 2200* (UKMB); Cameron Highlands, Robinson Waterfalls, 1340 m, 2009, *G.E. Lee 2300, 2301* (UKMB); Mentigi trail, 1365 m, 2009, *G.E. Lee 2296* (UKMB); tea plantation area, 1500 m, 2009, *G.E. Lee 2307* (UKMB). **Sabah:** Kinabalu National Park, power station to radio station, 1800 m, 1970, *T. Kodama 40317* as *L. mitracalyx* (NICH). **TANZANIA.** Uluguru Mts., near Magari, 1500-1800 m, 1970, *T. Pócs, Kondela & Nchimbi 6296/AH* (GOET). **SEYCHELLES.** Mahé: near Salazie, 450 m, 1973, *Norkett 16401* (NICH). **INDONESIA.** Sumatra: Singalang, 1300-1400 m, *V. Schiffner 94* as *Taxilejeunea mitracalyx* (JE); Java: Mt. Pangerango, 1900 m, *V. Schiffner 3014* as *T. mitracalyx* (JE). **SAMOA.** Ipolu, 800 m, 1975, *Schultze-Motel 3223/b* (NICH).

**Distribution and habitat in Malaysia:** Pahang\*, Sabah; mostly epiphytic, rarely epilithic, ca 800-1800 m.

**General distribution:** Africa, tropical Asia, Pacific region.

**Discussion:** *Lejeunea alata* is easily recognized by its 1) clavate perianth with sharp keels which extend above as auricles, 2) quadrate to hexagonal laminal cells with well-developed trigones and without intermediate thickenings, 3) suborbicular underleaves, 4) flat free margin of the leaf lobules, and 5) frequently reduced lobules on leaf lobes and female bracts. *Lejeunea alata* is most closely related to *L. eifrigii*, which was recovered as sister to *L. alata* in a phenetic and phylogenetic analysis (Lee *et al.*, submitted). Both species have similar perianths and leaf areolation and can easily be confused. However, *L. eifrigii* differs in the apiculate leaf apex, perianth without auriculate keels and small, reniform (wider than long) underleaves. Differences also can be seen in the angle between the ventral margin of the lobe and the keel (when the leaf is flattened), which is usually 180° in



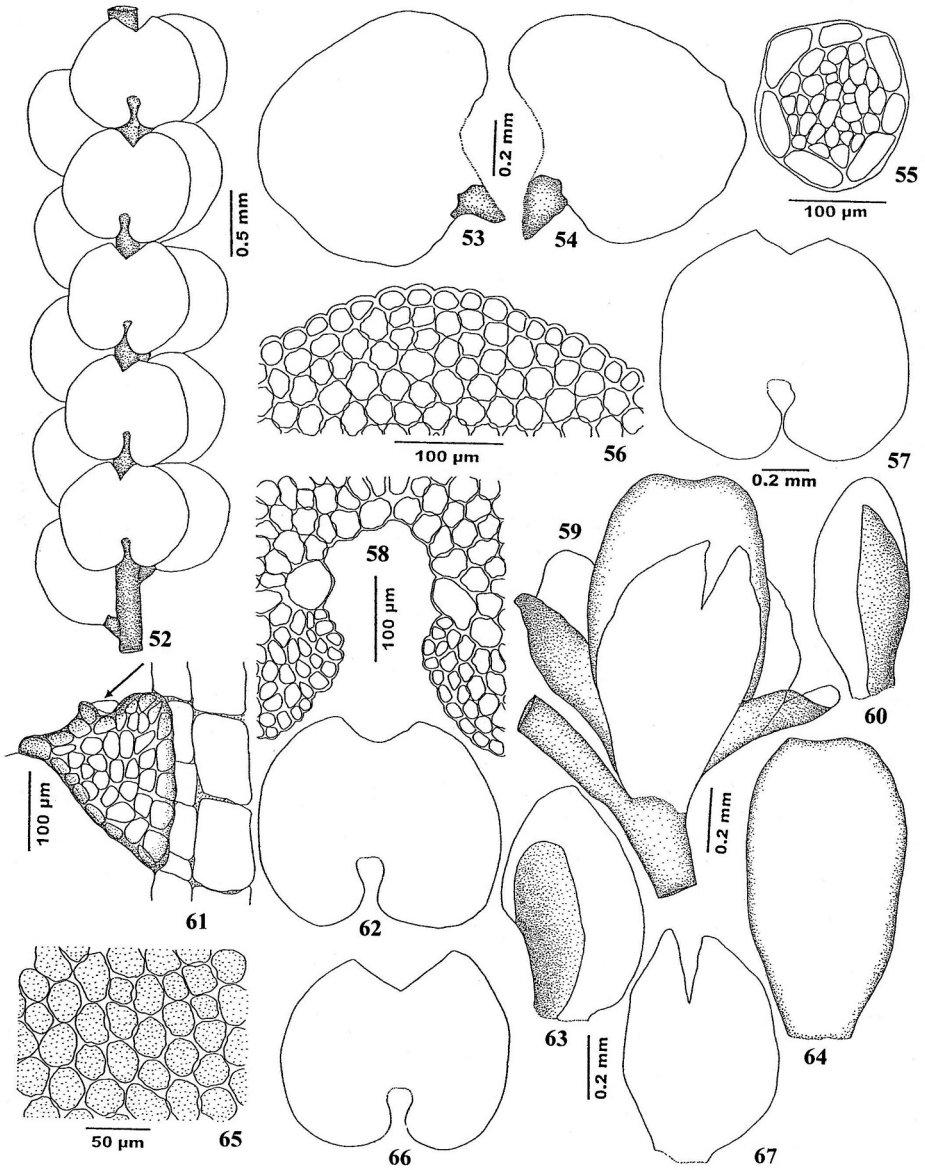
*L. eifrigii* and  $120^\circ$  in *L. alata*, and in the number of medullary cells (16-30 in *L. eifrigii* vs 8-16 in *L. alata*).

*Lejeunea alata* varies in the size of the leaf lobules and underleaves, in the morphology of the perianth and in the crenulations of the leaves and underleaves margin. The size of the leaf lobules varies considerably in association with habitat. Epiphyllous plants with imbricate leaves (including the type specimen) have larger, better-developed leaf lobules than plants with contiguous leaves and growing on other substrates. Reduced and well-developed leaf lobules can be found on the same plant, particularly those from Peninsular Malaysia, in which reduced leaf lobules are mostly located on the main shoot whereas well-developed lobules are found on the branches. Small (0.25 mm wide) and large (0.40 mm wide) underleaves can also be present on the same plants. The perianth auricles vary somewhat in size and are smaller in the Malaysian plants (0.10-0.15 mm wide) than in those from Africa (Tanzania) in which they are to 0.25 mm wide. The margins of leaves and underleaves are usually entire but crenulate margins are also observed in this species.

## 2. *Lejeunea albescens* (Steph.) Mizut., *J. Hattori Bot. Lab.* 33: 245 (1970) **Figs 52-67**

Basionym: *Taxilejeunea albescens* Steph., *Hedwigia* 35: 132 (1896). TYPE: Philippines, Insula Luzon, 1884/85, *Micholitz* 25 (holotype: G!).

**Plants** dioicous, relatively large, flexuous, 0.9-1.2 (1.5) mm wide, whitish green when fresh to dark brown when dry, irregularly and densely branched, sometimes pinnately branched, branches spreading, collar with three large lobes. **Stems** 0.1-0.2 mm in diameter, about 8-9 cells high in cross-section, epidermal cells 7, 40-60  $\mu\text{m}$  wide, medullary cells 20-32, 8-29  $\mu\text{m}$  wide. **Leaves** contiguous to imbricate, slightly recurved when dry, erect-spreading and slightly recurved when moist. **Leaf lobes** 0.6-0.8 mm long, 0.4-0.5 mm wide (when flattened), ovate-triangular; leaf apex broadly rounded, slightly recurved; leaf margin crenulate; ventral margin forming an angle of  $90^\circ$ - $110^\circ$  with the keel when flattened; insertion line 10-14 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregularly quadrate to rectangular towards the leaf margin; apical cells 21-28  $\mu\text{m}$  long and 12-18  $\mu\text{m}$  wide, median cells 31-47  $\mu\text{m}$  long and 25-40  $\mu\text{m}$  wide, basal cells 44-53  $\mu\text{m}$  long and 25-31  $\mu\text{m}$  wide; cell walls yellowish, with relatively large trigones and conspicuous intermediate thickenings, 1-3 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies glistening-botryoidal, *Calypogeia*-type, made up of 6-12 large granules (each 2-3  $\mu\text{m}$  wide), slightly rough externally; marginal cells with 5-7 oil bodies per cell, 2-3  $\mu\text{m}$  long and 2-3  $\mu\text{m}$  wide, mostly globose; median cells with 8-10 oil bodies per cell, 10-15  $\mu\text{m}$  long and 3-5  $\mu\text{m}$  wide, ellipsoid; basal cells with 8-17 oil bodies per cell, 3  $\mu\text{m}$  long and 3  $\mu\text{m}$  wide, mostly globose. **Leaf lobules** rarely reduced, 0.1-0.3 mm long, 0.08-0.10 mm wide, to 1/5-1/4 the length of the lobe, at an angle of  $40^\circ$ - $50^\circ$  to the stem, ovate-triangular, inflated along the keel; apex obliquely truncate; keel straight to curved; free margin incurved partially; apical tooth 42-44  $\mu\text{m}$  long, oblong, somewhat erect, apex obtuse; margin between tooth and sinus 3-4 cells long, large disc cell lacking, cell below the apical tooth 16-24  $\mu\text{m}$  long and 14-20  $\mu\text{m}$  wide. **Underleaves** 0.5-0.6 mm long, 0.6-0.8 mm wide, to 5-6 times wider than the stem, contiguous, reniform (wider than long), always covering the lobules; bilobed, lobes to 1/6-1/4 of underleaf length, about 15 cells wide, very shallowly triangular, sometimes slightly recurved; sinus broad, acute to obtuse, U-shaped to V-shaped; underleaf margin slightly crenulate; base auriculate; two large basal underleaf



Figs 52-67. *Lejeunea albescens* (Steph.) Mizut. 52. Part of plant in ventral view; 53, 54. Leaves; 55. Cross-section of stem; 56. Apical cells of leaf lobe; 57, 62, 66. Underleaves; 58. Basal cells of underleaf; 59. Perianth with bracts and bracteole; 60, 63. Female bracts; 61. Stem portion and leaf lobule (hyaline papilla shown by arrow); 64. Perianth; 65. Median cells of leaf lobe; 67. Female bracteole. 52-58, 61, 66 drawn from *G.E. Lee 1157* (UKMB); 59, 60, 62-64, 65, 67 from *A. Damanhuri 08-9* (UKMB).

cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.9-1.0 mm long, 0.6-0.7 mm wide with bracts, on short or long lateral branches, occasionally on the main shoot. Male bracts in 3-6 pairs, entire without wing, apex obtuse, keels inflated. Male bracteoles 1-2 (3), smaller than underleaves, margin entire. Antheridia 2 per bract, 5-10  $\mu\text{m}$  in diameter; somewhat yellowish with a long and hyaline stalk, 7-15  $\mu\text{m}$  in length. **Gynoecia** on short or long branches, female bracts somewhat crowded, with one innovation, usually with one gynoecium in a lateral position. Female bracts slightly smaller than the leaf, erect-spreading when moist, slightly enveloping the perianth. Lobes 0.6-0.7 mm long, 0.3-0.4 mm wide, ovate, apex obtuse, margin crenulate. Lobules 0.5-0.6 mm long, 0.1-0.2 mm wide, rarely reduced, 1/2 the width and 4/5 the length of the lobe, oblong to ovate, apex obtuse, keels straight, smooth, 0.3-0.4 mm long. Female bracteoles 0.6-0.7 mm long, 0.4-0.5 mm wide, 2/3 of the perianth length, ovate with tips acute, lobes to 1/3 of female bracteole length, sinus narrow, acute, margin crenulate. Perianths 0.8-0.9 mm long, 0.4-0.5 mm wide, emergent to 1/3 of the perianth length, obovoid, without keels and beak, cells of the perianth smooth on surface, stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined. MALAYSIA. Pahang:** Cameron Highlands, Gunung Brinchang, 1965, *Hiroshi Inoue 11198, 11238* as *Taxilejeunea albescens* (TNS), *ibid.*, *A. Damanhuri 08-9* (UKMB), *ibid.*, *G.E. Lee 2303* (UKMB); Fraser's Hill, 1524 m, 1962, *M. Togashi s.n.* (NICH), roadside to Clock Tower, 1220-1245 m, 2009, *G.E. Lee 1157, 1158* (UKMB). **Sabah:** Mt. Kinabalu, 1463-1500 m, 1963, *M. Mizutani 3258* (NICH), *ibid.*, 1450-1550 m, 1974, *T. Kodama 48137* (NICH), *ibid.*, 1530 m, 2010, *G.E. Lee 1533, 1823, 1825, 1842, 1843* (UKMB), Botanical Garden, around Power station road, 1515 m, 2010, *G.E. Lee 1744, 1747, 2044* (UKMB). **INDONESIA.** Seram: Manusela Nat. Park, 700-800 m, 1985, *H. Akiyama 9108* (NICH). Java: Halimun Salak National Park, 1200 m, 2009, *M.S. Sofiyana 023* (BIOT). **PHILIPPINES.** Luzon: Mt. Polis, 1978, *F. Rodriguez 78772* (NICH). **PAPUA NEW GUINEA.** Morobe Prov., Mt. Kaindi, 2350 m, 1981, *Gradstein 3844, 3887* (GOET); Southern Highlands Prov., Tari Gap, Mendi-Tari road, 2660 m, 1982, *H. Streimann 32457* (NICH).

**Distribution and habitat in Malaysia:** Pahang, Sabah; mostly epiphytic, occasionally terrestrial, *ca* 1400-2000 m.

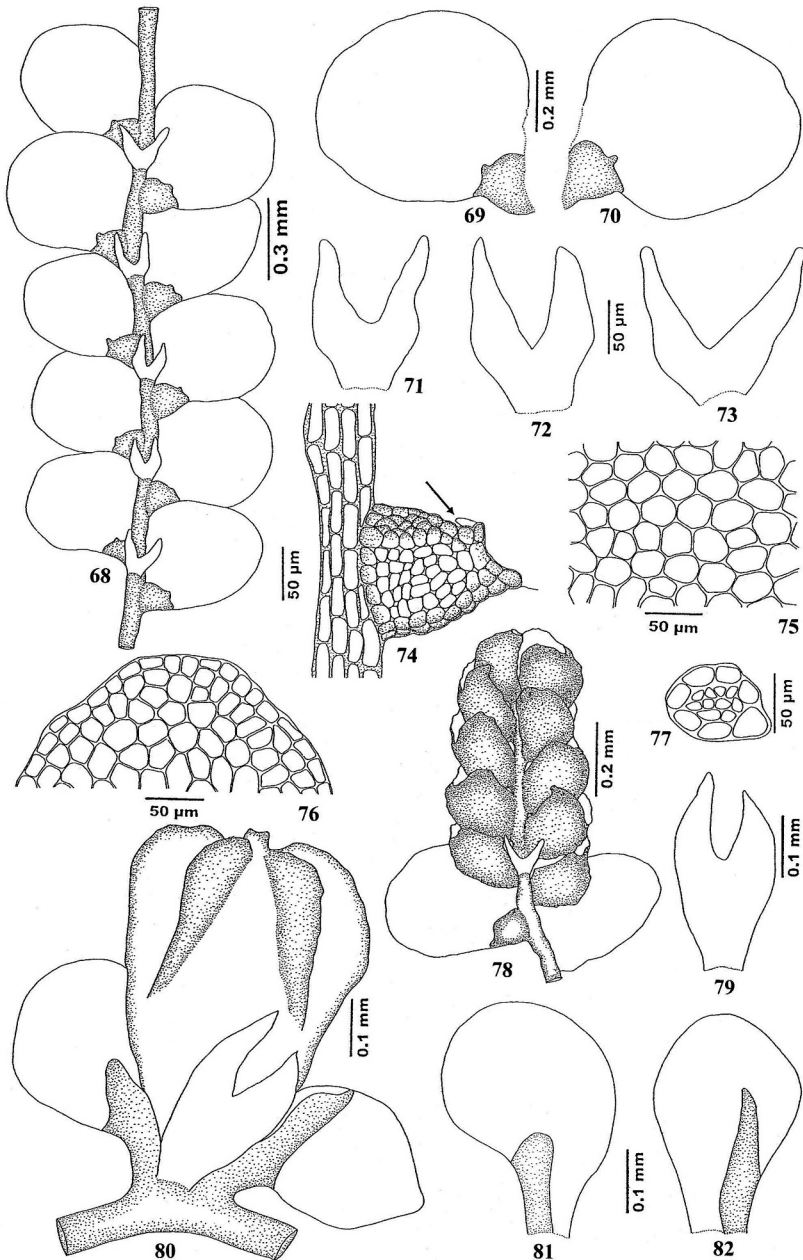
**General distribution:** Malesia.

**Discussion:** The most outstanding characters of *L. albescens* are the large underleaves with a prominently cordate-auriculate base and the very small leaf lobules. *Lejeunea albescens* may be confused with *L. kinabalensis*, especially in the field; both are whitish-green in color and have long, flexuous stems. *Lejeunea albescens* differ from *L. kinabalensis* by 1) eplicate perianths, 2) more shallowly bifid underleaves, and 3) *Calypogeia*-type oil bodies. *Lejeunea albescens*, *L. microloba* and *L. umbilicata* clustered into a group characterized by eplicate, beakless perianths in a phenetic and phylogenetic analysis (Lee *et al.*, submitted). However, *L. albescens* is easily recognized from *L. microloba* and *L. umbilicata* by having leaf lobe margins strongly crenulate and more shallowly bifid underleaves. Some variation is observed in the recurvature of the leaves and in the size of the perianth. Plants from the Philippines (*Rodriguez 78772*) stand out by strongly recurved leaf apices, undulate leaves and long, emergent perianths.

### 3. *Lejeunea anisophylla* Mont., *Ann. Sci. Nat., Bot.*, sér. 2. 19: 263 (1843) **Figs 68-82**

TYPE: Hawaii, "ad cortices inter muscos in insulis Sandwich", *Gaudichaud s.n. & s.d.* (isotype: G!)

= *Lejeunea boninensis* Horik., *J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot.* 1: 24 (1931). TYPE: Japan, Bonin Islands, Hahajima I., 1930, *Horikawa 2027*



Figs 68-82. *Lejeunea anisophylla* Mont. 68. Part of plant in ventral view; 69, 70. Leaves; 71-73. Underleaves; 74. Stem portion and leaf lobule (hyaline papilla shown by arrow); 75. Median cells of leaf lobe; 76. Apical cells of leaf lobe; 77. Cross-section of stem; 78. Androecial shoot; 79. Female bracteole; 80. Perianth with bracts and bracteole; 81, 82. Female bracts. 68, 71-73 drawn from G.E. Lee & H.Y. Tang 1443 (UKMB); 69, 70, 74-80 from G.E. Lee 1054a (UKMB); 81, 82 from G.E. Lee 1443 (UKMB).

(holotype: HIRO!), syn. *fide* Mizutani (1971, under *L. borneensis*) and Hürlimann (1993).

For further synonyms see Mizutani (1961, 1971), Zhu & So (2001) and Pócs (2010, 2011).

**Plants** autoicous, rather minute, delicate, (0.6) 0.75-0.95 mm wide, usually light green when fresh to dark brown when dry, irregularly and slightly branched, branches erect-spreading to spreading, collar with three very small (to reduced) lobes. **Stems** 0.06-0.08 mm in diameter, about 5 cells high in cross-section, epidermal cells 7, 13-25  $\mu\text{m}$  wide, medullary cells 5-10, 8-13  $\mu\text{m}$  wide. **Leaves** contiguous to distant, somewhat plane when dry, usually erect-spreading to spreading and plane when moist. **Leaf lobes** 0.35-0.55 mm long, 0.30-0.35 mm wide (when flattened), ovate; leaf apex broadly rounded, always flat; leaf margin entire; the ventral margin forming an angle of  $120^\circ$ - $140^\circ$  with the keel when flattened; insertion line about 12 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually pentagonal, sometimes rounded, irregular quadrate to rectangular towards the leaf margin; apical cells 18-20  $\mu\text{m}$  long and 15-18  $\mu\text{m}$  wide, median cells 28-30  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide, basal cells 30-38  $\mu\text{m}$  long and 18-25  $\mu\text{m}$  wide; cell walls hyaline, with small trigones, sometimes indistinct and without intermediate thickenings. Cuticle smooth. Oil bodies glistening-botryoidal, *Calypogeia*-type, made up of 8-13 large granules (each 2-3  $\mu\text{m}$  wide), slightly rough externally; marginal cells 5-7 oil bodies per cell, 2-3  $\mu\text{m}$  long and 2-3  $\mu\text{m}$  wide, mostly globose; median cells with 10-12 oil bodies per cell, 5-10  $\mu\text{m}$  long and 3-5  $\mu\text{m}$  wide, globose to somewhat ellipsoid; basal cells with 8-12 oil bodies per cell, 5-12  $\mu\text{m}$  long and 3-5  $\mu\text{m}$  wide, mostly ellipsoid. **Leaf lobules** sometimes reduced, 0.12-0.15 mm long, 0.10-0.12 mm wide, to 1/3 the length of the lobe, at an angle of  $60^\circ$ - $80^\circ$  to the stem, ovate-triangular, inflated along the keel; apex obliquely truncate; keel curved; free margin incurved partially; apical tooth 20-23  $\mu\text{m}$  long, oblong, somewhat erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 25  $\mu\text{m}$  long and 18-20  $\mu\text{m}$  wide. **Underleaves** 0.10-0.15 mm long, 0.10-0.12 mm wide, to 2 times wider than the stem, distant, triangular (slightly longer than wide), not covering the lobules; bilobed, lobes to 1/2-2/3 of underleaf length, about 2-5 cells wide, lanceolate, oblique, somewhat divergent; sinus broad, acute to rounded, U-shaped to V-shaped; underleaf margin entire; base  $\pm$  cuneate, insertion line straight to curved; two large basal underleaf cells lacking; underleaves attached to the stem by 2 superior central cells. **Androecia** 0.3-0.4 (0.6) mm long, 0.20-0.25 mm wide with bracts, on short or long lateral branches, occasionally terminal on the main shoot. Male bracts in 3-6 (8-10) pairs, crenulate with wing, apex obtuse, keels inflated. Male bracteoles 1-2, somewhat smaller than underleaf, margin entire. Antheridia not seen. **Gynoecea** on short or on long branches, occasionally on the main shoot, female bracts loosely arranged, with one innovation, usually with one gynoeceium, sometimes 2 gynoecea in a lateral row due to repeatedly fertile innovations. Female bracts slightly smaller than the leaf, erect-spreading when moist, not enveloping the perianth. Lobes 0.3-0.4 mm long, 0.25-0.35 mm wide, ovate to obovate, apex broadly rounded to acute, margin entire. Lobules 0.15-0.30 mm long, 0.06-0.10 mm wide, rarely reduced, 1/5-1/4 the width and 1/2-2/3 the length of the lobe, oblong to lanceolate, apex acute to obtuse, sometimes truncate or acuminate, keels straight, smooth, 0.15-0.20 mm long. Female bracteoles 0.25-0.35 mm long, 0.15-0.20 mm wide, 1/2 of the perianth length, ovate to oblong with tips acuminate, lobes to 1/3-2/3 of female bracteole length, distant, sinus narrow, acute to obtuse, margin entire to crenulate. Perianths 0.5-0.6 mm long, 0.4-0.5 mm wide,

emergent to 1/2 of the perianth length, obovoid, with 5 sharp keels, sometimes 4 keels with 1 indistinct dorsal keel; beak 2-3 cells long; stalk-like elongation lacking. **Sporophyte:** seta to 0.5 mm long; capsule *ca* 0.3 mm in diameter, valves 0.3 mm long, 0.15 mm wide at middle, scarcely spreading after dehiscence; elaters *ca* 0.2 mm long; spores rectangular to irregular-shaped, 25-38  $\mu$ m long and 13-20  $\mu$ m wide. **Vegetative propagation** not seen.

**Further specimens examined. MALAYSIA. Perlis:** Perlis State Park, 160 m, 2010, *G.E. Lee 2240, 2241* (UKMB); Gua Kelam, 70 m, 2010, *G.E. Lee 2242, 2244* (UKMB). **Pulau Langkawi:** trail to Gunung Jaya, 665 m, 2010, *G.E. Lee 2239, 2242* (UKMB). **Pulau Pinang:** Penang Hill, Bellevue Hotel, 800 m, 2008, *G.E. Lee 1201* (UKMB); Bukit Panchor, 150 m, 2008, *G.E. Lee 1054a* (UKMB). **Perak:** Trolak, trail to recreation park, 30 m, 2009, *Daniel 1, 3, 4* (UKMB). **Pahang:** Genting Highlands, stream near pumping plant, *ca* 1200 m, 1996, *N. Ohnishi 2827* (HIRO); Goh Tong Jaya, near waterfall, 845 m, 2011, *G.E. Lee 2208* (UKMB). **Selangor:** Taman Pertanian. Bukit Cahaya, 50 m, 2009, *G.E. Lee 1372* (UKMB); Hulu Langat, Sungai Gabai waterfall, 100 m, 2010, *Daniel 11-10, 11-11, G.E. Lee 2275* (UKMB). **Johor:** Kota Tinggi, Jason Bay, 1966, *J. Sinclair 10870* (SING), *ibid.*, Sungai Pellepah, 150 m, 1930, *F. Verdoorn 197* (SING). **Kuala Lumpur:** Bird Park, *ca* 50 m, 1996, *N. Ohnishi 2408* (HIRO). **Sarawak:** Bintulu, Bukit Setiam, 440-445 m, 2010, *G.E. Lee & H.Y. Tang 1439, 1440, 1441, 1443, 1448, 1452, 1454, G.E. Lee 2243, 2245* (UKMB); Kuching, Sungai Lalang, road to Bau, 30 m, 2009, *G.E. Lee & H.Y. Tang 1180* (UKMB); Sibiu, Sungai Merah, 30 m, 2011, *Daniel 11-1, 11-2* (UKMB). **Sabah:** Gaya Island near Jesselton, 50 m, 1963, *M. Mizutani 3298, 3300, 3300a, 3304, 3310*, all as *L. boninensis* (NICH); Kebun China Forest near Sandakan, East Coast, 1963, *M. Mizutani 3359* as *L. boninensis* (NICH); Sandakan, East Coast, 1963, *M. Mizutani 3365* as *L. boninensis* (NICH); Kinabalu National Park, along Mamut Road, 1000-1300 m, *T. Kodama 40816* as *L. borneensis* (NICH); from Ranau to Poring, 600 m, *T. Kodama 40857* as *L. borneensis* (NICH); Botanical Garden, around Power station road, 1515 m, 2010, *G.E. Lee 2062* (UKMB); Beaufort district, Klias Forest reserve, 50 m, 2007, *M. Suleiman 1859* (BORH); Tawau district, Golden Hope Plantation, 30 m, 2008, *M. Suleiman & D.P. Masundang 2523* (BORH); Kunak district, Golden Hope Plantation, Mostyn Forest Reserve, 200 m, 2008, *M. Suleiman & D.P. Masundang 2442, 2451, 2464* (BORH); Kota Kinabalu, Kionsom Waterfall, 180 m, 2001, *M.J. Madjapuni 78* (BORH); 200 m, 2010, *G.E. Lee 2145* (UKMB). **INDONESIA.** Kalimantan: B. Bangkirai, 2007, *T. Yamaguchi 293* (BO); Nusa Barong: 100-200 m, 1965, *D. Balázs com. T. Pócs 10-11.111* as *L. borneensis* (NICH); Ambon: 1965, *D. Balázs com. T. Pócs s.n.* as *L. borneensis* (NICH); Sulawesi: Lore Lindu National Park, Toro, 800-900 m, *N.S. Aryanti D3/P5/Q3/50-100/W/6* (BIOT). **SINGAPORE.** Pulau Ubin, Maman Beach, 2 m, 2007, *R.L. Zhu 20070126-10, 20070126-18C* (SING); Upper Peirce Canal, 2007, *R.L. Zhu 20070124-11A* (SING); Bukit Timah, 2007, *R.L. Zhu 20070203-13, 20070203-14* (SING). **PHILIPPINES.** Luzon: Quezon National Park, 1978, *A.R. Alvareg 781142* as *L. borneensis* (NICH). **JAPAN.** Ryukyu: Okinawa, 150 m, 2004, *T. Yamaguchi 24461* (GOET).

**Distribution and habitat in Malaysia:** Perlis\*, Pulau Langkawi\*, Pulau Pinang, Perak\*, Pahang, Selangor\*, Kuala Lumpur, Johor, Sarawak\*, Sabah; epiphytic on trees at low elevations, below 500 m.

**General distribution:** tropical Africa, Asia, Australia, Pacific region.

**Discussion:** *Lejeunea anisophylla* is one of the most common species of the genus in Malaysia. The most outstanding feature of *L. anisophylla* is the long androecial shoot, which is usually terminal on main stems or lateral branches and has male bracts which are often strongly crenulate and winged. The small, somewhat divergent, usually two cells wide underleaf lobes are also characteristic. Superficially, *L. anisophylla* is similar to *L. papilionacea* in the ovate-triangular leaf lobules with a partially incurved free margin, the long, terminal androecial shoots and the morphology of female bracts and bracteoles. The latter species, however, differs in the rounded laminal cells with well-developed trigones and intermediate thickenings, and the oblong-rectangular leaf lobes.

Plants of *L. anisophylla* vary in the size of the underleaf, which are large and rounded with upright lobes in the type materials of *Microlejeunea catanduana* and of *L. boninensis*, whereas small, triangular and with divergent lobes in the type material of *L. kiiensis* and Malaysian specimens. Some variation is also observed in the shape of the laminal cells and the presence of trigones and intermediate thickenings. Quadrate to pentagonal cells usually do not have trigones or very small ones and no intermediate thickenings, whereas rounded cells usually have distinct trigones and intermediate thickenings.

**4. *Lejeunea apiculata* Sande Lac., *Ned. Kruidk. Arch.* 3: 421 (1854) [1855] **Figs 83-100****

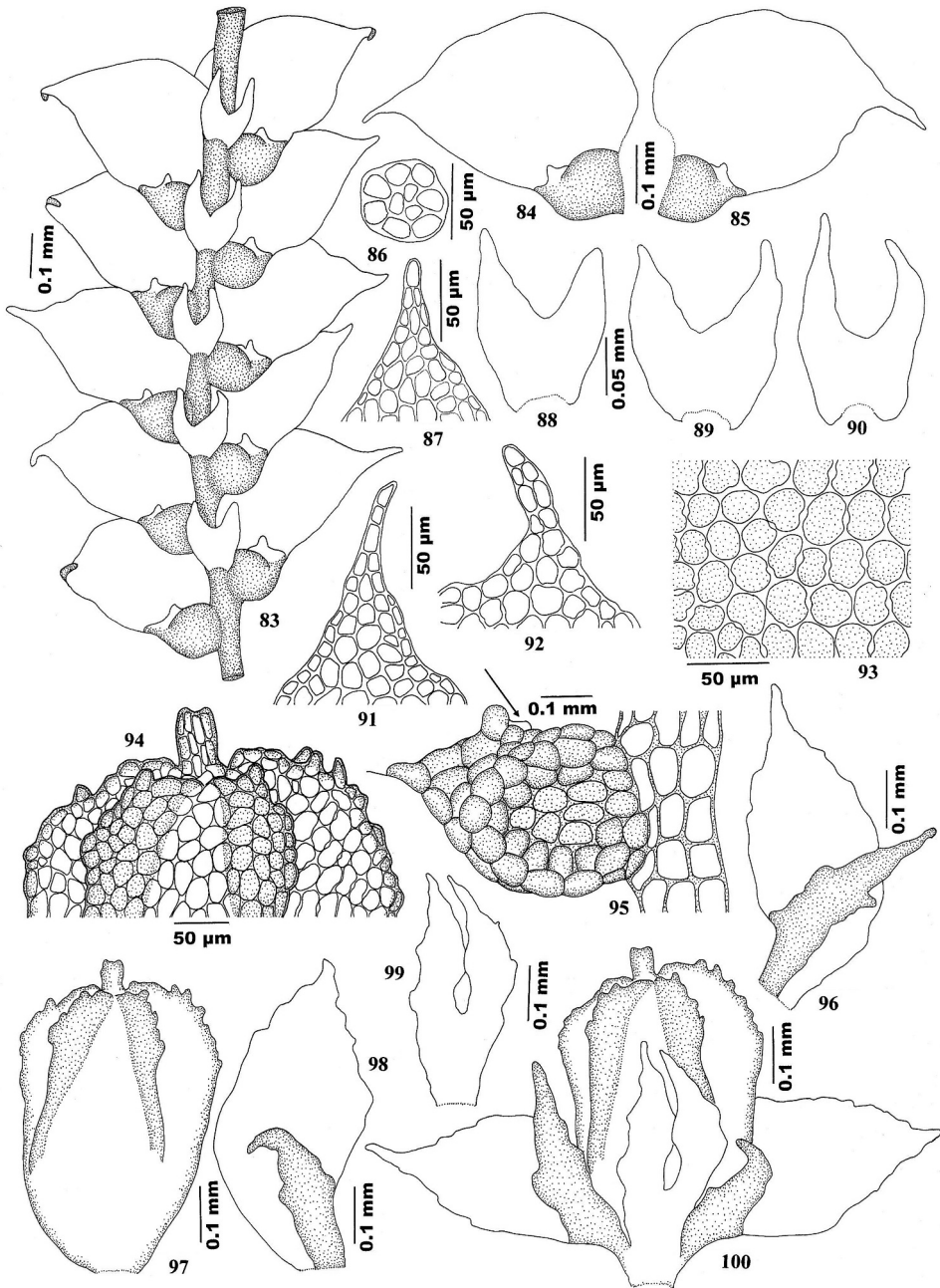
≡ *Eulejeunea apiculata* (Sande Lac.) Schiffn., *Consp. Hepat. Arch. Ind.*: 247 (1898) ≡ *Hygrolejeunea apiculata* (Sande Lac.) Steph., *Sp. Hepat.* 5: 556 (1914) ≡ *Taxilejeunea apiculata* (Sande Lac.) Eifrig, *Ann. Bryol.* 9: 99 (1937) [1936] [*non Taxilejeunea apiculata* (Gottsche) Steph., *Sp. Hepat.* 5: 459 (1913)] ≡ *Stenolejeunea apiculata* (Sande Lac.) R.M.Schust., *Beih. Nova Hedwigia* 9: 144 (1963) syn. *fide*

Söderström *et al.* (2010). TYPE: Indonesia, Java, collector unknown (holotype: L, not seen).

≡ *Prionolejeunea ungulata* Herzog, *J. Hattori Bot. Lab.* 14: 45 (1955). TYPE: China, Taiwan "Formosa". Botel Tobago, Kamm, 380-400 m, an Borke, 1947, *Schwabe 115* (holotype: JE, not seen) syn. *fide* Zhu & So (2001).

For further synonyms see Zhu & So (2001).

**Plants** autoicous, rather minute, delicate, (0.6) 0.75-0.95 mm wide, light brown or pale yellow when dry, irregularly and slightly branched, branches erect-spreading to spreading, collar with three very small (to reduced) lobes. **Stems** 0.04-0.06 mm in diameter, about 4 cells high in cross-section, epidermal cells 7, 10-20 µm wide, medullary cells 3, 6-10 µm wide. **Leaves** imbricate to contiguous, plane when dry, erect-spreading to spreading and plane when moist. **Leaf lobes** 0.3-0.4 mm long, 0.15-0.20 mm wide (when flattened), ovate; leaf apex apiculate; leaf margin entire; the ventral margin forming an angle of 130°-140° with the keel when flattened; insertion line about 11 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, rounded to hexagonal, irregular quadrate to oblong towards the leaf margin; apical cells 10-16 µm long and 10-14 µm wide, median cells 12-20 µm long and 10-16 µm wide, basal cells 16-26 µm long and 10-14 µm wide; cell walls hyaline, with well-developed trigones and conspicuous intermediate thickenings, 1-2 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies not seen. **Leaf lobules** sometimes reduced, *ca* 0.1 mm long, 0.07-0.09 mm wide, to 1/3-1/4 the length of the lobe, at an angle of 60°-70° to the stem, ovate-triangular, inflated along the keel; apex obliquely truncate; keel curved; free margin flat, sometimes slightly incurved partially; apical tooth 14-16 µm long, oblong, somewhat erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 16-20 µm long and 10-12 µm wide. **Underleaves** *ca* 0.1 mm long and wide, to 2 times wider than the stem, distant, ovate (slightly longer than wide), not covering the lobules; bilobed, lobes to 2/3 of underleaf length, about 3-4 cells wide, lanceolate, oblique, distant; sinus broad, obtuse, U-shaped; underleaf margin entire; base ± cuneate, insertion line curved; two large basal underleaf cells differentiated, sometimes lacking; underleaves attached to the stem by 2 superior central cells. **Androecia** 0.2-0.4 mm long, 0.20-0.25 mm wide with bracts, on short or long lateral branches.



Figs 83-100. *Lejeunea apiculata* Sande Lac. 83. Part of plant in ventral view; 84, 85. Leaves; 86. Cross-section of stem; 87, 91, 92. Apical cells of leaf lobe; 88-90. Underleaves; 93. Median cells of leaf lobe; 94. Upper portion of perianth; 95. Stem portion and leaf lobule (hyaline papilla shown by arrow); 96, 98. Female bracts; 97. Perianth; 99. Female bracteole; 100. Perianth with bracts and bracteole. 83-86, 88-90, 92-100 drawn from *V. Schiffner 2962/a* (JE); 87, 91 from *M. Mizutani 250a* (NICH).



Male bracts in 3-4 pairs, crenulate without wing, apex obtuse, keels inflated. Male bracteoles 1, somewhat smaller than underleaf, margin entire. Antheridia not seen. **Gynoecea** on short or on long branches, occasionally on the main shoot, female bracts loosely arranged, with one innovation, usually with one gynoeceium in a lateral position. Female bracts slightly larger than the leaf, erect-spreading when moist, not enveloping the perianth. Lobes 0.5-0.6 mm long, 0.2-0.3 mm wide, elliptical, apex apiculate, margin entire. Lobules 0.3-0.4 mm long, *ca* 0.10 mm wide, rarely reduced, 1/3-1/2 the width and 1/2-4/5 the length of the lobe, lanceolate, apex acute to acuminate, keels straight, smooth, 0.12-0.15 mm long. Female bracteoles 0.4 mm long, 0.2 mm wide, 4/5 of the perianth length, oblong with tips acuminate, lobes to 3/5 of female bracteole length, sinus narrow, obtuse, margin entire. Perianths 0.5-0.6 mm long, 0.3-0.4 mm wide, emergent to 1/3 of the perianth length, obovoid, with 5 sharp keels, cells of the perianth at the keels usually irregularly dentate at apex; beak 2-3 cells long; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined.** **MALAYSIA. Sabah:** In a virgin forest near Forest Dept. Bungalow, Sosopodon, Kundasang, Kinabalu area, 1350 m, 1963, *M. Mizutani 250a, 2039*, both as *Prionolejeunea ungulata* (NICH). **INDONESIA.** Sumatra: Singalang, 1400-1600 m, *V. Schiffner 2962/a* as *Taxilejeunea acutiloba* (JE).

**Distribution and habitat in Malaysia:** Sabah, epiphyllous at elevations above 1000 m.

**General distribution:** Asia, Australia, Pacific region.

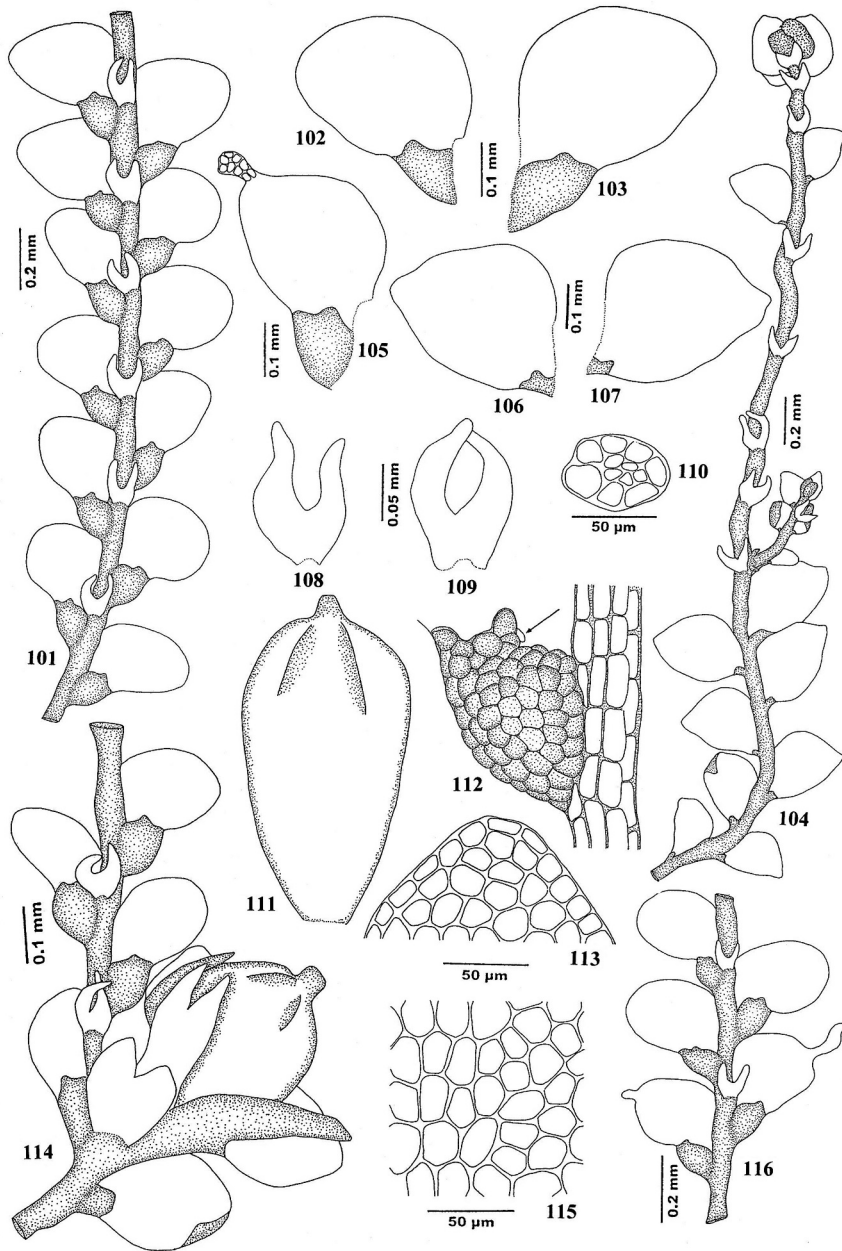
**Discussion:** *Lejeunea apiculata* is easily recognized from other *Lejeuneas* in Malaysia by 1) the strongly apiculate apex of leaf lobe, 2) laminal cells with well-developed trigones and intermediate thickenings, 3) underleaves distant with lanceolate lobes, and 4) the dentate keels at the apex of the perianth. In its apiculate apex of leaf lobe, *L. apiculata* resembles *L. eifrigii* and *L. microloba*. However, *L. apiculata* has ovate underleaves attached to the stem by 2 superior central cells whereas *L. eifrigii* and *L. microloba* have reniform underleaves attached to the stem by 4 superior central cells. The relationships between these three species are distant (Lee *et al.*, submitted). Among the Malaysian *Lejeuneas*, *L. apiculata* is most closely related to *L. tamsapocsi*; for differences see under *L. tamsapocsi*. *Lejeunea apiculata* is quite variable as mentioned by Zhu & So (2001). The materials from Mt. Kinabalu, which were previously identified as *Prionolejeunea ungulata*, have very small, indistinct trigones and no intermediate thickenings. *Lejeunea apiculata* was previously placed in the genus *Stenolejeunea* (as *S. apiculata* (Sande Lac.) R.M.Schust.) but ribbon-like propagules characteristic of the *Stenolejeuneas* have not been seen in the specimens examined.

### 5. *Lejeunea cocoes* Mitt., *J. Proc. Linn. Soc., Bot.* 5: 114 (1861) **Figs 101-116**

TYPE: Sri Lanka, Balagom, Oct. 1848, on *Cocos nucifera*, *Gardner 1399* (erroneously "1499" in Mitten (1861: 114) (holotype: NY!; isotype: BM!)).

For further synonyms see So & Zhu (1998).

**Plants** dioicous, relatively small, delicate, 0.3-0.6 mm wide, green when fresh to pale brown when dry, irregularly and slightly branched, branches erect-spreading, collar with three small lobes. **Stems** 0.05-0.07 mm in diameter, about 3-5 cells high in cross-section, epidermal cells 7, 14-23  $\mu$ m wide, medullary cells 5, 8-14  $\mu$ m wide. **Leaves** distant, plane when dry, erect-spreading and slightly convex when moist. **Leaf lobes** 0.3-0.4 mm long, 0.15-0.20 mm wide (when flattened), ovate; leaf apex narrowly rounded, sometimes obtuse; flat; leaf margin entire; the ventral margin forming an angle of 100°-150° with the keel when



Figs 101-116. *Lejeunea cocoes* Mitt. **101, 104.** Part of plant in ventral view; **102, 103.** Leaves; **105.** Leaf with ribbon-like regenerants; **106, 107.** Caducous leaves; **108, 109.** Underleaves; **110.** Cross-section of stem; **111.** Perianth; **112.** Stem portion and leaf lobule (hyaline papilla shown by arrow); **113.** Apical cells of leaf lobe; **114.** Part of plant, with perianth-bearing branch; **115.** Basal cells of leaf lobe; **116.** Part of plant, some leaves with ribbon-like regenerants. 101-103, 105, 108-111, 113-116 drawn from the holotype, *Gardner 1399* (NY); 104, 106, 107, 112 from *G.E. Lee 2184* (UKMB).

flattened; insertion line 9-10 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregular quadrate to rectangular towards the leaf margin; apical cells 20-25  $\mu\text{m}$  long and 13-20  $\mu\text{m}$  wide, median cells 25-30  $\mu\text{m}$  long and 13-20  $\mu\text{m}$  wide, basal cells 30-38  $\mu\text{m}$  long and 13-20  $\mu\text{m}$  wide; cell walls hyaline, with small trigones and without intermediate thickenings. Cuticle smooth. Oil bodies not seen. **Leaf lobules** often reduced, 0.10-0.15 mm long, 0.07-0.10 mm wide, to 1/3 the length of the lobe, at an angle of 40°-50° to the stem, ovate-triangular, inflated along the keel; apex obliquely truncate; keel curved; free margin incurved partially; apical tooth *ca* 25  $\mu\text{m}$  long, oblong, erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 25-30  $\mu\text{m}$  long and 13-15  $\mu\text{m}$  wide. **Underleaves** 0.08-0.10 mm long and wide, about as wide as the stem, distant, ovate (slightly longer than wide), not covering the lobules; bilobed, lobes to 1/2-2/3 of underleaf length, about 2-3 cells wide, lanceolate, oblique, distant; sinus broad, obtuse, widely U-shaped; underleaf margin entire; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 2 superior central cells. **Androecia** 0.4-0.7 (0.8) mm long, 0.35-0.45 mm wide with bracts, on short or long lateral branches, sometimes terminal on short branches. Male bracts in 3-4 (6) pairs, entire without wing, apex obtuse, keels inflated. Male bracteoles 1-2, larger than underleaf, margin entire. Antheridia not seen. **Gynoecea** terminal on main shoots, sometimes on short or long branches, female bracts somewhat crowded, with one or two innovations, 1-2 gynoecea in a lateral row due to repeatedly fertile innovations. Female bracts smaller than the leaf, erect-spreading when moist, slightly enveloping the perianth. Lobes 0.2-0.3 mm long, 0.10-0.15 mm wide, ovate to obovate, apex narrowly rounded, margin entire. Lobules 0.2-0.3 mm long, *ca* 0.05 mm wide, rarely reduced, 1/3 the width and 4/5 the length of the lobe, oblong-lanceolate, apex acute, keels straight, smooth, *ca* 0.1 mm long. Female bracteoles 0.2-0.3 mm long, 0.15-0.20 mm wide, 2/3 of the perianth length, ovate with tips acute, lobes to 1/3-1/2 of female bracteole length, distant, sinus narrow, acute, margin entire. Perianths 0.6-0.7 mm long, 0.3-0.4 mm wide, emergent to 1/2-2/3 of the perianth length, obovoid, with 5 weak keels; beak 2-3 cells long; cells of the perianth at the keels smooth; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** by means of ribbon-like regenerants from leaf margins and caducous leaves with ribbon-like and plantlet regenerants; ribbon-like regenerants oblong to lanceolate, 2 cells wide and 3-5 (11-20) cells long; caducous leaves ovate-triangular, 0.3-0.5 mm long and 0.2-0.3 mm wide, lobules strongly reduced.

**Further specimens examined.** **MALAYSIA.** **Perlis:** Perlis State Park, Prince of Denmark trail, 160 m, 2010, *G.E. Lee 2339* (UKMB). **Pahang:** Genting Highlands, Goh Tong Jaya, area around the waterfall, 845 m, 2011, *G.E. Lee 2177, 2179, 2184* (UKMB); Cameron Highlands, front gate of Cool Point Hotel, 2009, 1300 m, *G.E. Lee 2338* (UKMB). **SINGAPORE.** Botanical Garden, 1998, *A. Juslén 698* (SING); Sg. Buloh Nature Park, 1998, *A. Juslén 630* (SING).

**Distribution and habitat in Malaysia:** Perlis\*, Pahang\*, Sarawak (Mt. Poe; Mizutani, 1963); epiphytic at elevations below 1500 m.

**General distribution:** tropical Asia.

**Discussion:** *Lejeunea cocoes* together with *L. exilis* is the smallest species in the genus in Malaysia. Characteristic features of *L. cocoes* include 1) plants less than 0.6 mm wide, 2) leaf cells with relatively small or poorly developed trigones and without intermediate thickenings, 3) leaf lobules without large disc cell below the apical tooth, 4) underleaves small and distant, usually hardly wider than the stem, deeply bifid to 1/2-2/3 and with lanceolate lobes, 5) leaf margins sometimes with

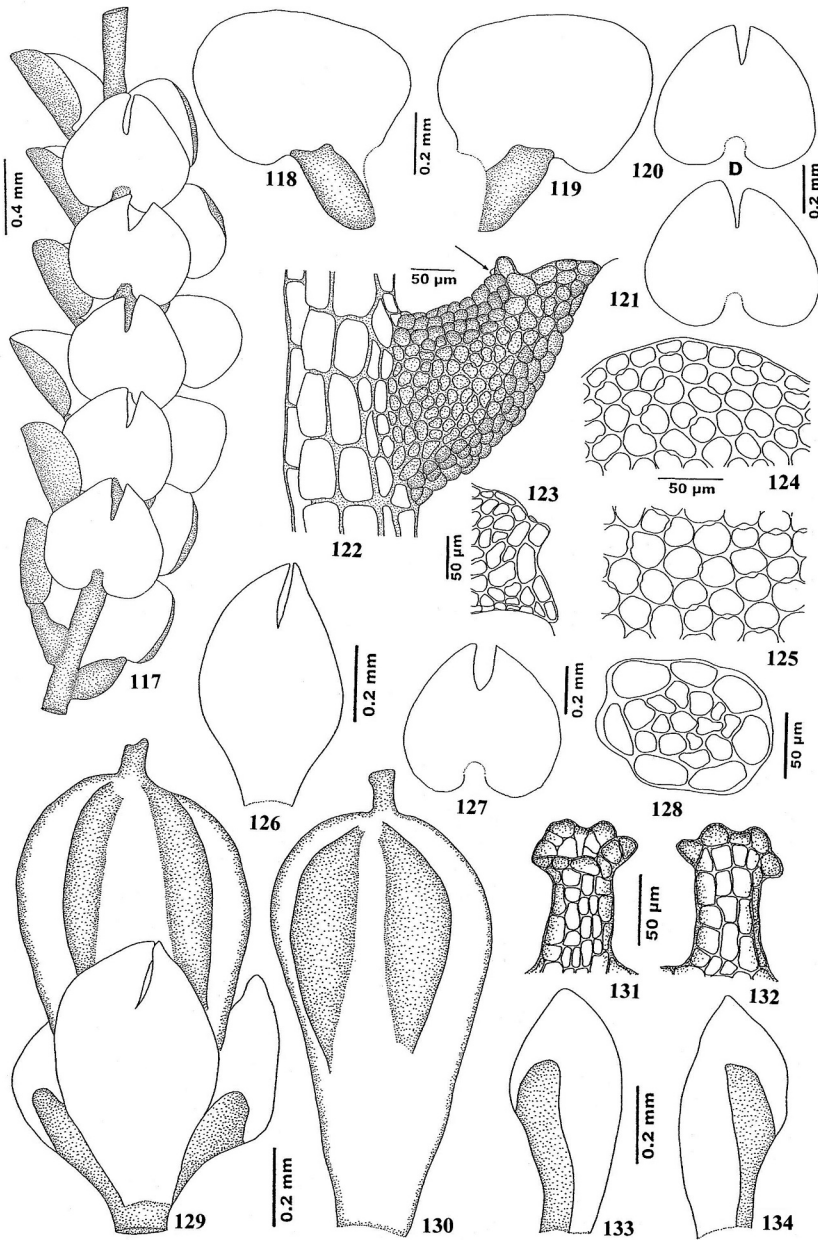
ribbon-like propagules, and 6) plants sometimes with strongly caducous leaves. The underleaves of *L. cocoes* are very similar to those of *L. anisophylla* and immature forms of *L. cocoes* are similar to *L. exilis*. In a phenetic and phylogenetic analysis (Lee *et al.*, submitted), *L. cocoes* was recovered as sister to *L. exilis*. However, *L. cocoes* is dioicous whereas *L. anisophylla* is autoicous. Furthermore, *L. cocoes* differs by the weakly 5-keeled perianth, rounded leaf cells, ribbon-like propagules, caducous leaves, and underleaves being consistently bifid (underleaves undivided and bifid in *L. exilis*).

**6. *Lejeunea compacta* (Steph.) Steph., Sp. Hepat. 5: 771 (1915) Figs 117-134**

Basionym: *Eulejeunea compacta* Steph., *Bull. Herb. Boissier* 5: 93 (1897). TYPE: Japan, Usami, 20 Febr 1895, *Faurie 15266* (holotype: G!).

For further synonyms see Mizutani (1961).

**Plants** dioicous, relatively large, *ca* 1.0 mm wide, usually light green to pale green when fresh to brown when dry, irregularly and loosely branched, branches erect-spreading, collar with three small lobes. **Stem** 0.12-0.14 mm in diameter, about 5-7 cells high in cross-section, epidermal cells 7, 25-44  $\mu$ m wide, medullary cells 14-20, 13-22  $\mu$ m wide. **Leaves** contiguous to imbricate, strongly recurved when dry, erect-spreading, recurved and slightly convex when moist. **Leaf lobes** 0.6-0.8 mm long, 0.4-0.5 mm wide (when flattened), ovate; leaf apex somewhat broadly rounded, slightly recurved; leaf margin entire; the ventral margin forming an angle of 90°-120° with the keel when flattened; insertion line about 16 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregularly quadrate to rectangular towards the leaf margin; apical cells 16-20  $\mu$ m long and 16-20  $\mu$ m wide, median cells 20-30  $\mu$ m long and 20-30  $\mu$ m wide, basal cells 30-44  $\mu$ m long and 16-24  $\mu$ m wide; cell walls yellowish, with well-developed trigones and conspicuous intermediate thickenings, 1-2 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies not seen. **Leaf lobules** sometimes reduced, 0.2-0.3 mm long, *ca* 0.15 mm wide, to 2/5-1/2 the length of the lobe, at an angle of 50-70° to the stem, ovate-oblong, inflated along the keel; apex obliquely truncate; keel curved; free margin incurved partially; apical tooth 26-30  $\mu$ m long, oblong, erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 40-50  $\mu$ m long and 20-24  $\mu$ m wide. **Underleaves** 0.4-0.6 mm long, 0.5-0.7 mm wide, to 3-4 times wider than the stem, contiguous to imbricate, orbicular (somewhat as long as wide), covering the entire leaf lobules; bilobed, lobes to 1/3-1/2 of underleaf length, about 13-15 cells wide, triangular, oblique; sinus narrow to broad, acute to obtuse, U-shaped to V-shaped; underleaf margin entire; base cordate, insertion line curved; two large basal underleaf cells somewhat differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** not seen. **Gynoecia** on short or long branches, female bracts loosely arranged, with one innovation, 2-3 gynoecia in a lateral row due to repeatedly fertile innovations. Female bracts slightly larger than the leaf, erect-spreading when moist, not enveloping the perianth. Lobes 0.5-0.7 mm long, 0.25-0.35 mm wide, obovate, apex acute to obtuse, margin entire. Lobules 0.4-0.6 mm long, 0.12-0.16 mm wide, rarely reduced, 1/3 the width and 2/3 the length of the lobe, lingulate, apex obtuse, keels straight, smooth, 0.3 mm long. Female bracteoles 0.6-0.7 mm long, 0.40-0.45 mm wide, 1/2 of the perianth length, elliptical with tips acute, lobes to 1/3 of female bracteole length, sinus narrow, acute, margin entire. Perianths 0.9-1.1 mm long, 0.5-0.6 mm wide, emergent to 1/2 of the perianth length, pyriform, with 5 sharp



Figs 117-134. *Lejeunea compacta* (Steph.) Steph. 117. Part of plant in ventral view; 118, 119. Leaves; 120, 121, 127. Underleaves; 122. Stem portion and leaf lobule (hyaline papilla shown by arrow); 123. Upper part of leaf lobule when flattened; 124. Apical cells of leaf lobe; 125. Median cells of leaf lobe; 126. Female bracteole; 128. Cross-section of stem; 129. Perianth with bracts and bracteole; 130. Perianth; 131, 132. Beak of perianth; 133, 134. Female bracts. All figures drawn from *G.E. Lee 1574* (UKMB).

keels; beak 3-4 cells long; cells of the perianth at the keels smooth; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined. MALAYSIA. Sabah:** Kinabalu Park, Kandis shelter to Ubah shelter, 2000 m, 2010, *G.E. Lee 1521* (UKMB), Lowii shelter to Mempening shelter, 2300-2500 m, 2010, *G.E. Lee 1537, 1574, 1591, 1594, 1991, 1992, 2005, 2006* (UKMB), Mempening shelter to Layang-layang staff quarters, 2500-2800 m, 2010, *G.E. Lee 1518, 1529, 1585, 1613, 1616, 2011, 2090, 2091, 2092, 2095, 2096* (UKMB), Villosa shelter to Paka shelter, 2900-3050 m, 2010, *G.E. Lee 1968* (UKMB), Paka cave, 2900-3050 m, 2010, *G.E. Lee 1491* (UKMB). **JAPAN.** Toyama Pref., between Keyaki-daira and Sarutok Kurobe valley, 650 m, 1964, *M. Mizutani s.n.* (NICH).

**Distribution and habitat in Malaysia:** Sabah\* (Mt. Kinabalu); epiphytic and epilithic in upper montane forest, 2000-3050 m.

**General distribution:** Asia.

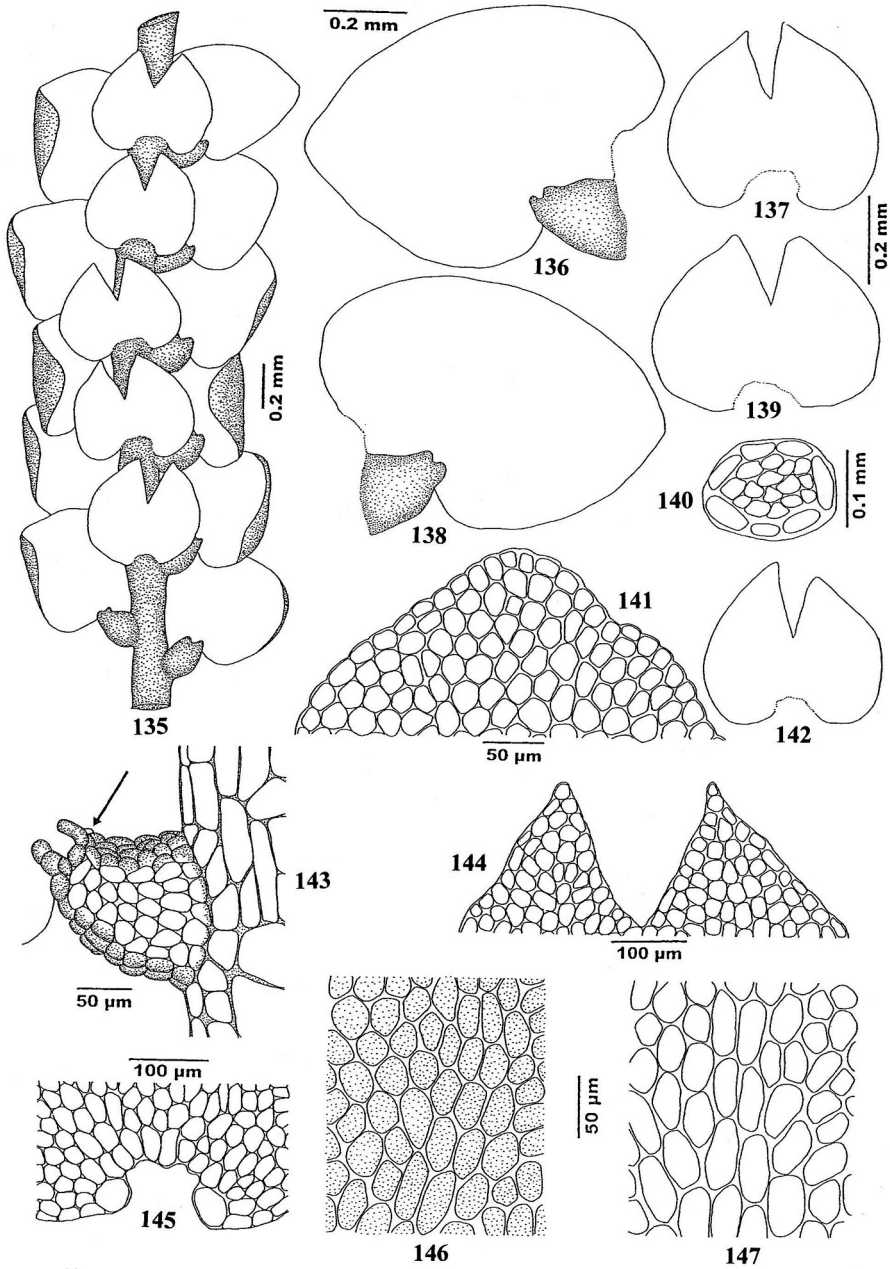
**Discussion:** *Lejeunea compacta* is characterized by 1) the erect-spreading, recurved and convex leaves when moist, 2) laminal cells with well-developed trigones and intermediate thickenings, 3) relatively large ovate-oblong leaf lobules, 4) large, imbricate underleaves with a cordate base, and 5) the pyriform perianth with 5 sharp keels. By its recurved leaves, *L. compacta* resembles the two species *L. stephaniana* and *L. mizutanii* from Borneo, but the latter two differ by straight underleaf bases (not cordate) and leaf cells without conspicuous trigones and intermediate thickenings.

*Lejeunea compacta* can be confused with *L. gradsteinii*; the latter species differs by 1) leaf lobules with flat free margin and two teeth, the first tooth consisting of (1-)2 cells, 2) leaf cells without intermediate thickenings, and 3) deeply bifid underleaves (to 2/3 of underleaf length) with rounded tips. As noted by Mizutani (1961), the type specimen of *L. compacta* (very scanty) is a mixture of *L. compacta* and *L. rotundistipula*.

**7. *Lejeunea contracta* Mizut., *J. Hattori Bot. Lab.* 33: 248 (1970)      **Figs 135-147****

TYPE: Sabah, Kinabalu area, between Tenompok and Kambaranga, south slope of Mt. Kinabalu, 1400-1900 m, 1970, *Iwatsuki 388* (holotype: NICH!).

**Plants** dioicous, relatively large, 1.0-1.3 mm wide, dark brown when dry, irregularly and slightly branched, branches erect-spreading, collar with three small (sometimes reduced) lobes. **Stem** 0.14-0.16 mm in diameter, about 6 cells high in cross-section, epidermal cells 7, 36-68  $\mu\text{m}$  wide, medullary cells 15-25, 15-26  $\mu\text{m}$  wide. **Leaves** closely imbricate to contiguous, slightly recurved when dry, erect-spreading and slightly convex when moist. **Leaf lobes** 0.5-0.7 mm long and 0.4-0.5 mm wide (when flattened), ovate-triangular; leaf apex narrowly rounded, occasionally recurved; leaf margin entire, sometimes weakly crenulate; the ventral margin forming an angle of 50°-90° with the keel when flattened; insertion line 10-11 lobe cells long. **Leaf cells** somewhat differentiated from base to apex, abruptly becoming smaller at the middle of the leaf, mostly quadrate to hexagonal, irregular quadrate towards the leaf margin, basal cells more or less elongated; apical cells 17-28  $\mu\text{m}$  long and 10-18  $\mu\text{m}$  wide, median cells 25-50  $\mu\text{m}$  long and 14-21  $\mu\text{m}$  wide, basal cells 35-57  $\mu\text{m}$  long and 17-25  $\mu\text{m}$  wide; cell walls hyaline, with small trigones and without intermediate thickenings. Cuticle rough by numerous minute papillae. Oil bodies not seen. **Leaf lobules** seldom reduced, 0.15-0.18 mm long and *ca* 0.1 mm wide, to 1/4-1/3 the length of the lobe, at an angle of 50°-60° to the stem, ovate, inflated along the keel; apex truncate, U-shaped; keel curved; free margin flat; apical tooth 25-30  $\mu\text{m}$  long, oblong, erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 25  $\mu\text{m}$  long and 15  $\mu\text{m}$  wide. **Underleaves** 0.3-0.35 mm



Figs 135-147. *Lejeunea contracta* Mizut. **135.** Part of plant in ventral view; **136, 138.** Leaves; **137, 139, 142.** Underleaves; **140.** Cross-section of stem; **141.** Apical cells of leaf lobe; **143.** Stem portion and leaf lobule (hyaline papilla shown by arrow); **144.** Apical cells of underleaf; **145.** Basal cells of underleaf; **146.** Median cells of leaf lobe; **147.** Basal cells of leaf lobe. 135, 139, 140, 142, 143, 145 drawn from the paratype, *M. Mizutani* 2205 (NICH); 136-138, 141, 144, 146, 147 from the holotype, *Z. Iwatsuki* 388 (NICH).

long, 0.3-0.5 mm wide, to 3 times wider than the stem, contiguous, ovate (slightly wider than long), covering 3/4 of the lobules; bilobed, lobes to 1/2 of underleaf length, about 12 cells wide, triangular, oblique to almost straight, sometimes slightly connivent; sinus narrow, acute, V-shaped; underleaf margin entire; base cordate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.4-0.5 mm long, 0.3-0.4 mm wide with bracts, on short lateral branches. Male bracts in 2-3 pairs, entire without wing, apex obtuse, keels inflated. Male bracteole 0-1, smaller than underleaf, margin smooth. Antheridia not seen. **Gynoecia** on short or on long branches, female bracts loosely arranged, with one innovation, usually with one gynoecium in a lateral position. Female bracts slightly smaller than the leaves, erect-spreading when moist, not enveloping the perianth. Lobes 0.4-0.7 mm long, 0.3-0.4 mm wide, elliptic, apex obtuse to subacute, margin entire. Lobules 0.2-0.4 mm long, 0.05-0.10 mm wide, rarely reduced, 1/2 the width and 3/4 the length of the lobe, oblong, apex obtuse to subacute, keels straight, smooth, 0.2-0.3 mm long. Female bracteoles 0.5-0.7 mm long, 0.4-0.5 mm wide, 1/2 of the perianth length, ovate with tips acute, lobes to 1/3 of female bracteole length, distant, sinus acute to obtuse, margin entire. Perianths 0.7-0.9 mm long, 0.4-0.6 mm wide, emergent to 1/2 of the perianth length, obovoid, with 5 sharp keels; beak 3-4 cells long; cells of the perianth at the keels smooth, rarely mammillose; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined. MALAYSIA. Sabah:** Mt. Kinabalu, between Tenompok Pass and Kamaranga Radio Station, 1400-1900 m, 1963, *M. Mizutani 2205* (NICH); near Paca Cave, 2950 m, 1970, *T. Kodama 40569* (NICH).

**Distribution and habitat in Malaysia:** Sabah; terrestrial on rocks at high elevations, above 1400 m.

**General distribution:** only known from Mt. Kinabalu, Sabah.

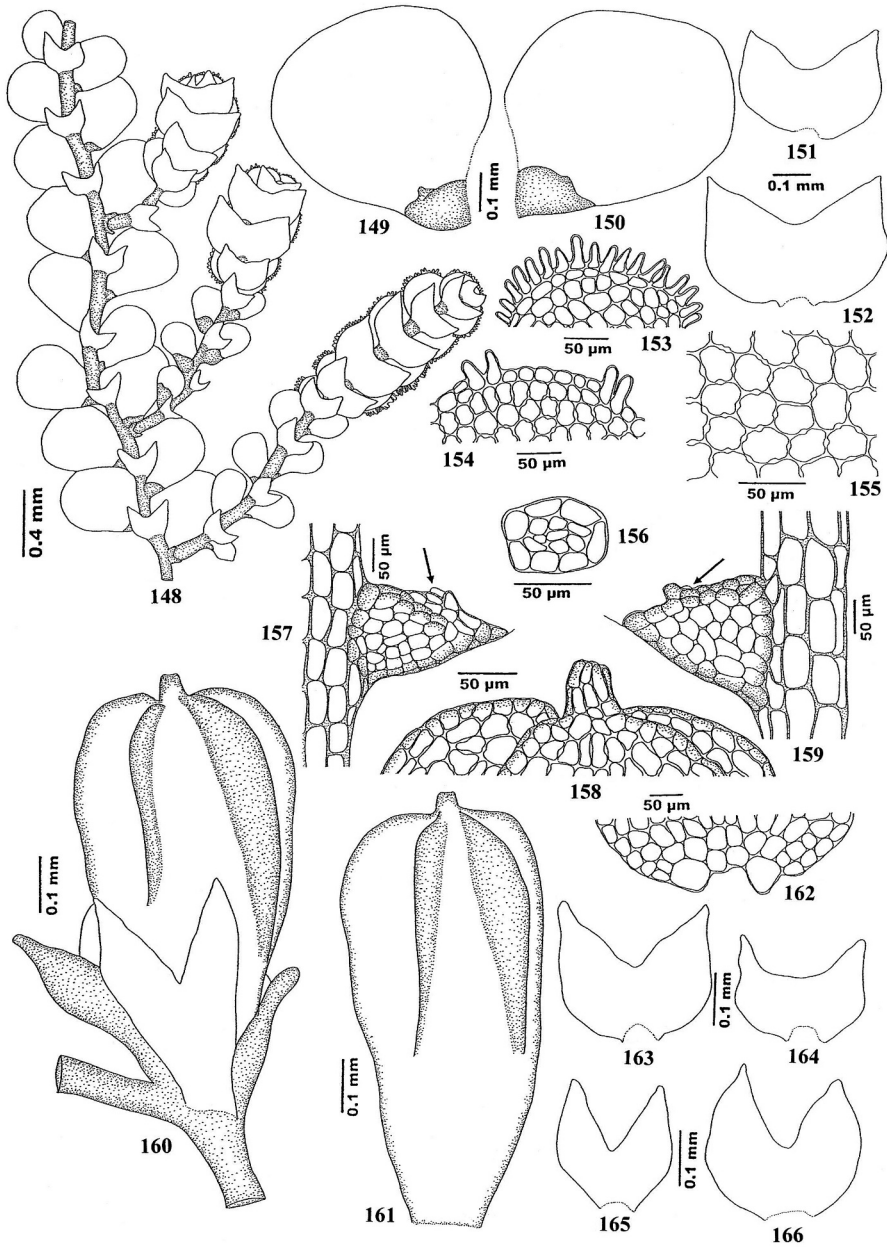
**Discussion:** *Lejeunea contracta* is characterized by the ovate-triangular leaves and the peculiar apex of the lobules, which is curved and U-shaped when flattened. Similar lobule apices are found in *L. umbilicata*, however, the latter species can be distinguished by the eplicate perianth. *Lejeunea contracta* resembles *L. compacta* and *L. kinabalensis* by the large underleaves with a cordate base; characters separating these species are discussed under the *L. kinabalensis*. In a phenetic analysis (Lee *et al.*, submitted), *Lejeunea contracta* and *L. compacta* clustered at a moderately high similarity level.

#### 8. *Lejeunea dimorpha* Kodama, *J. Hattori Bot. Lab.* 41: 383 (1976) **Figs 148-166**

TYPE: Malaysia. Sabah, Kinabalu National Park, near Mamut Mine, 1300 m, 1970, *Kodama 40916* (isotype: NICH!).

**Plants** autoicous, relatively large, 1.1-1.3 mm wide, light green when fresh to light brown when dry, irregularly and densely pinnate, sometimes bipinnately branched, branches erect-spreading to spreading, collar with three small lobes. **Stems** 0.07-0.10 mm in diameter, about 5 cells high in cross-section, epidermal cells 7, 37-52  $\mu\text{m}$  wide, medullary cells 8-16, 12-20  $\mu\text{m}$  wide. **Leaves** contiguous to imbricate, sometimes somewhat distant, rarely recurved when dry, spreading and plane when moist. **Leaf lobes** 0.5-0.8 mm long, 0.35-0.55 mm wide, ovate to ovate-orbicular; leaf apex broadly rounded; leaf margin entire; the ventral margin forming an angle of 160°-180° with the keel when flattened; insertion line about 12 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded to hexagonal, irregularly rounded to quadrate towards the leaf margin; apical cells 20-25  $\mu\text{m}$  long and 12.5-17.5  $\mu\text{m}$  wide, median





Figs. 148-166. *Lejeunea dimorpha* Kodama. 148. Part of plant in ventral view; 149, 150. Leaves; 151, 152, 164. Underleaves of vegetative propagules; 153, 154. Apical cells of the vegetative propagules; 155. Median cells of leaf lobe; 156. Cross-section of stem; 157, 159. Stem portion and leaf lobules (hyaline papilla shown by arrow); 158. Upper portion of perianth; 160. Perianth with bracts and bracteole; 161. Perianth; 162. Basal cells of underleaf; 163, 165, 166. Underleaves. 148-155, 157, 163-166 drawn from the isotype, *T. Kodama* 40916 (NICH); 156, 158-162 from *Tsutomu Kodama* 48129 (NICH).

cells 25-32  $\mu\text{m}$  long and 15-20  $\mu\text{m}$  wide, basal cells 37.5-50  $\mu\text{m}$  long and 17.5-25  $\mu\text{m}$  wide; cell walls hyaline, with well-developed trigones and conspicuous intermediate thickenings, 4-5 (6) per cell, 1-2 (3) between 2 adjacent trigones. Cuticle smooth. Oil bodies glistening-homogeneous, *Massula*-type, smooth, rarely segmented with indistinct granules; marginal cells with 10-20 oil bodies per cell, 2-3  $\mu\text{m}$  long and 2-3  $\mu\text{m}$  wide, mostly globose; median cells with 20-30 oil bodies per cell, 5-7  $\mu\text{m}$  long and 2-3  $\mu\text{m}$  wide, somewhat ellipsoid; basal cells with 40-50 oil bodies per cell, 4-5  $\mu\text{m}$  long and 2-3  $\mu\text{m}$  wide, globose to ellipsoid. **Leaf lobules** occasionally reduced, 0.15-0.20 mm long, 0.10-0.13 mm wide, to 1/4-1/3 the length of the lobe, at an angle of (70°) 100°-120° to the stem, ovate, inflated along the keel; apex obliquely truncate; keel slightly curved to straight; free margin slightly incurved, sometimes flat; apical tooth 20-25  $\mu\text{m}$  long, ovate to oblong, somewhat erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 20-23  $\mu\text{m}$  long and 15-17.5  $\mu\text{m}$  wide. **Underleaves** 0.2-0.3 mm long, 0.2-0.25 mm wide, to 2-3 times wider than the stem, distant, ovate to orbicular (slightly longer than wide), covering half of the lobules; bilobed, lobes to 1/2-2/3 of underleaf length, about 6-8 cells wide, triangular, oblique, somewhat divergent; sinus broad, obtuse, U-shaped; underleaf margin entire to slightly crenulate with projecting cells; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.4-0.5 (1.0) mm long, 0.3-0.4 mm wide with bracts, on short or long lateral branches. Male bracts in 3-6 (10) pairs, crenulate without wing, apex obtuse, keels inflated. Male bracteole 1, smaller than the underleaf, margin entire. Antheridia not seen. **Gynoeceia** on short or on long branches, female bracts loosely arranged, with one innovation, usually with one gynoeceium in a lateral position. Female bracts slightly smaller than the leaves, erect-spreading when moist, not enveloping the perianth. Lobes 0.35-0.45 mm long, 0.10-0.16 mm wide, oblanceolate to obovate, apex obtuse, sometimes apiculate, margin entire. Lobules 0.25-0.40 mm long, 0.05-0.08 mm wide, 1/2 the width and 4/5 the length of the lobe, sometimes as long as the lobe, oblong, apex acute to obtuse, keels straight and smooth, 0.12-0.24 mm long. Female bracteoles 0.73-0.75 mm long, 0.44-0.50 mm wide, 1/2 of the perianth length, ovate to obovate with tips acute, lobes to 1/3-1/2 of female bracteole length, distant, sinus narrow, acute, margin entire. Perianths 0.7-1.0 mm long, 0.4-0.5 mm wide, emergent to 1/2 of the perianth length, obovoid, with 5 keels; beak 2-3 cells long; cells of the perianth at the keels smooth, rarely mammillose; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** by specialized caducous branches with leaf margins with numerous and hyaline rhizoids, and with large, more or less imbricate underleaves which are larger than normal underleaves.

**Further specimens examined.** **MALAYSIA.** **Kelantan:** Gua Musang, Gunung Chamah, trail from Kem Abdullah Sani to Kem Barat, 1165 m, 2011, *A. Damanhuri* 11-85 (UKMB); foot of Gunung Chamah, Dakota trail, 770 m, 2011, *A. Damanhuri* 11-370, 11-373, 11-374, 11-376, 11-378, 11-380, 11-382, 11-384, 11-386, 11-389, 11-391, 11-394, 11-398, 11-401, 11-404, 11-406, 11-409, 11-411, 11-413, 11-416, 11-419, 11-422, 11-425, 11-428, 11-431, 11-435 (UKMB). **Pahang:** Genting Highlands, Goh Tong Jaya, near waterfall, 845 m, 2011, *G.E. Lee* 2211, 2222, 2237 (UKMB). **Sabah:** Kinabalu National Park, along Sungai Liwagu Trail, 1450-1550 m, 1974, *T. Kodama* 48128, 48129 (NICH); Tawau, Maliau Basin, NNW of Kalabakan, 980 m, 1999, *H. Akiyama* 177 (BORH); Keningau district, Crocker Range Park, 1100 m, 2008, *M. Suleiman & D.P. Masundang* 3889 (BORH). **INDONESIA.** Kalimantan: Balikpapan, Kutei Peak, 1952, *W. Meijer* B1872b, B2705b, B2722 (BO), summit, *W. Meijer* B2705b (BO); terrace Berikan Bulu, *W. Meijer* B2321c, B2174a, B2172c (BO). **PAPUA NEW GUINEA.** Morobe Prov., Wau-Salamaua Track towards Black Cat, 15 km NE of Wau, 2000 m, *H. Streimann* 25323 (NICH).

**Distribution and habitat in Malaysia:** Kelantan\*, Pahang\*, Sabah; epiphyllous at elevations above 700 m.

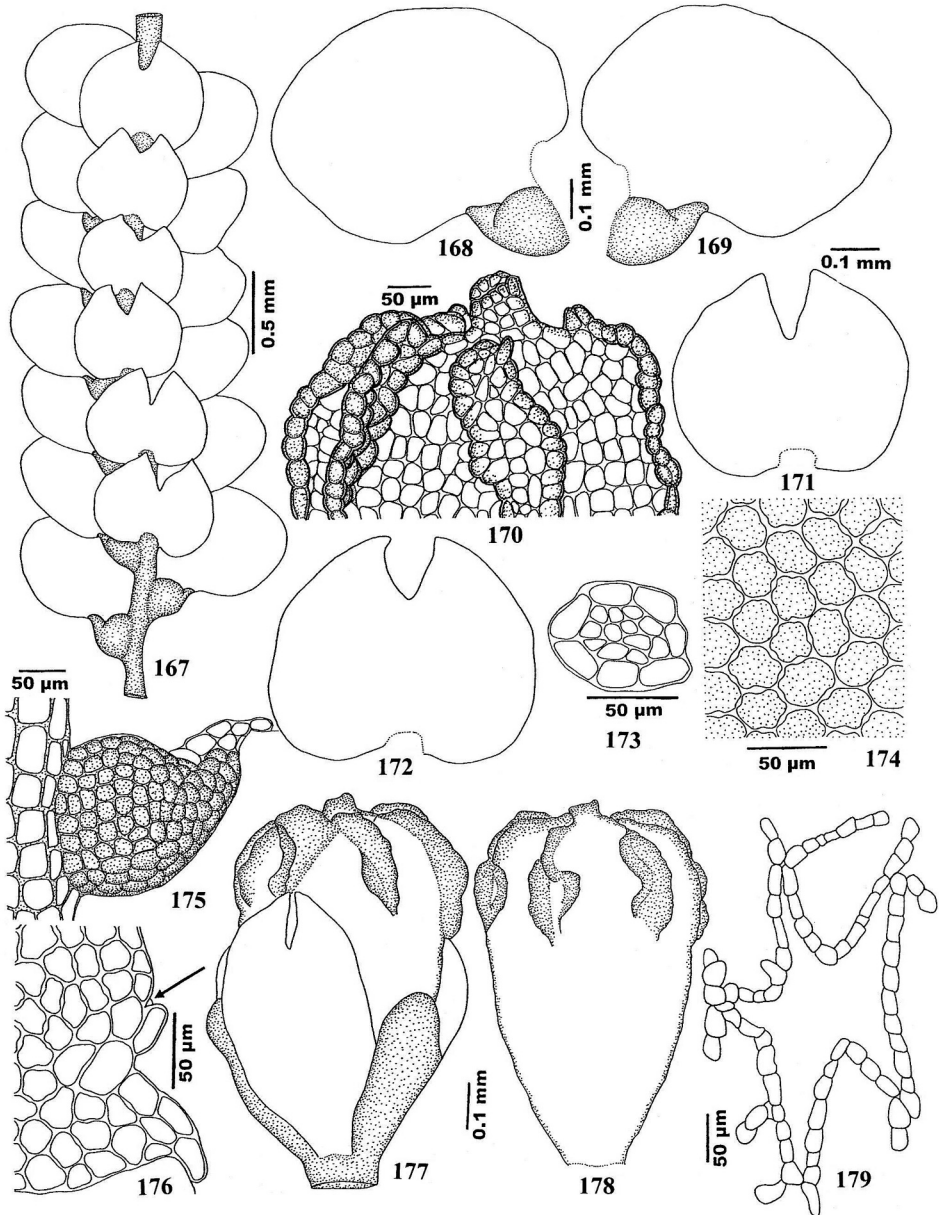
**General distribution:** Malesia.

**Discussion:** *Lejeunea dimorpha* is characterized by the peculiar caducous branches (= cladia), which are unique to this species. Pócs *et al.* (1995) first described the function of these branches for vegetative propagation. Following their breaking away from the stem, the cladia attach to the surfaces of living leaves by their rhizoids on leaf margins and, subsequently, new plantlets sprout from the leaf surfaces. The glistening-homogeneous, *Massula*-type oil bodies and the presence of two intermediate thickenings in the basal leaf cells between adjacent trigones are also characteristic. *Lejeunea dimorpha* was recovered as being most closely related to *L. micholitzii* in a phenetic and phylogenetic analysis (Lee *et al.*, submitted); for differences between the two species see under *L. micholitzii*.

**9. *Lejeunea dipterota* (Eifrig) G.E. Lee, *Polish J. Bot.* 58(1): 61 (2013) Figs 167-179**

Basionym: *Taxilejeunea dipterota* Eifrig, *Ann. Bryol.* 9: 96 (1937). TYPE: Java, "Prov. Preanger. In decliv. Austral. Montis Pangerango; in silvis primaevis supra Tjibodas ad arborum truncos, 18.4.1894, 1500 m, Iter Indicum 1893/94," *Schiffner 3020* (holotype: FH!).

**Plants** dioicous, relatively large, 1.0-1.3 mm wide, light green when fresh to pale green or light brown when dry, irregularly and slightly branched, branches spreading, collar with three small lobes. **Stems** 0.10-0.12 mm in diameter, about 6 cells high in cross-section, epidermal cells 7, 20-33  $\mu\text{m}$  wide, medullary cells 10-12, 13-18  $\mu\text{m}$  wide. **Leaves** imbricate, plane when dry, spreading and plane when moist. **Leaf lobes** 0.6-0.8 mm long, 0.4-0.6 mm wide (when flattened), ovate to ovate-oblong; leaf apex narrowly rounded, always flat; leaf margin entire; the ventral margin forming an angle of 90°-100° with the keel when flattened; insertion line about 13 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregularly quadrate to rectangular towards the leaf margin; apical cells 20-30  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide, median cells 25-33  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide, basal cells 33-45  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide; cell walls hyaline, with well-developed trigones and conspicuous intermediate thickenings, 3-5 per cell, 0-1 (2) between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies not seen. **Leaf lobules** sometimes reduced, 0.25-0.30 mm long and 0.15-0.17 mm wide, to 1/3 the length of the lobe, at an angle of 80°-90° to the stem, ovate-triangular, inflated along the keel; apex obliquely truncate; keel curved; free margin incurved fully, sometimes abruptly flattened towards the apex; apical tooth 33-38  $\mu\text{m}$  long, oblong, erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell present, cell below the apical tooth 45-50  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide. **Underleaves** 0.3-0.4 mm long, 0.5-0.6 mm wide, to 5-6 times wider than the stem, contiguous, reniform (wider than long), always covering the entire lobules; bilobed, lobes to 1/3 of underleaf length, about 10 cells wide, triangular, distant; sinus narrow to broad, acute to slightly obtuse, slightly U-shaped to V-shaped; underleaf margin entire; tips acute; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells lacking; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.5-0.6 mm long, 0.3-0.4 mm wide with bracts, on short or long branches. Male bracts in 3-4 pairs, crenulate without wing, apex truncate, keels inflated. Male bracteole 1, smaller than the underleaf, margin entire. Antheridia not seen. **Gynoecia** on short or long branches, rarely on main shoots, female bracts loosely arranged, with one innovation, usually with one gynoecium in a lateral position. Female bracts



Figs 167-179. *Lejeunea dipterota* (Eifrig) G.E. Lee. 167. Part of plant in ventral view; 168, 169. Leaves; 170. Upper portion of perianth; 171, 172. Underleaves; 173. Cross-section of stem; 174. Median cells of leaf lobe; 175. Stem portion and leaf lobule; 176. Leaf lobule when flattened (hyaline papilla shown by arrow); 177. Perianth with bracts and bracteole; 178. Perianth; 179. Cross-section of perianth. All figures drawn from *G.E. Lee 1801* (UKMB).

slightly smaller than the leaf, erect-spreading when moist, not enveloping the perianth. Lobes 0.7-0.8 mm long, 0.3-0.4 mm wide, ovate to obovate, apex acute to obtuse, margin entire. Lobules 0.4-0.5 mm long, 0.15-0.20 mm wide, rarely reduced, 1/3 the width and 2/3 the length of the lobe, oblong to slightly obovate, apex usually truncate, sometimes slightly obtuse, keels straight, smooth, 0.2-0.3 mm long. Female bracteoles 0.6-0.7 mm long, 0.40-0.45 mm wide, 1/2 of the perianth length, ovate with tips acute to acuminate, lobes to 1/3 of female bracteole length, distant, sinus narrow, acute, margin entire. Perianths 0.8-1.0 mm long, 0.4-0.5 mm wide, emergent to 1/3 of the perianth length, obovoid, with 5 keels, the keels 2-winged, undulate, wings 2-3 cells wide, dorsal keel shorter and less pronounced, lateral keels somehow expanded above as auricles; beak 2-3 cells long; cells of the perianth sometimes bulging on surface; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined.** MALAYSIA. Sabah: Kinabalu Park, trail from Timponoh gate to Kandis shelter, 1900 m, 2010, G.E. Lee 1801, 1802 (UKMB). INDONESIA. Java: G. Malabar, Tjitaroem, 1700 m, 1930, Veldhuis 1930 as *Taxilejeunea dipterota* (FH); Cibodas Botanical Garden, 1420 m, V. Schiffner 2880, 3078, 3139, 3170 as *T. dipterota* (JE), *ibid.*, 1953, W. Meijer B 3676 (SING).

**Distribution and habitat in Malaysia:** Sabah\*; epiphytic at higher elevations, above 1200 m.

**General distribution:** Sabah, Indonesia (Java).

**Discussion:** *Lejeunea dipterota* is characterized by 1) the light green to somewhat glossy green color of the plant when fresh, 2) large, reniform underleaves which always cover the leaf lobules, 3) fully incurved free margin of the lobule, 4) large disc cell below the apical tooth of the leaf lobule, 5) leaf cells with well-developed trigones and intermediate thickenings, and 6) 2-winged and undulate perianth keels. *Lejeunea dipterota* resembles *L. sordida* in the large and reniform underleaves and *L. flava* in shape of the leaf lobes. However, the perianth with undulate, 2-winged keels readily separate *L. dipterota* from the latter two species.

*Lejeunea dipterota* varies in the base of the underleaf. Eifrig (1937) described and illustrated the underleaf bases as being strongly cordate. In the type material, however, the underleaf bases are shallowly curved only. In some collections, underleaves with cordate or shallowly curved bases may be found on a single shoot.

#### 10. *Lejeunea discreta* Lindenb., in Gottsche, Lindenb. & Nees, *Syn. Hepat.*: 361 (1845)

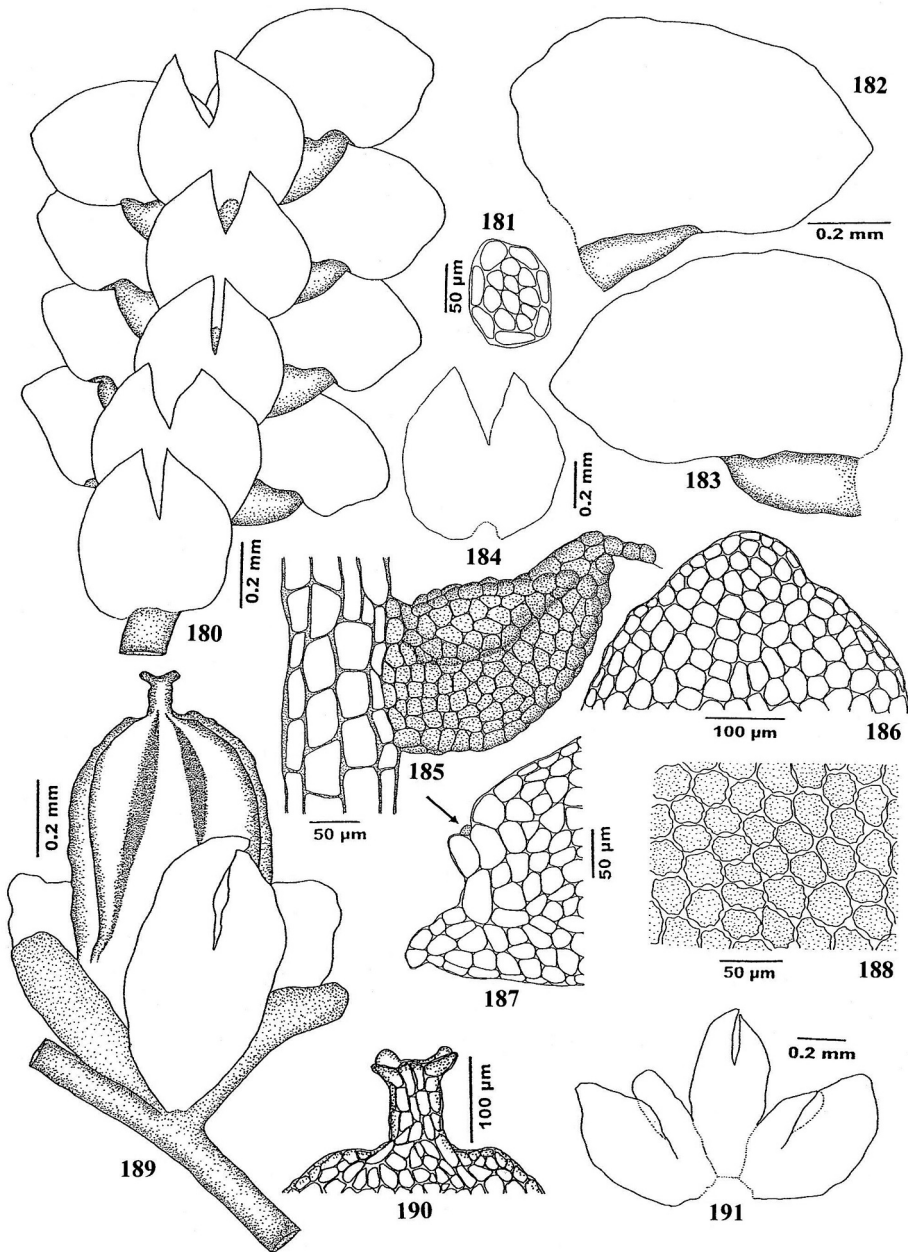
**Figs 180-191**

Basionym: *Hygrolejeunea discreta* (Lindenb.) Schiffn., *Consp. Hepat. Arch. Ind.*: 266 (1898)  $\equiv$  *Taxilejeunea discreta* (Lindenb.) R.M. Schust., *Beih. Nova Hedwigia* 9: 138 (1963). TYPE: Java, "inter *L. thymifolium*  $\beta$  *discretam* (Hb. N[Nees])", collector unknown (holotype: STR, not seen).

= *Lejeunea vaginata* Steph., *Sp. Hepat.* 5: 791 (1915). TYPE: Japan, Kochi Pref., 1904, Okamura 186 (holotype: G!), *syn. fide* Mizutani (1970).

For further synonyms see Mizutani (1961, 1970).

**Plants** dioicous, relatively large, 1.1-1.2 mm wide, usually yellowish green when fresh to dark brown when dry, irregularly and densely pinnate, sometimes bipinnately branched, branches erect-spreading to spreading, collar with three small lobes. **Stems** 0.1-0.2 mm in diameter, about 5 cells high in cross-section, epidermal cells 7, 33-40  $\mu$ m wide, medullary cells 9-12, 16-30  $\mu$ m wide. **Leaves** closely imbricate to contiguous, slightly recurved and somewhat convex when dry, erect-spreading, plane to slightly recurved and slightly convex when moist. **Leaf lobes** 0.7-0.8 mm long, 0.5-0.6 mm wide (when flattened), ovate; leaf apex narrowly rounded, flat to occasionally slightly recurved; leaf margin entire; the ventral



Figs 180-191. *Lejeunea discreta* Lindenb. **180**. Part of plant in ventral view; **181**. Cross-section of stem; **182**, **183**. Leaves; **184**. Underleaf; **185**. Stem portion and leaf lobule; **186**. Apical cells of leaf lobe; **187**. Upper portion of leaf lobule when flattened (hyaline papilla shown by arrow); **188**. Median cells of leaf lobe; **189**. Perianth with bracts and bracteole; **190**. Upper portion of perianth; **191**. Female bracts and bracteole. 180-188 drawn from *G.E. Lee 1146* (UKMB); 189-191 from *G.E. Lee 1037* (UKMB).

margin forming an angle of 110°-150° with the keel when flattened; insertion line about 10 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded to pentagonal, irregular quadrate to rectangular towards the leaf margin; apical cells 13-33 µm long and 7-13 µm wide, median cells 40-53 µm long and 33-53 µm wide, basal cells 53-86 µm long and 33-66 µm wide; cell walls hyaline, with well-developed trigones and conspicuous intermediate thickenings, 1-2 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies somewhat glistening to faintly opaque-granular, fine *Jungermannia*-type, with minute granules, somewhat rough externally; marginal cells with 5-7 oil bodies per cell, 4-5 µm long and 4-5 µm wide, mostly globose; median cells with 7-10 (15) oil bodies per cell, 5-7 µm long and 2-3 µm wide, somewhat ellipsoid; basal cells with 9-12 oil bodies per cell, 4-5 µm long and 4-5 µm wide, mostly globose. **Leaf lobules** sometimes reduced, 0.2-0.4 mm long, 0.10-0.16 mm wide, to 1/2 the length of the lobe, at an angle of 60°-80° to the stem, ovate-oblong to ovate-rectangular, inflated along the keel; apex truncate; keel curved; free margin incurved fully, sometimes abruptly flattened towards the apex; apical tooth 30-35 µm long, oblong, erect, apex somewhat truncate to obtuse; margin between tooth and sinus 3 cells long, large disc cell present, cell below the apical tooth 50 µm long and 33 µm wide. **Underleaves** 0.4-0.5 mm long, 0.40-0.43 mm wide, to 3-4 times wider than the stem, contiguous to imbricate, suborbicular (slightly wider than long), covering half of the lobules; bilobed, lobes to 1/2 of underleaf length, about 7 cells wide, triangular, sometimes slightly connivent; sinus narrow, acute, V-shaped; underleaf margin entire; base ± cuneate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.7-0.9 mm long, 0.5-0.6 mm wide with bracts, terminal on short or long branches, occasionally on the main shoots. Male bracts in 4-6 pairs, entire without wing, apex truncate, keels inflated. Male bracteoles 1-2, smaller than the underleaf, margin entire. Antheridia not seen. **Gynoecea** on short or long branches, sometimes on the main shoot, female bracts loosely arranged, sometimes somewhat crowded, with one innovation, 1-2 gynoecea in a lateral row due to repeatedly fertile innovations. Female bracts larger than the leaves, erect spreading when moist, not enveloping the perianth. Lobes 0.7-0.8 mm long, 0.5-0.6 mm wide, ovate, apex obtuse to acute, margin entire. Lobules 0.5-0.6 mm long, 0.1-0.2 mm wide, rarely reduced, 1/2 the width and 2/3 the length of the lobe, oblong to lanceolate, apex obtuse to truncate, keels straight, smooth, 0.3-0.4 mm long. Female bracteoles 0.6-0.7 mm long, 0.4-0.6 mm wide, 1/2 of the perianth length, ovate with the tips acute, lobes to 1/2 of female bracteole length, connivent, sinus narrow, acute, margin entire. Perianths 1.0-1.2 mm long, 0.5-0.6 mm wide, emergent to 1/2 of the perianth length, oblong, with 5 keels; beak 3-4(-6) cells long, trumpet-shaped; cells of the perianth at the keels smooth, rarely mammillose; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined.** **MALAYSIA. Perak:** Gunung Korbu, summit of Gunung Korbu, 2183 m, 2009, *Damanhuri 09-11* (UKMB). **Pahang:** Cameron Highlands, Brinchang, 1830 m, 1965, *H. Inoue 11191* (TNS); tea plantation area, 1500 m, 2009, *G.E. Lee 1460, 2295, 2298, 2307, 2331* (UKMB); Robinson Waterfalls, 1340 m, 2009, *G.E. Lee 2304, 2328* (UKMB); Genting Highlands, theme park, 1500 m, 2008, *G.E. Lee 1037, 1146* (UKMB); summit of Gunung Ulu Kali, 1600 m, 1996, *N. Ohnishi 2514* (HIRO); along stream near pumping plant, ca 1200 m, 1996, *N. Ohnishi 2836* (HIRO); Fraser's Hill, along road, 1275 m, 2008, *G.E. Lee 1181, 1423, 1427* (UKMB). **Sabah:** Mt. Kinabalu, between Tenompok Pass and Kamaranga Radio Station, 1400-1900 m, 1963, *M. Mizutani 2110e* (NICH), between Kamaranga Radio Station and waterfalls, 2000-2146 m, 1963, *M. Mizutani 2383, 2396, 2601* (NICH), between Tenompok Pass and Ulu Damaian, 1463-

1500 m, 1963, *M. Mizutani* 3239 (NICH), near Forest Department Bungalow, 1350 m, 1963, *M. Mizutani* 6123, 6125, 6142 (NICH), roadside from Headquarters to Timpohon gate, 1530 m, 2010, *G.E. Lee* 1532, 1705 (UKMB), between Timpohon gate and Kandis shelter, 1900 m, 2010, *G.E. Lee* 1734, 1771, 1774, 1778, 1782, 1795, 1798 (UKMB), between Kandis shelter and Ubah shelter, 2000 m, 2010, *G.E. Lee* 1979 (UKMB), Botanical Garden, around Power station road, 1515 m, 2010, *G.E. Lee* 1741, 1742, 1745, 2033, 2035, 2038, 2042, 2043, 2045, 2046, 2047, 2050, 2051, 2053, 2057, 2060, 2063, 2064, 2065, 2066, 2068, 2069, 2070, 2071, 2073, 2074, 2076, 2078, 2079, 2080, 2081, 2082, 2083, 2084 (UKMB), trail from Lowii shelter to Mempoening shelter, 2300-2500 m, 2010, *G.E. Lee* 1986, 1987, 1990 (UKMB), trail from Mempoening shelter to Layang-layang Staff Quarters, 2500-2800 m, 2010, *G.E. Lee* 1465, 1892, 1909, 2101 (UKMB), between Bundu Tuhan View and Liwagu trails, 1530 m, *G.E. Lee* 1689, 1832, 1837, 1838, 1839, 1841, 1845, 1847 (UKMB), Paka cave, 2900-3050 m, 2010, *G.E. Lee* 1511, 1603, 1667, 1942, 1943, 1952, 1954 (UKMB). **INDIA.** Eastern Himalaya: Sikkim, Dalapchand, 1650 m, 2006, *M. Dey & D. K. Singh* 36998, 39609 (CAL). **JAPAN.** Honshu: Fukushima-ken, Futaba-gun, 120 m, 1979, *M. Mizutani* 5665, 5681 (NICH). **INDONESIA.** Java: Mt. Patuha SW of Bandung, 2000-2100 m, 2009, *Afiatri Putrika* 2 (GOET); Cibodas Botanical Garden, 2007, *G.E. Lee & Nova Indri* 15 (BIOT). **PHILIPPINES.** Luzon: Benguet Prov., Mt. Santo Tomas, 1550-2350 m, 1984, *M. Onraedt* 10654 (NICH); Bagio, 1500 m, 1984, *M. Onraedt* 11804c (NICH); Bagio-Bontoc, 1880 m, 1984, *M. Onraedt* 10888g (NICH). **PAPUA NEW GUINEA.** Southern Highlands, Iaro River, Onim, 2230 m, 1982, *H. Streimann* 23863 (NICH). **AUSTRALIA.** Queensland: Barron State Forest, Herberton Range, 13 km S of Atherton, 1000 m, 1983, *H. Streimann* 27207 (NICH). **NEW CALEDONIA.** Mt. Aoui, 500 m, 1951, *Guillaumin & Baumann* 10333, 10516 (GOET); Col de Vulcain, ca 900 m, *Guillaumin & Baumann* 8143b (GOET).

**Distribution and habitat in Malaysia:** Perak, Pahang, Sabah; on various substrates but especially on trees, above 1000 m.

**General distribution:** widespread in Southeast Asia, from India to Papua New Guinea; also in northern Australia (Queensland) and New Caledonia.

**Discussion:** *Lejeunea discreta* is recognized by 1) the narrowly rounded leaf apex, 2) large leaf lobules (to 1/2 the length of the lobe), 3) large disc cell below the apical tooth, 4) incurved free margin of leaf lobule, 5) leaf cells with well-developed trigones and intermediate thickenings, and 6) the trumpet-shaped beak of the perianth. *Lejeunea discreta* resembles *L. pectinella*; both have a large lobule with strongly incurved free margin and the leaf cells with well-developed trigones and intermediate thickenings. Differences between the two species can be seen in the shape of the leaf lobe apex, which is usually narrowly rounded in *L. discreta* and broadly rounded in *L. pectinella*, and in the shape and length of the beak of the perianth where it is trumpet-shaped and 3-4(-6) cells long in *L. discreta* while short-cylindrical and 8-10 cells long in *L. pectinella*.

Plants of *L. discreta* vary in size, in recurvature of the leaves, in the width of underleaves and in the length and shape of the perianth beak. Epiphyllous plants often have shorter length of leaf (0.38-0.40 mm) and width of underleaves (0.16-0.18 mm). Furthermore, leaves are plane when moist with the underleaves distantly arranged and lobule occasionally reduced. Plants with larger leaves (0.7-0.8 mm long) and underleaves (0.40-0.44 mm long) normally occur in highland forest. In plants from Gunung Korbu, Cameron Highlands and Genting Highlands, the apices of leaves are strongly recurved when moist and the underleaves are larger and overlapping each other. The leaves are more erect-spreading with lobules at an angle of 45°-60° to the stem. On the other hand, the apices of leaves from the lowland forest (< 500 m) are rarely recurved when moist and usually spreading with the lobule at an angle of 70°-90° to the stem. Plants from Java have a longer, 5-6 cells long beak and the trumpet-shaped beak is not so prominent as compared to the perianth of plants from Peninsular Malaysia which are 3-4 cells

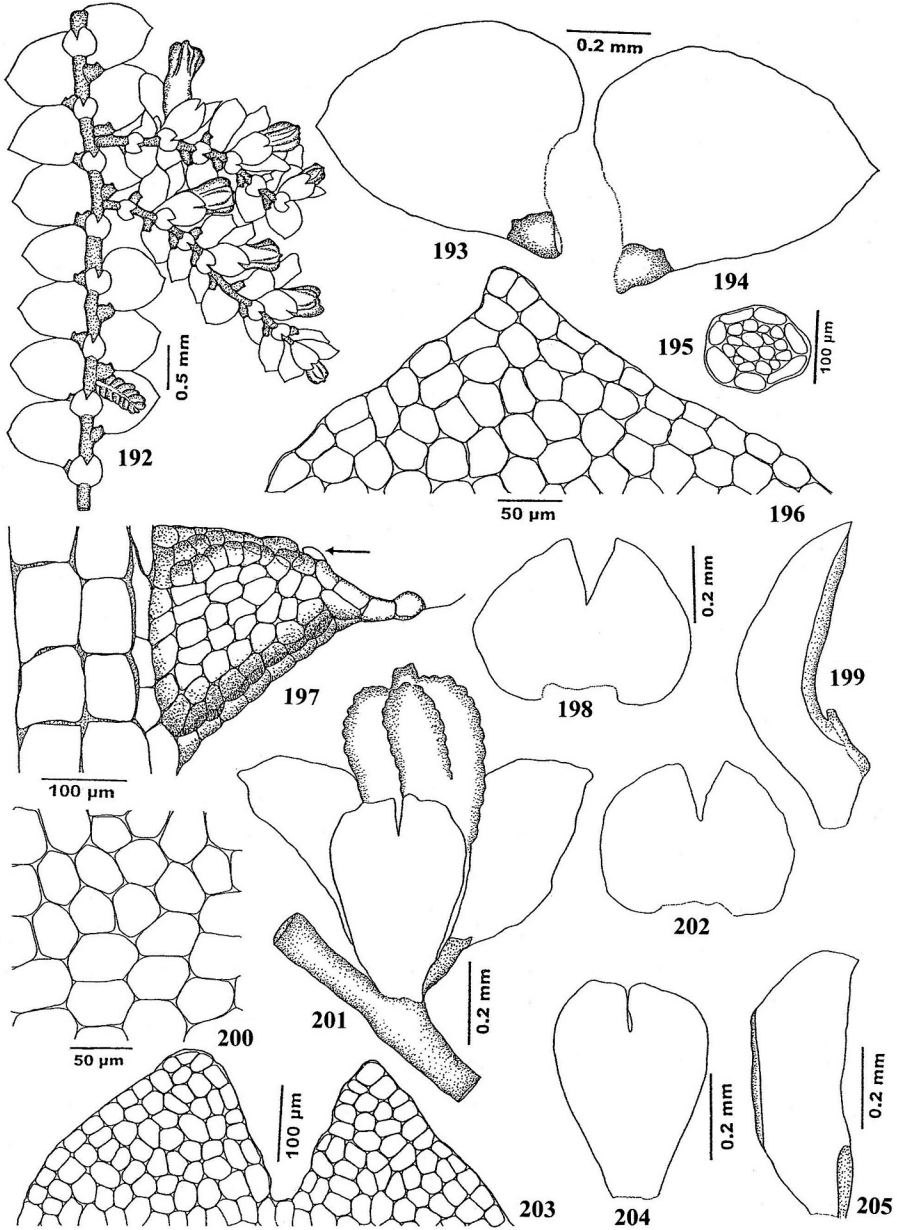


long and more prominently trumpet-shaped. Some interesting variation, finally, is seen among the synonyms of *L. discreta*, e.g., strongly crenulated leaf margins in the type of *Hygrolejeunea norfolkiensis* and strongly recurved leaves with broadly rounded apices and cordate underleaf base in the type of *H. rostrata*.

**11. *Lejeunea eifrigii* Mizut., *J. Hattori Bot. Lab.* 33: 244 (1970) **Figs 192-204****

Basionym: *Taxilejeunea acutiloba* Eifrig, *Ann. Bryol.* 9: 94 (1937) (non *Lejeunea acutiloba* (Hook.f. & Tayl.) Gott., *Lindenb. et Nees, Syn. Hepat.*: 321 (1845) = *Taxilejeunea acutiloba* forma *major* Eifrig, *Ann. Bryol.* 9: 96 (1937). TYPE (lectotype designated by R. Grolle in sched., see Lee *et al.*, 2011b): Indonesia. Java, Salak, *Schiffner 3223* (JE!).

**Plants** autoicous, relatively large, 1.7-2.0 mm wide, usually yellowish green to pale green when fresh to dark green when dry, irregularly and densely to loosely branched, branches erect-spreading, collar with three small lobes, the lobes often reduced, sometimes only with two distinct lobes at the lateral sides and one indistinct dorsal lobe. **Stems** 0.13-0.17 mm in diameter, about 6 cells high in cross-section, epidermal cells 7, 30-60  $\mu$ m wide, medullary cells 16-30, 20-40  $\mu$ m wide. **Leaves** contiguous, often somewhat crisped and slightly recurved when dry, erect-spreading to spreading and plane when moist. **Leaf lobes** 0.4-0.8 mm long, 0.6-0.7 mm wide (when flattened), ovate; leaf apex apiculate, sometimes slightly acute to obtuse; leaf margin entire, branch leaf margin sometimes crenulate; the ventral margin forming an angle of 120°-170° with the keel when flattened; insertion line about 10 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually quadrate to hexagonal, irregularly rectangular towards the leaf margin; apical cells 20-30  $\mu$ m long and 12-17  $\mu$ m wide, median cells 50-58  $\mu$ m long and 20-30  $\mu$ m wide, basal cells 62-80  $\mu$ m long and 20-33  $\mu$ m wide; cell walls hyaline, with small trigones and without intermediate thickenings. Cuticle smooth. Oil bodies opaque-papillose, rough *Jungermannia* type, with minute granules, rough externally; marginal cells with 3-5 oil bodies per cell, 3-5  $\mu$ m long and 3-5  $\mu$ m wide, mostly globose; median cells with 5-20 oil bodies per cell, 7-10  $\mu$ m long and 4-5  $\mu$ m wide, ovoid to ellipsoid; basal cells with 18-20 oil bodies per cell, 5-6  $\mu$ m long and 5-6  $\mu$ m wide, mostly globose to ovoid. **Leaf lobules** frequently reduced, 0.13-0.16 mm long and 0.09-1.10 mm wide, to 1/5-1/4 the length of the lobe, at an angle of 50°-70° to the stem, ovate, inflated along the keel; apex obliquely truncate; keel curved; free margin flat; apical tooth 33-35  $\mu$ m long, oblong, somewhat erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 40  $\mu$ m long, 20  $\mu$ m wide. **Underleaves** 0.1-0.3 mm long, 0.6-0.7 mm wide, to 2 times wider than the stem, very distant, reniform (wider than long), covering half of the lobules; bilobed, lobes to 1/2 of underleaf length, about 10 cells wide, triangular, somewhat oblique; sinus narrow, acute to obtuse, U-shaped to V-shaped; margin entire; base  $\pm$  cuneate, insertion line straight; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.3-0.8 mm long, 0.3-0.5 mm wide with bracts, on short or long lateral branches, occasionally on the main shoots. Male bracts in 3-6 pairs, entire without wing, apex obtuse, keels inflated. Male bracteoles 0-2, smaller than the underleaf, margin entire. Antheridia not seen. **Gynoecia** on short or long branches, female bracts loosely arranged and sometimes somewhat crowded, with one innovation, 1-3 gynoecia in a lateral row due to repeatedly fertile innovations. Female bracts smaller than the leaf, sometimes almost same size as



Figs 192-204. *Lejeunea eifrigii* Mizut. **192.** Part of plant in ventral view; **193, 194.** Leaves; **195.** Cross-section of stem; **196.** Apical cells of leaf lobe; **197.** Stem portion and leaf lobule (hyaline papilla shown by arrow); **198, 202.** Underleaves; **199, 205.** Female bracts; **200.** Median cells of leaf lobe; **201.** Perianth with bracts and bracteole; **203.** Apical cells of underleaf; **204.** Female bracteole. All figures drawn from *G.E. Lee 1185* (UKMB).

the leaf, erect-spreading when moist, not enveloping the perianth. Lobes 0.6-0.8 mm long, 0.20-0.25 mm wide, oblong to lanceolate, apex acute, margin entire. Lobules 0.20-0.23 mm long, 13-15  $\mu$ m wide, very small, sometimes reduced, 1/6 the width and 1/3 the length of the lobe, linear, apex rounded to obtuse, keels straight, smooth, 1.5-1.6 mm long. Female bracteoles 0.5-0.6 mm long, 0.40-0.43 mm wide, 1/2 of the perianth length, obovate with tips rounded, lobes to 1/4 of female bracteole length, sinus narrow, acute, margin entire. Perianths 1.0 mm long, 0.5 mm wide, emergent to 1/3-1/2 of the perianth length, clavate, with 5 keels; beak 2 cells long; cells of the perianth at the keels strongly mammillose; stalk-like elongation sometimes present, 0.3-0.4 mm long. **Sporophyte:** seta to 0.4-0.6 mm long; capsule 0.3-0.4 mm in diameter, valves 0.3 mm long, 0.2 mm wide at middle, somewhat spreading after dehiscence; elaters *ca* 0.2 mm long; spores not seen. **Vegetative propagation** not seen.

**Further specimens examined. MALAYSIA. Pahang:** Cameron Highlands, Mentigi trail, 1360 m, 2009, *G.E. Lee 1168, 1170, 1185, 2297* (UKMB); Parit Waterfalls, 1340 m, 2009, *G.E. Lee 1367, 2334* (UKMB); Genting Highlands, along the road to Gunung Ulu Kali, 1650 m, 2009, *G.E. Lee 1192, 1194* (UKMB). **Sabah:** Mt. Kinabalu, between Kamaranga Radio Station and Waterfalls, 2000-2146 m, 1963, *M. Mizutani 2482* (NICH); mossy forest between Tenompok Pass and Ulu Damaian, 1463-1500 m, 1963, *M. Mizutani 3244* (NICH), between Sosopodon and S. Kelinggen, 1963, *M. Mizutani 3849* (NICH), trail from Timpohon gate to Kandis Shelter, 1900 m, 2010, *G.E. Lee 1662, 1783, 1784, 1789, 1792, 1815* (UKMB), Botanical Garden, around Power station road, 1515 m, 2010, *G.E. Lee 2079* (UKMB), between Bundu Tuhan View trail and Liwagu trail, 1530 m, 2010, *G.E. Lee 1852* (UKMB). **INDIA.** Sikkim: Rate chhu, East district, 1788 m, 2005, *D. Singh & M. Dey 36042* (CAL). **INDONESIA.** Sumatra: Singalang, 1800 m, *V. Schiffner 2972, 3209* as *Taxilejeunea acutiloba* (JE); W Java, Salak, 700 m, *V. Schiffner 3032* as *T. acutiloba* f. *major* (JE). **PHILIPPINES.** Mindoro: Paitan-Ramayan, 900 m, 1988, *E. Salgado 12245, 12286* (NICH). **JAPAN.** Kyushu: Miyaki Pref., Nichinan, Kobuze Falls, 1970, *M. Mizutani s.n.* (NICH); Kobuze Falls, northwest of Nichinan, Miyazaki Prefecture, 1957, *S. Hattori & M. Mizutani s.n.* (NICH).

**Distribution and habitat in Malaysia:** Pahang, Sabah; on various substrates at elevations above 900 m.

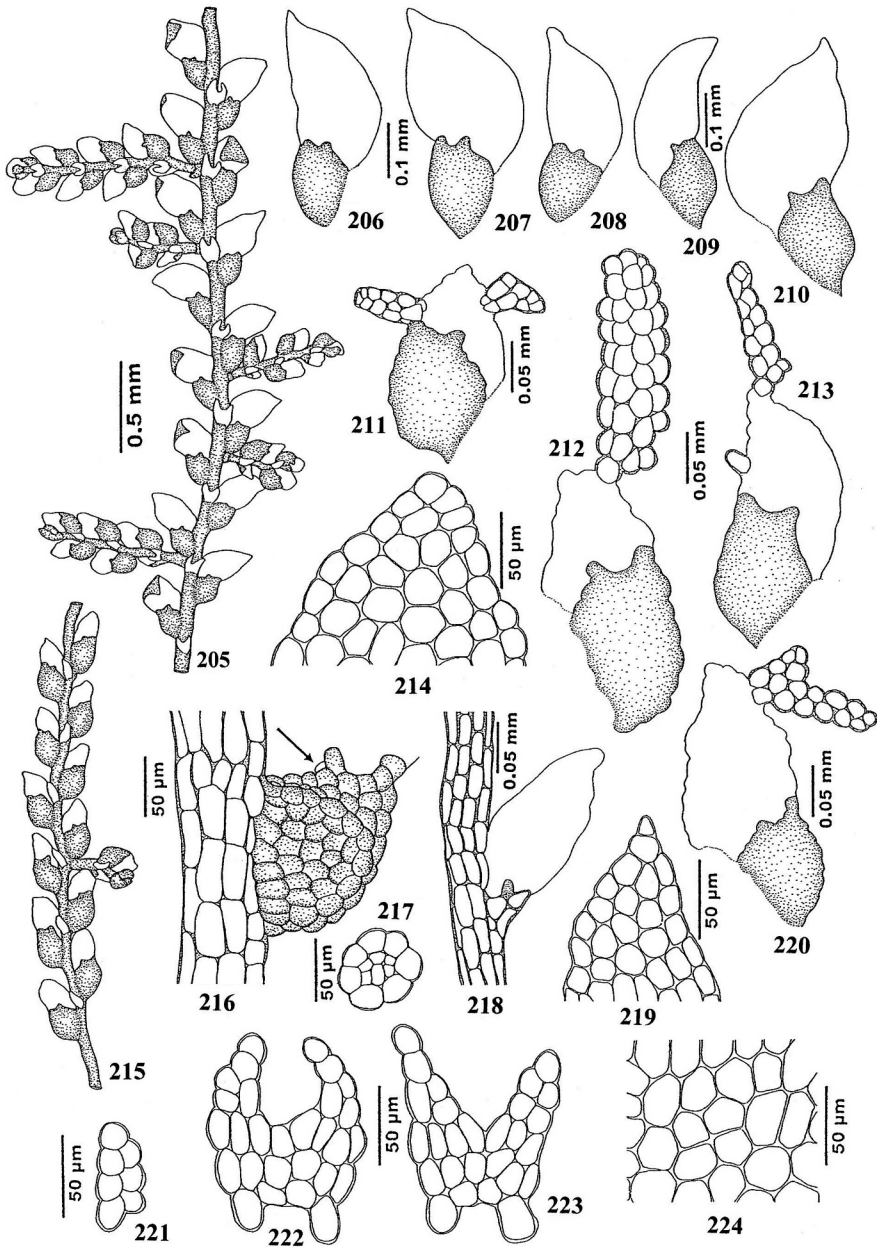
**General distribution:** tropical Asia.

**Discussion:** *Lejeunea eifrigii* is distinguished by 1) the long clavate perianth with 5 mammillose keels, 2) apiculate leaf apex, 3) small and reniform underleaves, 4) leaf cells with small trigones and without intermediate thickenings, 5) leaves somewhat crisped when dry, and 6) frequently reduced lobules on leaf lobes and female bracts. *Lejeunea eifrigii* was resolved as sister to *L. alata* in a phenetic and phylogenetic analysis (Lee *et al.*, submitted); differences between the two species are discussed under *L. alata*.

*Lejeunea eifrigii* varies particularly in the apices of leaf lobes, which may be sometimes being acute or obtuse instead of apiculate. Two specimens from Japan, collected from wet rock, consist of rather large, freely branched plants with numerous perianths and with unusually robust stems made up of 25-32 medullary rows of cells.

**12. *Lejeunea exilis* (Reinw., Blume et Nees) Grolle, *J. Hattori Bot. Lab.* 46: 353 (1979)  
Figs 205-224**

Basionym: *Jungermannia exilis* Reinw., Blume et Nees, *Nova Acta Caes. Leop. Nat. Cur.* 12: 227 (1825)  $\equiv$  *Jungermannia cucullata* var.  $\beta$  *exilis* (Reinw., Blume et Nees) Nees, *Enumer. Pl. Crypt. Jav. Hepat.*: 57 (1980)  $\equiv$  *Lejeunea cucullata* var.  $\beta$  *exilis* (Reinw., Blume et Nees) Gottsche *et al.*, *Syn. Hepat.*: 390 (1845)  $\equiv$



Figs 205-224. *Lejeunea exilis* (Reinw., Blume et Nees) Grolle var. *exilis*. 205, 215. Part of plants in ventral view; 206-210. Leaves; 211-213, 220. Leaves with marginal regenerants; 214, 216, 218. Stem portion and leaf lobules (hyaline papilla shown by arrow); 217. Cross-section of stem; 219. Apical cells of leaf lobe; 221-223. Cells of underleaves; 224. Median cells of leaf lobe. 205, 207, 210, 212, 214, 215-217, 221-224 drawn from G.E. Lee 1162 (UKMB); 206, 208, 209, 219 from M. Mizutani 6144 (NICH); 211, 213 from A. Damanhuri 09-5 (UKMB); 218 from A. Damanhuri 08-1 (UKMB); 220 from G.E. Lee 1181 (UKMB).

*Eulejeunea cucullata* var.  $\beta$  *exilis* (Reinw., Blume et Nees) Schiffn., *Consp. Hepat. Arch. Ind.*: 254 (1898)  $\equiv$  *Microlejeunea exilis* (Reinw., Blume et Nees) Bischl. et al., *Nova Hedwigia* 3: 452 (1962). TYPE: Java, without collector (holotype: STR, not seen).

For further synonyms see Zhu & Grolle (2003).

**Plants** dioicous, relatively very small, (0.3) 0.5-0.8 mm wide, yellowish green to light green when fresh, yellowish to pale brown when dry, irregularly and loosely branched, sometimes bipinnately branched on female plants, branches erect-spreading, collar with three small lobes. **Stems** (0.03) 0.06-0.08 mm in diameter, about 4 cells high in cross-section, epidermal cells 7, 25-35  $\mu$ m wide, medullary cells 3-6, 12-18  $\mu$ m wide. **Leaves** distant, never recurved when dry, erect-spreading and plane when moist. **Leaf lobes** (0.1) 0.3-0.6 mm long, 0.1-0.3 mm wide (when flattened), ovate to ovate-oblong; leaf apex narrowly rounded, acute to acuminate; leaf margin entire to slightly crenulate; the ventral margin forming an angle of 120°-170° with the keel when flattened; insertion line about 9 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually quadrate to hexagonal, irregularly rectangular towards the leaf margin; apical cells 18-20  $\mu$ m long and 18-20  $\mu$ m wide, median cells 25-28  $\mu$ m long and 18-20  $\mu$ m wide, basal cells 25-33  $\mu$ m long and 17-25  $\mu$ m wide; cell walls hyaline, with small or indistinct trigones and without intermediate thickenings. Cuticle smooth. Oil bodies somewhat glistening to faintly opaque-granular, fine *Jungermannia*-type, with minute granules, somewhat rough externally, 3-5 per cell, 5-7  $\mu$ m long and 2-3  $\mu$ m wide, mostly ellipsoid in all cells. **Leaf lobules** occasionally reduced, 0.2-0.3 mm long, 0.10-0.15 mm wide, to 2/5-1/2 the length of the lobe, at an angle of 40°-50° to the stem, ovate-oblong, inflated along the keel; apex obliquely truncate; keel curved; free margin incurved partially, sometimes flat; apical tooth 33-40  $\mu$ m long, oblong, erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 25-30  $\mu$ m long and 20-22  $\mu$ m wide. **Underleaves** minute, 0.06-0.08 mm long, 0.06-0.07 mm wide, as wide as or slightly wider than the stem, very distant, dimorphic, bilobed and unlobed; bilobed underleaves orbicular (slightly longer than wide), not covering the lobules, lobes to 1/2 of underleaf length, about 3 cells wide, lanceolate, oblique to almost straight, sinus broad, acute to obtuse, U-shaped to V-shaped, underleaf margin crenulate, base  $\pm$  cuneate, insertion line curved, two large basal underleaf cells differentiated, underleaves attached to the stem by 2 superior central cells; unlobed underleaves lanceolate, 4-5 cells long, 2-3 cells wide. **Androecia** 0.25-0.40 (0.6) mm long, 0.2-0.3 (0.4) mm wide with bracts, on short lateral branches. Male bracts in 2-6 pairs, crenulate with wing, apex obtuse, keels inflated. Male bracteoles 0-2, smaller than the underleaf, margin entire. Antheridia 2 per bract, 70-90  $\mu$ m in diameter, somewhat yellowish with a short and hyaline stalk, 50  $\mu$ m in length. **Gynoecia** on short or long lateral branches, female bracts loosely arranged, usually with one innovation, sometimes with 2 innovations, 1-2 gynoecia in a lateral row due to repeatedly fertile innovations. Female bracts almost same size as the leaf, erect-spreading when moist. Lobes 0.37-0.45 mm long, 0.15-0.20 mm wide, obovate to elliptical, apex obtuse, margin somewhat crenulate. Lobules 0.30-0.35 mm long, 0.10-0.13  $\mu$ m wide, 1/2-3/4 the width and 3/4 the length of the lobe, obovate to oblong, apex acute to rounded, keels straight, smooth, 0.15-0.25 mm long. Female bracteoles 0.3-0.4 mm long, 0.18-0.20 mm wide, oblong to obovate with tips obtuse, lobes to 1/4 of female bracteole length, distant, sinus narrow to wide, acute to obtuse, margin slightly crenulate. Perianth (*vide* Zhu & Grolle, 2003: 102) strongly emergent,

cylindrical, 0.72-0.92 mm long, 0.34-0.45 mm wide at middle, slightly compressed dorsiventrally, with 2 indistinct keels; beak 2-3 cells long. **Sporophyte** not seen. **Vegetative propagation** by means of ribbon-like regenerants from leaf margins; shape and size of the propagules variable: oblong to lanceolate, sometimes branched, usually 2 (4) cells wide, 5-7 (10) cells long.

**Further specimens examined.** **MALAYSIA.** **Sabah:** Mt. Kinabalu, near Forest Department Bungalow, Kundasang, 1350 m, 1963, *M. Mizutani* 247, 6106a, 6116, 6130, 6130a, 6138, 6144, 2001, 2012 all as *L. abnormis*, *M. Mizutani* 250a as *L. infestans* (NICH), Park Headquarters, 2000 m, 1972, *M. Okabe* 114a as *L. abnormis* (NICH), Tawau Hill Forest Reserve, 120-210 m, 1974, *G. Mikil* 133 as *L. abnormis* (NICH), Botanical Garden, around power station road, 1515 m, 2010, *G.E. Lee* 2040, 2046, 2048, 2052, 2054, 2055, 2056, 2060, 2066, 2068, 2072, 2073, 2079 (UKMB), between Bundu Tuhan View trail and Liwagu trail, 1530 m, 2010, *G.E. Lee* 1716 (UKMB), road from Headquarters to Timponoh gate, 1530 m, 2010, *G.E. Lee* 1532 (UKMB), Paka cave, 2900-3050 m, 2010, *G.E. Lee* 1935 (UKMB). **INDONESIA.** Kalimantan: Paid Bentuang Karimun, 1997, *Heri Sujadmiko* 089 (BO); Java: Cibodas Botanical Garden, 1400 m, 1972, *M. Okabe* 30b as *L. abnormis* (NICH), above Cibodas, 1420-1650 m, 1930, *Fr. Verdoorn* 2031 (GOET). **PAPUA NEW GUINEA.** Morobe Prov., Slate Creek & Gumi Creek Divide, 17 km W of Bulolo, 2100 m, *H. Streimann* 13886 (NICH).

**Distribution and habitat in Malaysia:** Sabah; epiphytic at wide elevational range, from 120 to 3050 m.

**General distribution:** tropical Asia, New Caledonia, Australia and the western Pacific.

**Discussion:** *Lejeunea exilis* can be easily separated from the other Malaysian species of *Lejeunea* by its small size (plants less than 0.8 mm wide), distant, ovate-lanceolate leaves, minute underleaves which are dimorphic (bifid, undivided) on single shoots, its ribbon-like propagules and its often winged male bracts. Immature plants or branch leaves of *L. exilis* can be mistaken for *Microlejeunea punctiformis*, which differs in the presence of ocelli, winged bracts, smaller leaf cells, 5-keeled perianth and absence of ribbon-like propagules in *M. punctiformis* (Zhu & Grolle, 2003). Most of the specimens of *L. exilis* examined were mixed with *Microlejeunea punctiformis* and *Metalejeunea cucullata*. Variation in *L. exilis* was discussed by Zhu & Grolle (2003). The stem and branch leaves of this species must be observed carefully because the stem leaves are more typical than those of the branches. Most of the specimens from Peninsular Malaysia produce ribbon-like propagules and occasionally the leaf apex also generates marginal rhizoids consisting of 2-3 projecting cells, a phenomenon occurring otherwise in *L. patriciae*. Female plants seem to produce smaller leaves, with rounded apices and regularly reduced leaf lobules, compared with male plants.

According to Zhu and Grolle (2003), the perianth of *L. exilis* is cylindrical and without any keels. However, in the original description of *Byssolejeunea abnormis* Herzog (1941), which was treated as a synonym of *L. exilis* by Zhu & Grolle (2003), the perianth is described as being ovoid in shape and with 5 keels: "Perianthia ovoidea, anguste 5-carinata". As stated by Herzog (1948: 237), the 5 keels of the perianth can be seen clearly: "Dazu kommt dann noch das bei typischen Exemplaren von *Byssolejeunea* stets etwas blasig aufgetriebene Perianth, das jedoch immerhin noch 5 Kanten erkennen last und dadurch an die Form des Perianthes von *Drepanolejeunea tenuis* erinnert." I have examined the type specimen of *B. abnormis* (Java, Prov. Preanger, *Schiffner* 2676 p.p.) and found two perianths which clearly showed 5 keels. Therefore, this plant is treated here as a separate variety instead of as a synonym of *L. exilis*.

**KEY TO THE VARIETIES OF *L. EXILIS***

Perianth cylindrical and without any keels. . . . . *L. exilis* var. *exilis*  
 Perianth ovoid to somewhat obovoid and with 5 keels. . . . . *L. exilis* var. *abnormis*

**a. *L. exilis* var. *exilis***

See under the species

**b. *L. exilis* var. *abnormis* (Herzog) G.E. Lee, *Polish J. Bot.* 58(1): 61(2013) Figs 225-235**

Basionym: *Byssolejeunea abnormis* Herzog, *Hedwigia* 80: 84 (1941) ≡ *Lejeunea abnormis* (Herzog) R.M. Schust., *J. Hattori Bot. Lab.* 25: 4 (1962) (non *Lejeunea abnormis* (Gottsche) Steph. in Renaud & Cardot, *Rev. Bryol.* 18: 57 (1891)) ≡ *Microlejeunea abnormis* (Herzog) Inoue et H. A. Mill., *Bull. Nat. Sci. Mus. Tokyo* 11: 9 (1968) ≡ *Lejeunea byssiformis* Grolle & Mizut., *J. Hattori Bot. Lab.* 43: 131 (1977). TYPE: Indonesia, Java, "Prov. Preanger. decliv. austr. M. Pangerango, prope Tjibodas, secus viam versus Sindanglaya, 1330 m, 1894", *Schiffner 2676 p.p.* (holotype: JE!).

This variety differs from var. *exilis* only in the perianth as mentioned in the key. Perianths 0.5-0.6 mm long, 0.4-0.5 mm wide, emergent to 1/2 of perianth length, obovoid, with 5 keels, sometimes with 4 keels with 1 indistinct dorsal keel; beak 3 cells long; cells of the perianth at the keels smooth, rarely mammillose, regularly rounded to quadrate, stalk-like elongation sometimes present, 0.2-0.3 mm long.

**Further specimens examined. MALAYSIA. Kelantan:** Gua Musang, foot of Gunung Chamah, Dakota trail, 770 m, 2011, *A. Damanhuri 11-373, 11-381, 11-384, 11-395, 11-404, 11-406, 11-409, 11-428, 11-431, 11-413* (UKMB). **Pahang:** Cameron Highlands, 1830 m, 1962, *M. Togashi 77b* as *L. abnormis* (NICH); Tanah Rata, Parit Waterfalls, 1340 m, 2009, *G.E. Lee 2161* (UKMB); Robinson Waterfalls, 1340 m, 2009, *G.E. Lee 1166, 2162, 2285, 2293, 2294, 2302, 2305, 2306* (UKMB); tea plantation, 1500 m, 2009, *G.E. Lee 2287* (UKMB); gate of Cool Point Hotel, 1300 m, 2009, *G.E. Lee 2279, 2281* (UKMB); Mentigi trail, 1365 m, 2009, *G.E. Lee 1162, 1163, 1177, 2160, 2278* (UKMB); Genting Highlands, trail to summit of Gunung Ulu Kali, 1650 m, 2009, *G.E. Lee 1186* (UKMB); summit of Gunung Ulu Kali, 1600 m, 1996, *N. Ohnishi 2441, 2470, 2754, 2777, 2779* (HIRO); Gunung Brinchang, below summit, 1600 m, 2008, *A. Damanhuri 08-1, 08-2* (UKMB); Goh Tong Jaya, around waterfall, 845 m, 2011, *G.E. Lee 2181, 2182, 2184, 2198, 2203* (UKMB); Fraser's Hill, road to the Clock Tower and Post Office, 1275 m, 2008, *G.E. Lee 1181* (UKMB), along Mayer trail, 1000 m, 2009, *G.E. Lee 1425* (UKMB); Perlok, Kem Lata Bujang, 205 m, 2009, *A. Damanhuri 09-5* (UKMB).

**Distribution and habitat in Malaysia:** Kelantan\*, Pahang\*; epiphytic at wide elevational range, from 200-2000 m.

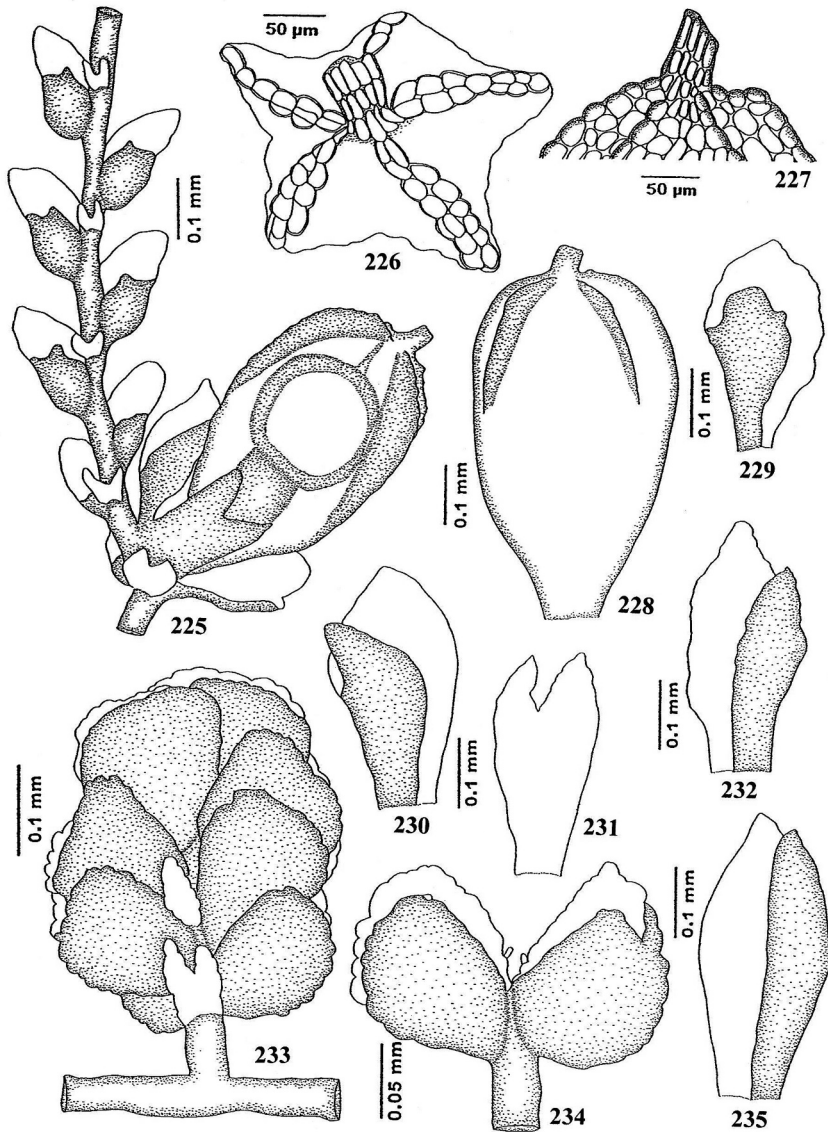
**General distribution:** thus far only known from Peninsular Malaysia and Indonesia (Java).

**13. *Lejeunea flava* (Sw.) Nees, *Naturgesch. Eur. Leberm.* 3: 277 (1838) Figs 236-249**

Basionym: *Jungermannia flava* Sw., *Prodr.* 144 (1788). TYPE: West Indies, Jamaica, *Swartz s.n.* (lectotype designated by Grolle (1976): UPS, not seen; isotype: BM!).

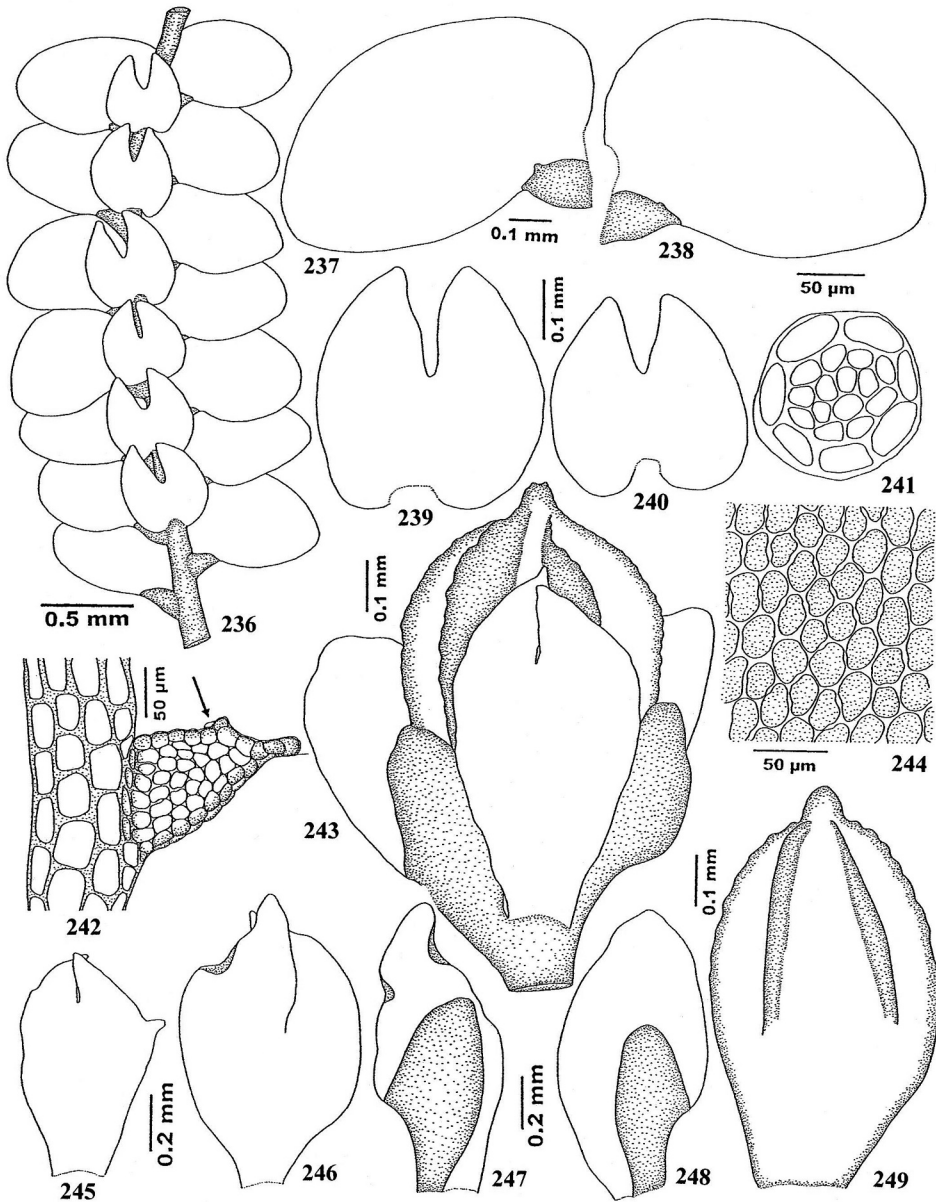
For further synonyms see Grolle (1981).

**Plants** autoicous, relatively large, (0.8) 1.3-1.6 mm wide, usually yellowish green when fresh to light brown when dry, irregularly and densely branched, sometimes loosely bipinnately branched, branches erect-spreading, collar with three small lobes. **Stems** 0.08-0.13 mm in diameter, about 6 cells high in cross-



Figs 225-235. *Lejeunea exilis* var. *abnormis* (Herzog) G.E. Lee. 225. Part of plant in ventral view, with perianth-bearing branch; 226. Keels of perianth; 227. Upper portion of perianth; 228. Perianth; 229, 230, 232, 235. Female bracts; 231. Female bracteole; 233. Androecial shoot; 234. Male bracts. 225-232, 235 drawn from *G.E. Lee 1186* (UKMB); 233, 234 from *A. Damanhuri 08-1* (UKMB).





Figs 236-249. *Lejeunea flava* (Sw.) Nees. 236. Part of plant in ventral view; 237, 238. Leaves; 239, 240. Underleaves; 241. Cross-section of stem; 242. Stem portion and leaf lobule (hyaline papilla shown by arrow); 243. Perianth with bracts and bracteole; 244. Median cells of leaf lobe; 245, 246. Female bracteoles; 247, 248. Female bracts; 249. Perianth. 236-239, 242 drawn from G.E. Lee 1836 (UKMB); 240, 246-248 from G.E. Lee 1186 (UKMB); 241, 244, 249 from G.E. Lee 1191 (UKMB); 243, 245 from G.E. Lee 1083 (UKMB).

section, epidermal cells 7, 15-25  $\mu\text{m}$  wide, medullary cells 14-17, 32.5-50.0  $\mu\text{m}$  wide. **Leaves** closely imbricate, slightly recurved and convex when dry, spreading, never recurved and slightly convex when moist. **Leaf lobes** (0.50) 0.70-0.85 mm long, (0.30) 0.45-0.55 mm wide (when flattened), ovate-oblong; leaf apex narrowly rounded, always flat; leaf margin entire; the ventral margin forming an angle of  $100^\circ$ - $130^\circ$  with the keel when flattened; insertion line about 12 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregularly quadrate to rectangular towards the leaf margin; apical cells 12.5-17.5  $\mu\text{m}$  long and 12.5-15.0  $\mu\text{m}$  wide, median cells 20-25  $\mu\text{m}$  long and 15-17.5  $\mu\text{m}$  wide, basal cells 25.0-42.5  $\mu\text{m}$  long and 17.5-25.0  $\mu\text{m}$  wide; cell walls hyaline, with well-developed trigones and infrequently with intermediate thickenings, 1-2 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies somewhat glistening to faintly opaque-granular, fine *Jungermannia*-type, with minute granules, somewhat rough externally; marginal cells with 2-3 oil bodies per cell, 2-3  $\mu\text{m}$  long and 2-3  $\mu\text{m}$  wide, mostly globose; median cells with 3-8 oil bodies per cell, 5-13  $\mu\text{m}$  long and 3-5  $\mu\text{m}$  wide, globular, ovoid to somewhat ellipsoid; basal cells with 3-11 oil bodies per cell, 5-13  $\mu\text{m}$  long and 3-5  $\mu\text{m}$  wide, globular, ovoid to somewhat ellipsoid. **Leaf lobules** rarely reduced, 0.15-0.20 mm long and 0.10-0.12 mm wide, to 1/5-1/4 the length of the lobe, at an angle of  $50^\circ$ - $60^\circ$  to the stem, ovate-triangular, inflated along the keel; apex obliquely truncate; keel straight to slightly curved; free margin incurved partially; apical tooth 17.5  $\mu\text{m}$  long, oblong, somewhat erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 25  $\mu\text{m}$  long and 20  $\mu\text{m}$  wide. **Underleaves** (0.3) 0.4-0.6 mm long, (0.3) 0.45-0.60 mm wide, to 4-5 times wider than the stem, contiguous to imbricate, orbicular, covering the lobules; bilobed, lobes to 1/2 of underleaf length, about 10-12 cells wide, triangular, sometimes connivent; sinus narrow, acute to obtuse, U-shaped to V-shaped; underleaf margin entire; base  $\pm$  cuneate to cordate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.45-0.50 mm long, 0.40-0.45 mm wide with bracts, on short or long lateral branches, occasionally on main shoots. Male bracts in 3-4 pairs, entire without wing, apex obtuse, keels inflated. Male bracteoles 2-3, smaller than underleaf, margin entire. Antheridia 2 per bract, 75  $\mu\text{m}$  in diameter, somewhat yellowish with a long and hyaline stalk, 50  $\mu\text{m}$  in length. **Gynoecia** on short or long lateral branches, occasionally on the main shoots, female bracts somewhat crowded, with one innovation, usually one gynoecium, sometimes 2-3 gynoecia in a lateral row due to repeatedly fertile innovations. Female bracts smaller than the leaf, erect-spreading when moist, somewhat enveloping the perianth. Lobes 0.60-0.95 mm long, 0.25-0.50 mm wide, narrowly elliptic to obovate, apex obtuse to acute, margin entire. Lobules 0.35-0.65 mm long, 0.15-0.30 mm wide, rarely reduced, 1/2 the width and 2/3 the length of the lobe, oblong to ovate, apex obtuse to acute, keels straight, smooth, 0.2-0.3 mm long. Female bracteoles 0.45-0.65 (0.9) mm long, 0.25-0.35 (0.55) mm wide, more or less of the perianth length, ovate with obtuse tips, lobes to 1/2-2/3 of female bracteole length, overlapping, sinus narrow, acute, margin entire. Perianths 0.60-0.75 (0.9) mm long, 0.35-0.45 (0.6) mm wide, emergent to 1/2-1/5 of the perianth length, obovoid, with 5 keels; beak 2-3 cells long; cells of the perianth at the keels strongly mammillose; stalk-like elongation lacking. **Sporophyte**: seta to 0.5 mm long; capsule 0.25-0.30 mm in diameter, valves 0.3 mm long, 0.15 mm wide at middle, scarcely spreading after dehiscence; elaters *ca* 0.2 mm long; spores rectangular to irregular-shaped, 38-50  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide. **Vegetative propagation** not seen.

**Further specimens examined. MALAYSIA. Kedah:** Kulim, trail to Gunung Inas, 1550 m, 2009, *Damanhuri s.n.* (2 packets) (UKMB). **Kelantan:** Gua Musang, foot of Gunung Chamah, 770 m, 2011, *A. Damanhuri 11-385* (UKMB). **Pulau Pinang:** Penang Hill, Bellevue Hotel, 800 m, 2008, *G.E. Lee 1083, 1084, 1086, 1087* (UKMB). **Perak:** Gunung Korbu, summit of Gunung Korbu, 2183 m, 2009, *A. Damanhuri 09-1, 09-2, 09-3, 09-4, 09-11* (UKMB). **Pahang:** Cameron Highlands, Robinson Waterfalls, 1340 m, 2009, *G.E. Lee 1172, 1175, 2285* (UKMB); Parit Waterfalls, 1340 m, 2009, *G.E. Lee 2246* (UKMB); tea Plantation, 1500 m, 2009, *G.E. Lee 2247, 2283, 2287* (UKMB); Mentigi trail, 1365 m, 2009, *G.E. Lee 1161a, 1161b, 1176, 2248, 2277, 2278, 2282, 2284, 2286, 2289, 2290, 2291* (UKMB); near gate of Cool Point Hotel, 1300 m, 2009, *G.E. Lee 2276, 2279, 2280, 2281* (UKMB); Gunung Brinchang, below summit, 1600 m, 2008, *A. Damanhuri 08-1, 08-2, 08-5, 08-6, 08-10* (UKMB); Brinchang, 1965, *Hiroshi Inoue 11191* (TNS); Genting Highlands, summit of Gunung Ulu Kali, ca 1600 m, 1996, *N. Ohnishi 2538, 2550, 2517, 2525, 2751, 2752, 2756, 2771, 2776, 2778, 2779, 2787* (HIRO), trail to summit of Gunung Ulu Kali, 1650 m, 2009, *G.E. Lee 1186, 1191, 1192, 1191a, 1194, 1200* (UKMB), theme park, 1500 m, 2008, *G.E. Lee 1036, 1037, 1144* (UKMB); Goh Tong Jaya, near waterfall, 845 m, 2011, *G.E. Lee 2185, 2186, 2188, 2191, 2201, 2206, 2206a, 2200, 2210, 2221, 2222* (UKMB). **Selangor:** Hulu Langat, Sungai Gabai, staircase to summit, 100 m, 2010, *G.E. Lee 2276* (UKMB). **Sabah:** Mt. Kinabalu, between Sosopodon and S. Kelinggen, 1350-1400 m, 1963, *M. Mizutani 3771* (NICH), Power station to Carson's camp, 1800-2500 m, 1969, *S. Kokawa & M. Hotta 3789bis* (NICH), headquarters, 2000 m, 1972, *M. Okabe 109* (NICH), trail from Timphoh gate to Kandis shelter, 1900 m, 2010, *G.E. Lee 1787, 1790, 1798, 1799, 1800, 2141* (UKMB), between Bundu Tuhan View trail and Liwagu trail, 1530 m, 2010, *G.E. Lee 1626, 1679, 1703, 1834, 1836, 1848* (UKMB), trail from Lowii Shelter to Mempening Shelter, 2300-2500 m, 2010, *G.E. Lee 1682, 1672, 1983, 1984, 1988, 1989, 2118* (UKMB), trail from Kandis Shelter to Ubah Shelter, 2000 m, 2010, *G.E. Lee 1977, 1978, 1980, 1981, 2009*, (UKMB), Botanical Garden, around Power station road, 1515 m, 2010, *G.E. Lee 1741, 1745, 1747, 2024, 2027, 2029, 2030, 2035, 2036, 2040, 2055, 2064, 2048, 2066, 2068, 2069, 2070, 2071, 2079, 2146* (UKMB), road from Headquarters to Timphoh gate, 1530 m, 2010, *G.E. Lee 1641* (UKMB), trail from Ubah Shelter to Lowii Shelter, 2000 m, 2010, *G.E. Lee 1611, 1618, 1621, 2111, 2112, 2113, 2115, 2130* (UKMB); trail from Mempening shelter to Layang-layang Staff Quarters, 2500-2800 m, 2010, *G.E. Lee 1529, 1592, 1880, 1881, 1902, 1908* (UKMB); Tambunan district, Mt. Trus Madi, 1600 m, 1996, *M. Suleiman 134* (BORH). **INDONESIA.** W Java: Mt. Kendeng, 1230 m, 2005, *Radhiah Zakaria 212c* (BIOT); Halimum Salak Mt. National Park, 1200 m, 2009, *M.S. Sofiyana 024, 025* (BIOT); Cikudapaeh trail, 1100 m, 2009, *NSA IIATIQI-4* (BIOT); Sulawesi: Lore Lindu National Park, trail to Mt. Nokilalaki, 2000-2100 m, 2005, *N.S. Ariyanti 733* (BIOT).

**Distribution and habitat in Malaysia:** Kedah\*, Kelantan\*, Pulau Pinang\*, Perak\*, Pahang, Selangor\*, Sabah; on various substrates, particularly epiphytic on tree trunks, 1000-2800 m.

**General distribution:** a very common, pantropical species.

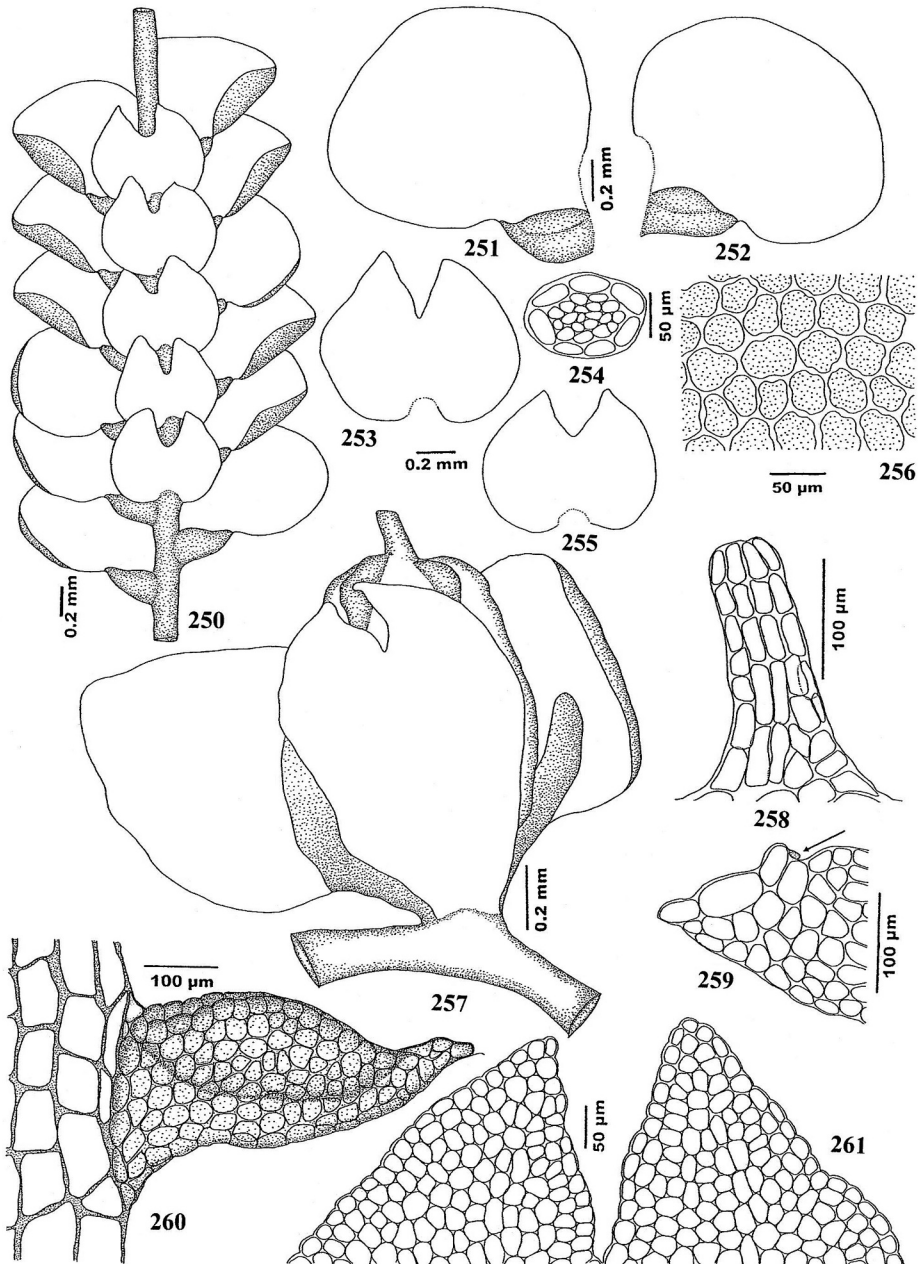
**Discussion:** *Lejeunea flava* is easily recognized by 1) the autoicous plants, usually with short androecial shoots, 2) plants yellowish to whitish-green when fresh, 3) leaves ovate-oblong, 4) rather large and imbricate underleaves with cordate bases, 5) small inflated leaf lobules, and 6) somewhat opaque and mammillose perianth. *Lejeunea flava* resembles *L. discreta* in the large and imbricate underleaves, however, the latter has much longer leaf lobules with incurved free margins. *Lejeunea flava* is also similar to *L. papilionacea* in the ovate-oblong leaves but the latter has small, distant underleaves and obovate to obcordate perianths with auriculate keels. *Lejeunea flava* varies in Malaysia mainly in the female bracts and bracteoles. Female bracts from Penang Hill sometimes produce a sinus on the lobule with a hyaline papilla on the lateral side, those from Mt. Kinabalu, Sabah are usually somewhat undulate. Furthermore, the female bracteoles in the latter plants are rather broad, rounded or widely ovate, and abruptly tapering towards the base.

**14. *Lejeunea fleischeri* (Steph.) Mizut., *J. Hattori Bot. Lab.* 33: 238 (1970)**

**Figs 250-261**

Basionym: *Hygrolejeunea fleischeri* Steph., *Sp. Hepat.* 5: 560 (1914). TYPE: Java, Diengplateau, 2/4 1901, *Fleischer* 22 (holotype: G!).

**Plants** dioicous, comparatively large, 1.5-2.0 (2.3) mm wide, light green when fresh to light brown when dry, irregular and somewhat densely branched, branches erect-spreading to spreading, collar with three small lobes. **Stem** ca 0.1 mm in diameter, about 7-8 cells high in cross-section, epidermal cells 7, 38-62  $\mu\text{m}$  wide, medullary cells (12) 20-30, 13-25  $\mu\text{m}$  wide. **Leaves** closely imbricate, slightly recurved when dry, erect-spreading to spreading, slightly recurved and convex when moist. **Leaf lobes** 0.8-1.0 (1.4) mm long, 0.6-0.8 (1.0) mm wide (when flattened); ovate to ovate-orbicular; leaf apex broadly rounded, usually slightly recurved; leaf margin slightly crenulate; the ventral margin forming an angle of 100°-120° with the keel when flattened; insertion line about 12 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregular quadrate to rectangular towards the leaf margin; apical cell 20-25  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide, median cell 25-33  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide, basal cell 38-50  $\mu\text{m}$  long and 18-25  $\mu\text{m}$  wide; cell walls yellowish, with well-developed trigones and conspicuous intermediate thickenings, 1-3 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies not seen. **Leaf lobules** rarely reduced, 0.3-0.4 (0.5) mm long, ca 0.2 mm wide, to 1/3 (1/2) the length of the lobe, at an angle of 40°-60° to the stem, ovate-oblong, inflated along the keel; apex obliquely truncate; keel curved; free margin incurved fully; apical tooth 40-50  $\mu\text{m}$  long, oblong, erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell present, cell below the apical tooth 75  $\mu\text{m}$  long and 20  $\mu\text{m}$  wide. **Underleaves** 0.45-0.60 (0.8) mm long, 0.5-0.6 (0.75) mm wide, to 5-6 times as wide as the stem, contiguous to subimbricate, ovate to somewhat orbicular (slightly longer than wide), covering 3/5-4/5 of the lobules; bilobed, lobes to 1/3-1/2 of underleaf length, about 13 cells wide, triangular, sometimes oblique, distant to slightly connivent; sinus narrow, acute, V-shaped; underleaf margin crenulate; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells lacking; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.40-0.55 mm long, 0.4-0.5 mm wide with bracts, on main shoots. Male bracts in 2-4 pairs, entire without wing, apex truncate, keels inflated. Male bracteoles 0-1, smaller than the underleaf, margin entire. Anteridia not seen. **Gynoeceia** on short or long branches, occasionally terminal on main shoots, female bracts somewhat crowded, with 1(-2) innovations, gynoeceia 1-3 in a lateral row due to repeatedly fertile innovations. Female bracts more or less the size of leaves, erect spreading when moist, somewhat enveloping the perianth. Lobes 0.7-0.9 mm long, 0.6-0.7 mm wide, obovate, apex obtuse, margin crenulate. Lobules 0.3-0.4 mm long, 0.1-0.2 mm wide, rarely reduced, 1/3 the width and 3/5 the length of the lobe, oblong to spatulate, apex obtuse to somewhat truncate, keels straight, smooth, 0.3-0.4 mm long. Female bracteoles 0.6-0.8 mm long, 0.4-0.6 mm wide, 4/5 of the perianth length, obovate to widely elliptic with the tips acute, lobes to 1/3-1/4 of female bracteole length, connivent, sinus narrow, acute, margin crenulate. **Perianth** 1.0-1.2 mm long, 0.5-0.6 mm wide, emergent to (1/2) 1/5 of the perianth length, oblong, with 5 keels, sometimes 4 keels and 1 indistinct dorsal keel; beak 5-6 cells long; cells of the perianth at the keels smooth, rarely mammillose; stalk-like elongation sometimes present, 0.2-0.3 mm long. **Sporophyte** not seen. **Vegetative propagation** not seen.



Figs 250-261. *Lejeunea fleischeri* (Steph.) Mizut. 250. Part of plant in ventral view; 251, 252. Leaves; 253, 255. Underleaves; 254. Cross-section of stem; 256. Median cells of leaf lobe; 257. Perianth with bracts and bracteole; 258. Beak of perianth; 259. Upper part of leaf lobule when flattened (hyaline papilla shown by arrow); 260. Stem portion and leaf lobule; 261. Apical cells of underleaf. All figures drawn from *A. Damanhuri 09-3* (UKMB).

**Further specimens examined. MALAYSIA. Perak:** Gunung Korbu, summit of Gunung Korbu, 2183 m, 2009, *A. Damanhuri 09-1, 09-2, 09-3, 09-4* (UKMB). **Pahang:** Genting Highlands, summit of Gunung Ulu Kali, 1600 m, 1996, *N. Ohnishi 2485, 2508, 2515* (HIRO), theme park, 1500 m, 2008, *G.E. Lee 1037* (UKMB), trail to summit of Gunung Ulu Kali, 1650 m, 2009, *G.E. Lee 1196* (UKMB); Cameron Highlands, Gunung Brinchang, 1600 m, 2008, *A. Damanhuri 08-1, 08-2* (UKMB). **INDONESIA.** Java: Mt. Patuha, SW of Bandung, 2000-2100 m, 2009, *S. Kornochalert 1401* (BIOT); Lake Situ Oatengen NW of Mt. Patuha, 1500 m, 2009, *Dian Apriana 1* (BIOT).

**Distribution and habitat in Malaysia:** Perak\*, Pahang\*; usually epiphytic, above 1500 m.

**General distribution:** Peninsular Malaysia, Indonesia (Java).

**Discussion:** The distinguishing characters of *L. fleischeri* are 1) leaves closely imbricate and recurved when dry or moist, 2) lobules large, rarely reduced, 3) leaf cells with well-developed trigones and intermediate thickenings, 4) underleaves ovate to somewhat orbicular, and 5) perianth oblong and with 5-6 cells long beak. *Lejeunea fleischeri* is very close to *L. pectinella*, both species having similar leaves, lobules and perianths. The two species were clustered at a high similarity level (0.88) in a phenetic analysis and *L. pectinella* was resolved as sister to *L. fleischeri* in a phylogenetic analysis (Lee *et al.*, submitted). The differences between them are given in the Table 2.

*Lejeunea fleischeri* varies in plant size, in the recurvature and orientation of the leaves, in the size of the underleaves, in the number of medullary cells (stem cross-section), and in the number of innovations. Specimens from Peninsular Malaysia (Gunung Korbu, Genting Highlands, Cameron Highlands) and Java (Mt. Patuha) are somewhat different from the type of *L. fleischeri*. The type material has strongly recurved and erect-spreading leaves whereas in the other specimens the leaves are little recurved and less spreading, particularly in robust plants. However, this variation can be observed in single specimens. Furthermore, specimens from Genting Highlands have rather larger leaves (1.1-1.4 mm long and 0.9-1.0 mm wide) and underleaves (0.8 mm long and 0.5-0.75 mm wide); the shape of the underleaves tends to become orbicular instead of ovate in these plants. Furthermore, stems in the type material are made up of about 12 medullary cell rows while those in the other materials have more than 20 rows. In addition, the gynoecia have usually two innovations in the type material but often only one in other materials.

Table 2. Differences between *L. fleischeri* and *L. pectinella*

Characters	<i>L. fleischeri</i>	<i>L. pectinella</i>
Number of medullary cells (stem cross-section)	(12) 20-30	10-15
Leaf lobe orientation	Erect-spreading	Spreading to widely spreading
Shape of underleaves	Ovate to ovate-orbicular	Reniform
Shape of female bracts (lobule)	Oblong to spatulate	Widely obovate
Shape of female bracteoles	Obovate to widely elliptic	Orbicular to widely ovate
Perianth keels	Smooth	With 2-3 small teeth
Length of perianth beak	5-6 cells	8-10 cells
Position of perianth	Emergent to 1/5 (1/2) of the perianth length	Not emergent, hidden between the bracts

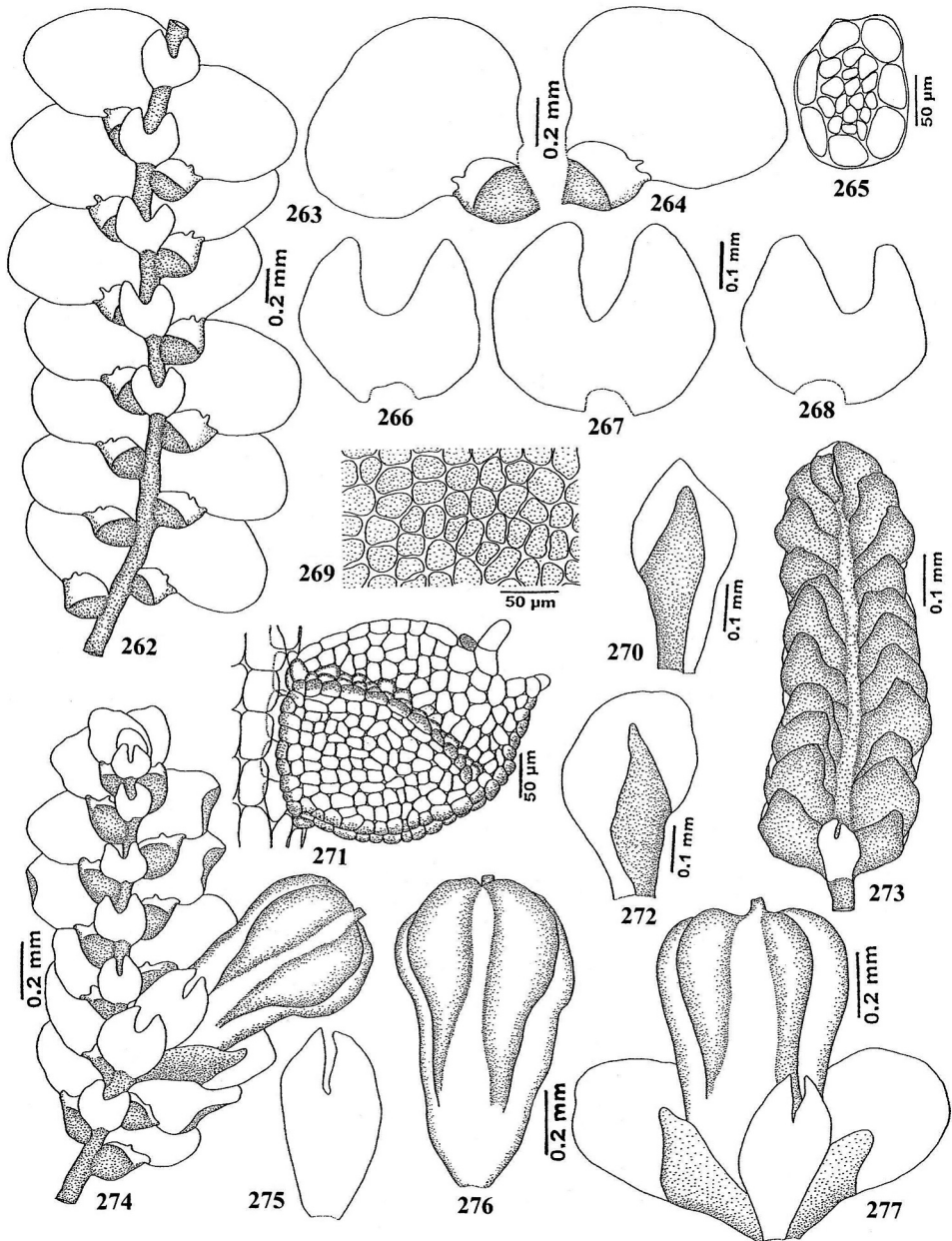
**15. *Lejeunea gradsteinii* G.E. Lee, A. Damanhuri et A. Latiff,**  
*Acta Biol. Pl. Agriensis* 1: 30 (2011a)

**Figs 262-277**

**TYPE:** Malaysia, Sabah, Mt. Kinabalu, trail from Mempening shelter to Layang-Layang staff quarters, montane forest, on tree trunk, 2500-2800 m, 12 November 2010, *G.E. Lee 1891* (holotype, UKMB!; isotype, PC!).

**Plants** dioicous, 1.3-1.4 mm wide, whitish green when fresh to brown when dry, irregularly and densely branched, branches erect-spreading to spreading, collar with three small lobes. **Stems** ca 0.1 mm in diameter, about 6 cells high in cross-section, epidermal cells 7, 38-63  $\mu\text{m}$  wide, medullary cells 12-17, 13-25  $\mu\text{m}$  wide. **Leaves** imbricate, rarely recurved and slightly convex when dry, erect-spreading to spreading and plane when moist. **Leaf lobes** (0.3-0.5) 0.6-0.9 mm long, (0.2-0.3)0.4-0.6 mm wide (when flattened), ovate; leaf apex obtuse, flat; leaf margin weakly crenulate; the ventral margin forming an angle of 120°-140° with the keel when flattened; insertion line 10-11 lobe cells long. **Leaf cells** rounded to oblong, abruptly becoming smaller towards the median cells and gradually becoming smaller towards the leaf margin, basal portion of cells are more or less elongate; apical cells 20-25  $\mu\text{m}$  long and 12.5-17.5  $\mu\text{m}$  wide, median cells 25-30  $\mu\text{m}$  long and 17.5-20  $\mu\text{m}$  wide, basal cells 25-42.5  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide; cell walls hyaline, with well-developed trigones, infrequently with intermediate thickenings. Cuticle rough by numerous minute papillae. Oil bodies not seen. **Leaf lobules** never reduced, 0.3-0.4 mm long and 0.2-0.3 mm wide, to 1/3 the length of the lobe, at an angle of about 90° to the stem, orbicular, inflated along the keel; apex obliquely truncate, with two teeth, the first tooth conspicuous, 1-2 cells long and 2 cells wide at base, the second tooth small and indistinct, 1-celled, obtuse; the keel curved; free margin flat; apical tooth 25-30  $\mu\text{m}$  long, oblong, erect, apex obtuse; margin between tooth and sinus 3-4 cells long, large disc cell lacking, cell below apical tooth 30-35  $\mu\text{m}$  long and 15-20  $\mu\text{m}$  wide. **Underleaves** 0.2-0.4 mm long, 0.2-0.4 mm wide, to 2 times as wide as the stem, distant, orbicular, covering 1/3 of the lobules; bilobed, lobes to 2/3 of underleaf length, about 6-8 cells wide, triangular, oblique, distant; sinus broad, obtuse, U-shaped; underleaf margin weakly crenulate; base  $\pm$  cuneate, insertion line curved; the two large basal cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** on short or long lateral branches, androecial shoot 0.4-0.7 (1.10) mm long, 0.3-0.4 mm wide with bracts. Male bracts in 4-13 pairs, entire without wing, apex obtuse, keels inflated. Male bracteole 0-1, slightly smaller than the underleaf, margin crenulate. Antheridia 2 per bract, 70-85  $\mu\text{m}$  in diameter, somewhat yellowish with a short and hyaline stalk, 40-50  $\mu\text{m}$  in length. **Gynoeceia** on short or long branches, female bracts loosely arranged, with one innovation, 1-3 gynoeceia in a lateral row due to repeatedly fertile innovations. Female bracts smaller than the leaf, erect-spreading when moist, somewhat not enveloping the perianth. Lobes 0.5-0.6 mm long, 0.2-0.3 mm wide, ovate to lanceolate, apex obtuse, margin weakly crenulate. Lobules 0.3-0.4 mm long, 0.1-0.2 mm wide, 1/2 the width and 3/4-5/6 the length of the lobe, sometimes almost same length as the lobe, ovate to linear, apex acute to obtuse, keels straight, smooth, 0.1-0.2 mm long. Female bracteoles 0.4-0.5 mm long, 0.2-0.3 mm wide, 1/2 of the perianth length, ovate with tips acute, lobes up 1/3 of female bracteole length, sinus narrow, acute, margin weakly crenulate. Perianths 0.8-1.0 mm long, 0.5-0.6 mm wide, emergent to 1/3 of the perianth length, obovate-clavate, with 5 sharp keels; beak 2-3 cells long; sometimes the keels extended above more or less as auricles; cells of the perianth at the keels mammillose; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined. Malaysia. Sabah:** Mt. Kinabalu, trail from Mempening shelter to Layang-Layang staff quarters, 2500-2800 m, 2010, *G.E. Lee 1884, 1885, 1886, 1887, 1888, 1889, 1890* (UKMB).



Figs 262-277. *Lejeunea gradsteinii* G.E. Lee, A. Damanhuri et A. Latiff. 262. Part of plant in ventral view; 263, 264. Leaves; 265. Cross-section of stem; 266-268. Underleaves; 269. Median cells of leaf lobe; 270, 272. Female bracts; 271. Stem portion and leaf lobule; 273. Androecial shoot; 274. Part of plant, with perianth-bearing branch; 275. Female bracteole; 276. Perianth; 277. Perianth with bracts and bracteole. All figures drawn from the holotype G.E. Lee 1891 (UKMB).



**Distribution and habitat in Malaysia:** Sabah, epiphytic on tree trunks, 2500-2800 m.

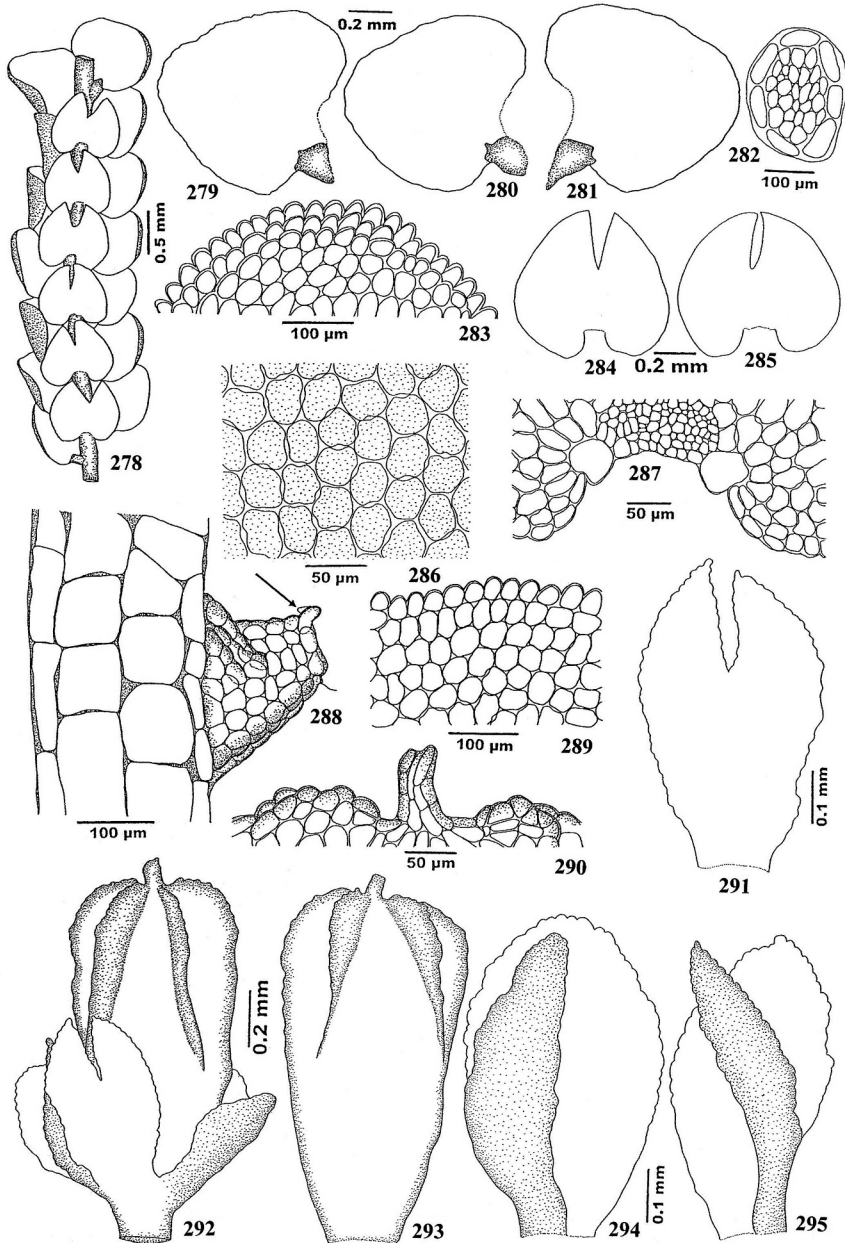
**General distribution:** only known from Mt. Kinabalu, Sabah.

**Discussion:** The distinguishing characters of *L. gradsteinii* are 1) the whitish green color when fresh, 2) weakly crenulate margin of leaves, underleaves, female bracts and bracteoles, 3) rather large, strongly inflated, never-reduced lobules with conspicuously flat free margins, 4) apex of lobules with 2 teeth, 5) basal leaf cells more or less elongate, 6) leaf cells with well-developed trigones and without intermediate thickenings, 7) the obovate-clavate perianths with 5 sharp keels, and 8) the long male shoot with up to 13 pairs of male bracts. *Lejeunea gradsteinii* is most closely related to *L. mimula*; in a phenetic analysis both species were clustered at a similarity level of 0.73 (Lee *et al.*, submitted). *Lejeunea mimula* is easily recognized from *L. gradsteinii* by having large, reniform and unlobed underleaves and the large, funnel-shaped beak of the perianth.

**16. *Lejeunea kinabalensis* Mizut., *J. Hattori Bot. Lab.* 33: 246 (1970) Figs 278-295**

TYPE: Malaysia, Sabah, Kinabalu area, Tenompok and Kamaranga, south slope of Mt. Kinabalu, 1400-1900 m, 1970, *Iwatsuki 417* (holotype: NICH!).

**Plants** dioicous, relatively large, flexuous, 1.0-1.5 mm wide, whitish green when fresh to pale green or dark brown when dry, irregularly and slightly branched, sometimes loosely pinnate to bipinnately branched, branches erect-spreading to spreading, collar with three small lobes. **Stem** 0.15-0.20 mm in diameter, about 8 cells high in cross-section, epidermal cells 7, 80-100  $\mu$ m wide, medullary cells 20-27, 26-53  $\mu$ m wide. **Leaves** contiguous to imbricate, recurved when dry, erect-spreading to spreading and slightly recurved when moist. **Leaf lobes** 1.0-1.2 mm long, 0.8-0.9 mm wide (when flattened); ovate to ovate-triangular; leaf apex narrowly rounded, recurved; leaf margin strongly crenulate with prominent projecting cells; the ventral margin forming an angle of 90°-100° with the keel when flattened; insertion line about 11 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregularly quadrate to pentagonal towards the leaf margin; apical cells 20-30  $\mu$ m long and 20-26  $\mu$ m wide, median cells 33-43  $\mu$ m long and 26-33  $\mu$ m wide, basal cells 33-56  $\mu$ m long and 23-30  $\mu$ m wide; cell walls hyaline to yellowish, with well-developed trigones and conspicuous intermediate thickenings, 0-2 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies somewhat glistening to faintly opaque-granular, fine *Jungermannia*-type, with minute granules, somewhat rough externally; marginal cells 3-5 oil bodies per cell, 5-10  $\mu$ m long and 3-5  $\mu$ m wide, ovoid to ellipsoid; median cells with 7-8 oil bodies per cell, 10-15  $\mu$ m long and 4-6  $\mu$ m wide, globose to somewhat ellipsoid; basal cells with 8-10 oil bodies per cell, 10-15  $\mu$ m long and 4-6  $\mu$ m wide, mostly ellipsoid. **Leaf lobules** sometimes reduced, 0.20-0.25 mm long and 0.13-0.18 mm wide, to 1/5-1/4 the length of the lobe, at an angle of 40°-50° to the stem, ovate, inflated along the keel; apex truncate; keel curved; free margin flat; apical tooth 20-25  $\mu$ m long, oblong, suberect, apex obtuse, slightly curved; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 25-30  $\mu$ m long and 18-20  $\mu$ m wide. **Underleaves** 0.7-0.8 mm long, 0.8-1.0 mm wide, to 4 times wider than the stem, contiguous, suborbicular (slightly wider than long), always covering the lobules; bilobed, lobes to 1/2 of underleaf length, about 15 cells wide, triangular, oblique, connivent to distant; sinus narrow, acute, V-shaped; underleaf margin strongly crenulate; base cordate, insertion line straight; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.5-0.8 mm long, 0.4-0.5 mm wide with bracts, on short lateral branches.



Figs 278-295. *Lejeunea kinabalensis* Mizut. 278. Part of plant in ventral view; 279-281. Leaves; 282. Cross-section of stem; 283, 289. Apical cell of leaf lobe; 284, 285. Underleaves; 286. Median cells of leaf lobe; 287. Basal cells of underleaf; 288. Stem portion and leaf lobule (hyaline papilla shown by arrow); 290. Upper portion of perianth; 291. Female bracteole; 292. Perianth with bracts and bracteole; 293. Perianth; 294, 295. Female bracts. 278-285, 288, 289 drawn from the holotype, *Z. Iwatzuki* 417 (NICH); 286, 287 from *G.E. Lee* 1827 (UKMB); 290-295 from *G.E. Lee* 1773 (UKMB).

Male bracts in 3-6 pairs, entire without wing, apex obtuse, keels inflated. Male bracteoles 2, smaller than underleaf, margin crenulate. Antheridia not seen. **Gynoecia** on short lateral branches, female bracts loosely arranged, with one innovation, usually with one gynoecium in a lateral position. Female bracts smaller than the leaf, erect-spreading when moist, not enveloping the perianth. Lobes 0.6-0.7 mm long, 0.3-0.4 mm wide, ovate, apex obtuse, margin strongly crenulate. Lobules 0.6-0.7 mm long, 0.2-0.3 mm wide, rarely reduced, 1/2 the width of the lobe, almost the length of the lobe, oblong to elliptic, apex acute to obtuse, keels straight to curved, smooth, 0.16-0.25 mm long. Female bracteoles 0.7-0.8 mm long, 0.3-0.4 mm wide, 1/2 of the perianth length, ovate to obovate with tips acute, lobes to 1/2-1/3 of female bracteole length, sinus narrow, acute, margin strongly crenulate. Perianths 1.2-1.3 mm long, 0.6-0.7 mm wide, emergent to 1/2 of the perianth length, somewhat obovoid, with 5 keels, sometimes 4 keels with 1 indistinct ventral keel; beak 3 cells long; cells of the perianth at the keels strongly mammillose; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined.** **MALAYSIA.** **Sabah:** Mt. Kinabalu, between Kamaranga Radio Station and Waterfalls, 2000-2146 m, 1963, *M. Mizutani 2486* (NICH); Kinabalu National Park, around Power Station, 1800 m, 1974, *T. Kodama 47225* (NICH), roadside from Headquarters to Timpohon gate, 1530 m, 2010, *G.E. Lee 1827* (UKMB), trail from Timpohon gate to Kandis shelter, 1900 m, 2010, *G.E. Lee 1733, 1737, 1770, 1773, 1803, 1804, 1805, 1821, 1822, 2138, 2139, 2140* (UKMB), Botanical Garden, around Power station road, 1515 m, 2010, *G.E. Lee 2042, 2082* (UKMB). **PHILIPPINES.** Mindanao: Agusan Norte Prov., trail Bo. San Antonio to summit Cabadbaran, 2000 m, 1984, *B.C. Tan & M. Navarez 84-452* (NICH).

**Distribution and habitat in Malaysia:** Sabah, only known from Mt. Kinabalu; on litter in humid montane forest, in open and shaded places, 1400-2150 m.

**General distribution:** Sabah, Philippines, Papua New Guinea.

**Discussion:** *Lejeunea kinabalensis* is a very distinct species characterized by 1) the relatively large whitish-green and flexuous plant, 2) the crenulate margin of leaf lobe, leaf lobule, underleaf, and female bract and bracteole, 3) the large underleaf with cordate base, 4) the small leaf lobule with flat free margin, 5) the obovoid perianth with 3 cells long beak, and 6) the rough cuticle. Superficially, *Lejeunea kinabalensis* is similar to *L. albescens* and *L. contracta*, all of which have relatively large plants with a flexuous long stem, small leaf lobules, and very large underleaves with a cordate base. The differences between these three species are summarised in Table 3.

Table 3. Morphological features of *L. kinabalensis*, *L. albescens* and *L. contracta*

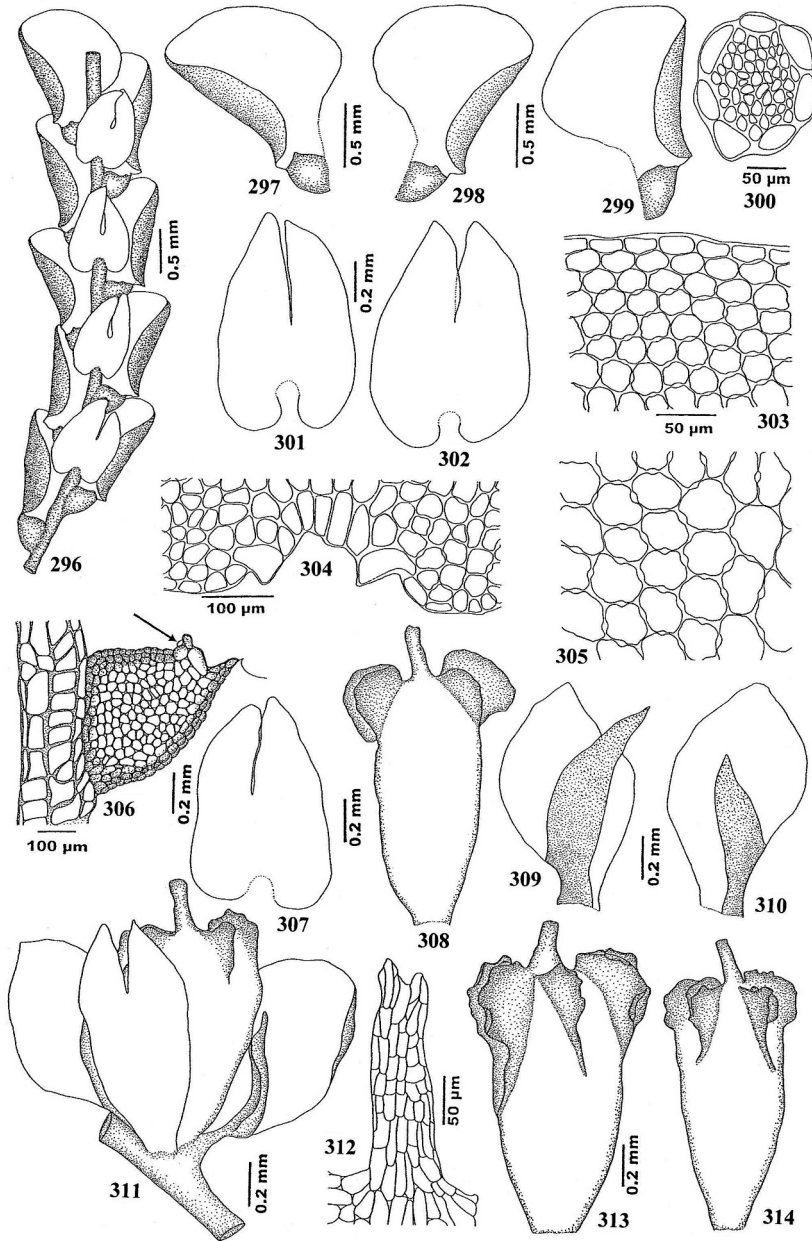
Characters	<i>L. kinabalensis</i>	<i>L. albescens</i>	<i>L. contracta</i>
Leaf apex	Broadly rounded, somewhat obtuse	Broadly rounded, somewhat obtuse	Narrowly rounded, somewhat acute
Leaf margin	Strongly crenulate	Crenulate	Entire or weakly crenulate
Leaf lobule apex	Spread out, somewhat curved	Spread out, obliquely truncate	Contracted, curved to U-shaped
Trigones	Well-developed	Well-developed	Small, indistinct
Number of medullary cells of stem in cross-section	20-27	20-32	15-25
Underleaf (lobes up to underleaf length)	Deeply bifid (1/2)	Shallowly bifid (1/6-1/4)	Deeply bifid (1/2)
Perianth keels	5 keels	without keel	5 sharp keels
Cells of the perianth at the keel	Strongly mammillose	Smooth	Smooth

**17. *Lejeunea lumbricoides* (Nees) Gottsche, Lindenb. et Nees,**  
*Syn. Hepat.*: 342 (1845)

**Figs 296-314**

Basionym: *Jungermannia lumbricoides* Nees, *Enum. Pl. Crypt. Jav.*: 40 (1830) ≡ *Omphalanthus lumbricoides* (Nees) Gottsche, Lindenb. et Nees, *Syn. Hepat.*: 748 (1847) ≡ *Taxilejeunea lumbricoides* (Nees) Schiffn., in Engler & Prantl, *Nat. Pflanzenfam.* 1, 3: 125 (1893). TYPE: Java, *Blume s.n.* (holotype: STR!).

**Plants** dioicous, relatively large, flexuous, 1.8-2.2 mm wide, pale green when fresh to dark brown when dry, pendent from twigs or branches; irregularly and densely pinnate to bipinnately branched, branches erect-spreading, collar with three rather large lobes. **Stems** 0.12-0.17 mm in diameter, about 10 cells high in cross-section, epidermal cells 7, 43-68 μm wide, medullary cells 35-50, 15-22 μm wide. **Leaves** closely imbricate, recurved when dry, erect-spreading to spreading and recurved when moist. **Leaf lobes** 1.5-1.7 mm long, 1.2-1.4 mm wide (when flattened), ovate-orbicular; leaf apex broadly rounded, always recurved; leaf margin entire; the ventral margin forming an angle of 140°-150° with the keel when flattened; insertion line 15-20 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregularly quadrate to rectangular towards the leaf margin; apical cells 21-28 μm long and 12-18 μm wide, median cells 31-47 μm long and 25-40 μm wide, basal cells 44-53 μm long and 25-31 μm wide; cell walls yellowish, with well-developed trigones and conspicuous intermediate thickenings, 1-2 per cell, 0-1 between 2 adjacent trigones. Cuticle smooth. Oil bodies not seen. **Leaf lobules** rarely reduced, 0.4-0.5 mm long, 0.2-0.3 mm wide, to 1/4-1/3 the length of the lobe, at an angle of 40°-50° to the stem, ovate-triangular, inflated along the keel; apex obliquely truncate; keel curved; free margin flat, sometimes the free margin incurved partially; apical tooth 42-44 μm long, oblong, somewhat erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell present, cell below the apical tooth 80 μm long and 40 μm wide. **Underleaves** 0.8-1.0 mm long, 0.6-0.7 mm wide, to 4 times wider than the stem, contiguous to distant, ovate (longer than wide), covering half of the lobules; bilobed, lobes to 1/2-2/3 of underleaf length, about 19 cells wide, narrowly triangular, slightly connivent to overlapping; sinus narrow, acute, V-shaped; underleaf margin entire; base cordate to auriculate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.9-1.0 mm long, 0.6-0.7 mm wide with bracts, on short or long lateral branches, occasionally on main shoots. Male bracts in 3-6 pairs, entire without wing, apex obtuse, keels inflated. Male bracteoles 1-2, smaller than underleaf, margin entire. Antheridia 2 per bract, 80-100 μm in diameter, somewhat yellowish with a long and hyaline stalk, 90 μm in length. **Gynoecia** on short or long branches, female bracts somewhat crowded, with one innovation, 2-3 gynoecia in a lateral row due to repeatedly fertile innovations. Female bracts slightly smaller than the leaf, erect-spreading when moist, not enveloping the perianth. Lobes 0.9-1.0 mm long, 0.5-0.6 mm wide, ovate, apex obtuse, margin entire. Lobules 0.5-0.7 mm long, 0.16-0.20 mm wide, rarely reduced, 1/2-2/3 the width and 2/3 the length of the lobe, sometimes longer than the length of the lobe, lanceolate, apex acute, keels straight, smooth, 0.2-0.3 mm long. Female bracteoles 0.8 mm long, 0.4 mm wide, 3/4 of the perianth length, ovate to elliptic with tips acute, lobes to 1/2-2/3 of female bracteole length, sinus narrow, acute, margin entire. Perianths 1.0-1.3 mm long, 0.5-0.6 mm wide, emergent to 3/4 of the perianth length, pyriform with 5 keels, sometimes 4 keels with 1 indistinct ventral keel, the keels often expanded above as auricles, ca 0.3 mm wide, at times 2-winged and strongly undulate at apex; beak 7-10 cells long; cells of the perianth at the keels somewhat



Figs 296-314. *Lejeunea lumbricoides* (Nees) Gottsche, Lindenb. et Nees. 296. Part of plant in ventral view; 297-299. Leaves; 300. Cross-section of stem; 301, 302, 307. Underleaves; 303. Apical cells of leaf lobe; 304. Basal cells of underleaf; 305. Median cells of leaf lobe; 306. Stem portion and leaf lobule (hyaline papilla shown by arrow); 308, 313, 314. Perianths; 309, 310. Female bracts; 311. Perianth with bracts and bracteole; 312. Beak of perianth. 296-303, 305, 306 drawn from G.E. Lee 1155 (UKMB); 304 from G.E. Lee 1428 (UKMB); 307-313 from S.R. Gradstein & N.S. Ariyanti 11028 (BIOT); 314 from S.R. Gradstein & N.S. Ariyanti 11053 (BIOT).

mammillose; stalk-like elongation lacking. **Sporophyte:** seta to 0.4 mm long; capsule *ca* 0.4 mm in diameter, valves 0.4 mm long, 0.3 mm wide at middle, scarcely spreading after dehiscence; elaters *ca* 0.2 mm long; spores not seen. **Vegetative propagation** not seen.

**Further specimens examined.** **MALAYSIA. Pahang:** Fraser's Hill, along road, 980 m, 2008, *G.E. Lee 1155* (UKMB), 1275 m, 2008, *G.E. Lee 1184* (UKMB), 1120 m, 2009, *G.E. Lee 1428, 1429* (UKMB). **Sabah:** West Coast Res., Mt. Tambuyokon, 1830-2130 m, 1961, *W. Meijer B 11317* (NICH); Mt. Kinabalu, Tenompok, 1524 m, 1931-1932, *J. & M.S. Clemens s.n.* (NICH), above Paca Cave, 2984-3200 m, 1963, *M. Mizutani 2965* (NICH), between Tenompok Pass and Kamaranga Radio Station, 1400-1900 m, 1963, *M. Mizutani 2101* (NICH), between Kamaranga Radio Station and Second Radio Station, 2146-2500 m, 1963, *M. Mizutani 2634* (NICH), below Paca Cave, 2500-2800 m, 1963, *M. Mizutani 2750, 3554* (NICH), between Kamaranga Radio Station and waterfalls, 2000-2146 m, 1963, *M. Mizutani 2396* (NICH), hot spring, 1800 m, 1972, *M. Okabe 106a, 125, 129* (NICH). **INDONESIA.** Seram: Manusela National Park, 1290-2000 m, 1985, *H. Akiyama 8777* (NICH); Sulawesi: Lore Lindu N. Park, Mt. Nokilalaki, 1900-2350 m, 2005, *S.R. Gradstein & N.S. Ariyanti 11028, 11053* (BIOT). **FIJI.** Viti Levu: summit Mt. Victoria, 1260 m, 1952, *H. Hürlimann T 1107* (GOET).

**Distribution and habitat in Malaysia:** Pahang, Sabah; epiphytic in montane forest, growing in pendulous festoons on branches of shrubs in open and developed area, occasionally on living leaves (Tixier, 1980), above 1000 m.

**General distribution:** Malesia.

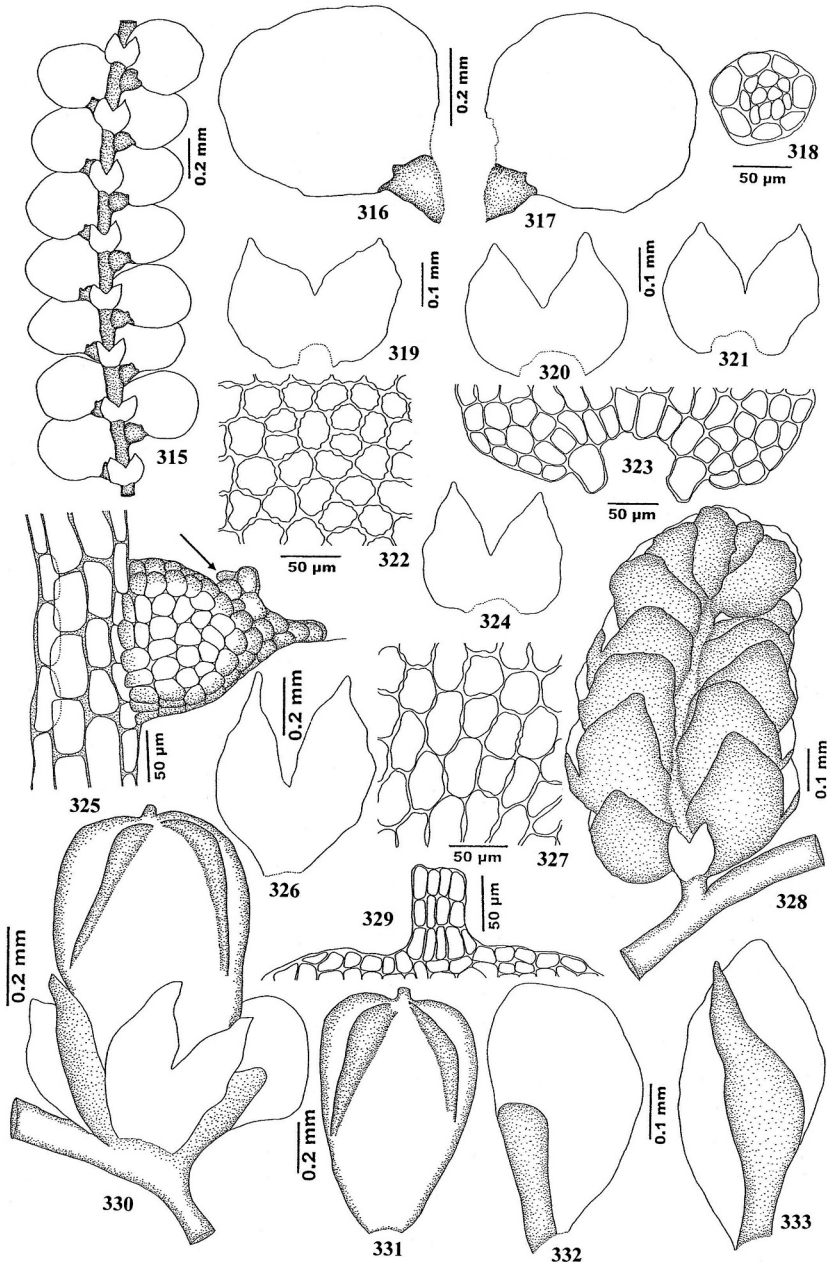
**Discussion:** The distinguishing characters of *L. lumbricoides* are 1) the flexuous habit, plant often large, growing pendulously from twigs or branches, 2) the apices of leaf lobe strongly recurved when dry or moist, 3) the cordate base of underleaf, sometimes with auricle, 4) the small leaf lobules, 5) the large, rectangular disc cell below the apical tooth, 6) the laminal cells with well-developed trigones and conspicuous intermediate thickenings, and 7) the peculiar long beak of the perianth. In its flexuous habit and strongly recurved leaves, *L. lumbricoides* resembles *L. stephaniana* from Borneo, however, in the latter species, the underleaves are smaller (0.3-0.4 mm long), rounded and without auricle at the base, the cells are without intermediate thickenings, and the perianth are obovoid with 3-4 cells long beak. In *L. lumbricoides*, the underleaves are larger (0.8-1.0 mm long), often with auricle at the base, the laminal cells are with well-developed trigones and conspicuous intermediate thickenings, and they have prominent pyriform perianth with 7-10 cells long beak. Both species are considerably robust plants of high elevations.

The specimens collected from Malaysia are always sterile and usually slightly smaller than the Indonesia plants. They also vary in the characters of the leaf lobule and in the number of keels on the perianth. In particular, Indonesian *L. lumbricoides* sometimes does not possess a very distinct disc cell and the apical tooth is also not so well-developed, usually with two rows of cell in width. Perianths have been seen in only two collections from Sulawesi (*S.R. Gradstein & N.S. Ariyanti 11028, 11053*). The perianths may have 4-5 keels or only 2 (lateral) ones, even within the same collection. The keels are often expanded above as auricles, especially the lateral keels. The auricles vary in size and are bigger and often undulate on large perianths.

**18. *Lejeunea micholitzii* Mizut., *J. Hattori Bot. Lab.* 33: 236 (1970)    **Figs 315-333****

Basionym: *Hygrolejeunea parvisaccata* Steph., *Sp. Hepat.* 5: 567 (1914) ≡ *Taxilejeunea parvisaccata* (Steph.) Eifrig, *Ann. Bryol.* 9: 90 (1937), *non Lejeunea parvisaccata* Steph., *Sp. Hepat.* 5: 567 (1914). TYPE: Philippines, Insula Luzon, 1884, *Micholitz s.n.* (holotype: G!).

For further synonyms see Mizutani (1961, 1970).



Figs 315-333. *Lejeunea micholitzii* Mizut. **315**. Part of plant in ventral view; **316**, **317**. Leaves; **318**. Cross-section of stem; **319-321**, **324**. Underleaves; **322**. Median cells of leaf lobe; **323**. Basal cells of underleaf; **325**. Stem portion and leaf lobule (hyaline papilla shown by arrow); **326**. Female bracteole; **327**. Basal cells of leaf lobe; **328**. Androecial shoot; **329**. Upper portion of perianth; **330**. Perianth with bracts and bracteole; **331**. Perianth; **332**, **333**. Female bracts. 315-317, 322, 325-327, 329 drawn from *Z. Iwatsuki 1383a* (NICH); 318, 320, 324, 328 from *G.E. Lee 1833* (UKMB); 319, 321, 323 from *G.E. Lee 1799* (UKMB); 330-333 from *M. Mizutani 3811* (NICH).

**Plants** dioicous, 0.8-1.3 mm wide, usually light green when fresh, dark green to brown when dry, irregularly and slightly branched, sometimes pinnately branched, branches erect-spreading to spreading, collar with three small lobes. **Stem** 0.07-0.10 mm in diameter, about 5 cells high in cross-section, epidermal cells 7, 20-30  $\mu\text{m}$  wide, medullary cells 10-15, 12-16  $\mu\text{m}$  wide. **Leaves** contiguous to subimbricate, occasionally distant, rarely recurved when dry, erect-spreading to spreading and plane when moist. **Leaf lobes** 0.6-0.8 mm long and 0.5-0.6 mm wide (when flattened), ovate to orbicular; leaf apex broadly rounded, always flat; leaf margin entire; the ventral margin forming an angle of  $120^\circ$ - $150^\circ$  with the keel when flattened; insertion line 10-11 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, quadrate to rectangular towards the leaf margin; apical cell 13-21  $\mu\text{m}$  long and 8-13  $\mu\text{m}$  wide, median cell 33-42  $\mu\text{m}$  long and 13-21  $\mu\text{m}$  wide, basal cell 38-42  $\mu\text{m}$  long and 13-21  $\mu\text{m}$  wide; cell walls hyaline, with well-developed trigones and conspicuous intermediate thickenings, 1-3 per cell, 0-1(2) between 2 adjacent trigones. Cuticle smooth. Oil bodies somewhat glistening to faintly opaque-granular, fine *Jungermannia*-type, with minute granules, somewhat rough externally; marginal cells with 10-14 oil bodies per cell, 3-4  $\mu\text{m}$  long and 2-3  $\mu\text{m}$  wide, mostly globose to ovoid; median cells with 16-20 oil bodies per cell, 5-10  $\mu\text{m}$  long and 3-4  $\mu\text{m}$  wide, globose, ovoid to ellipsoid; basal cells with 14-24 oil bodies per cell, 6-10  $\mu\text{m}$  long and 3-5  $\mu\text{m}$  wide, globose, ovoid to ellipsoid. **Leaf lobules** sometimes reduced, 0.1-0.2 mm long and *ca* 0.1 mm wide, to 1/4 the length of the lobe, at an angle of  $50^\circ$ - $60^\circ$  to the stem, ovate-triangular, inflated along the keel; apex obliquely truncate; keel curved; free margin incurved partially; apical tooth 25-30  $\mu\text{m}$  long, oblong, erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 30-35  $\mu\text{m}$  long and 25-28  $\mu\text{m}$  wide. **Underleaves** *ca* 0.2 mm long, 0.2-0.4 mm wide, to 2-3 times wider than the stem, distant, suborbicular to wider than long, sometimes reniform, covering half of the lobules; bilobed, lobes to 3/5-4/5 of underleaf length, sometimes more or less apiculate, about 7 cells wide, triangular, oblique; sinus narrow to broad, acute to obtuse, U-shaped to V-shaped; underleaf margin entire; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.3-0.8 mm long, 0.4-0.5 mm wide with bracts, on short or long lateral branches. Male bracts in 3-6 pairs, crenulate without wing, apex obtuse, keels inflated. Male bracteole 1, smaller than underleaf, margin entire. Antheridia 2 per bract, 100-110  $\mu\text{m}$  in diameter, hyaline, with a short and hyaline stalk, 75-80  $\mu\text{m}$  in length. **Gynoecia** on short or long branches, female bracts loosely arranged, with one innovation, usually with one gynoecium in a lateral position. Female bracts slightly smaller than the leaves, erect-spreading when moist, not enveloping the perianth. Lobes 0.4-0.5 mm long, 0.2-0.3 mm wide, ovate to obovate, apex obtuse, margin entire. Lobules 0.2-0.4 mm long, 0.05-0.10 mm wide, rarely reduced, 1/3 the width and 1/2 the length of the lobe, sometimes almost as long as the lobe, oblong to lanceolate, apex acute to obtuse, keels straight, smooth, 0.1-0.2 mm long. Female bracteoles 0.4-0.5 mm long, 0.2-0.3 mm wide, 1/2 of the perianth length, ovate to slightly obovate with tips acute, lobes to 3/5 of female bracteole length, distant, sinus acute, margin entire. Perianths 0.7-0.8 mm long, 0.4-0.5 mm wide, emergent to 1/2 of the perianth length, obovoid, with 5 keels, sometimes 4 keels with 1 indistinct ventral keel; beak 3 cells long; cells of the perianth at the keels smooth, rarely mammillose; stalk-like elongation sometimes present, 0.1-0.2 mm long. **Sporophyte** not seen. **Vegetative propagation** not seen.



**Further specimens examined. MALAYSIA. Kelantan:** Gua Musang, foot of Gunung Chamah, Dakota trail, 770 m, 2011, *A. Damanhuri 11-369, 11-436* (UKMB). **Pulau Langkawi:** along the trail to the summit of Gunung Jaya, 690 m, 2010, *G.E. Lee 1461, 1462* (UKMB). **Negeri Sembilan:** along the trail to Sungai Semong, 265 m, 2010, *A. Damanhuri 10-1* (UKMB). **Pahang:** Genting Highlands, along stream near pumping plant, ca 1200 m, 1996, *N. Ohnishi 2846* (HIRO); Goh Tong Jaya, bear waterfall, 845 m, 2011, *G.E. Lee 2205, 2206a, 2189, 2199, 2202* (UKMB); Cameron Highlands, trail to Gunung Brinchang, 1910 m, 2009, *G.E. Lee 2299* (UKMB); Parit Waterfalls, 1340 m, 2009, *G.E. Lee 2333* (UKMB). **Sabah:** between Sosopodon and S. Kelinggen, foot of Mt. Kinabalu, 1350-1400 m, 1963, *M. Mizutani 3811, 3843* (NICH); Kinabalu Park, trail from Timphohon gate to Kandis shelter, 1900 m, 2010, *G.E. Lee 1799, 1814, 1833* (UKMB); Botanical Garden, around Power station road, 1515 m, 2010, *G.E. Lee 1739, 1746, 1748, 2039, 2058, 2059, 2062, 2066, 2074, 2077* (UKMB). **INDONESIA.** W Java: Halimum Salak Mt. National Park, 1200 m, 2009, *M.S. Sofiyana 026* (BIOT); Mt. Kendeng, 1230 m, 2005, *Radhiah Zakaria 171c, 191c* (BIOT); trail to Ciismun waterfall, 2007, *G.E. Lee & Nova Indri 33* (BIOT); Cikudapaeh trail, 1100 m, 2009, *NSA IIATI Q2-2* (BIOT); Sulawesi: Lore Lindu National Park, Toro, 900-1100 m, 2005, *N.S. Ariyanti B1/Sp1/S13/3, B2/Sp2/S2/1* (BIOT). **PHILIPPINES.** Mindoro: Mt. Halcon, 1300 m, 1988, *M. Onraedt & E. Salgado 12090, 12130* (NICH).

**Distribution and habitat in Malaysia:** Kelantan\*, Pulau Langkawi\*, Negeri Sembilan\*, Pahang\*, Sabah; epiphyte at elevations above 700 m.

**General distribution:** Malesia, New Caledonia.

**Discussion:** The distinguishing characters of *L. micholitzii* include 1) small, reniform and distant, deeply bifid (3/4-4/5) underleaves with acute lobes, 2) leaf cells with well-developed trigones and intermediate thickenings, 3) two intermediate thickenings in the basal leaf cells between adjacent trigones, 4) the fine *Jungermannia*-type of oil bodies, and 5) the obovoid perianth with a 3 cells long beak. This species maybe confused with *L. anisophylla* and *L. papilionacea* but differs by being dioicous; moreover *L. papilionacea* differs by the auriculate perianth keels and orbicular underleaves and *L. anisophylla* by leaf cells without well-developed trigones and intermediate thickenings. Among the Malaysian *Lejeuneas*, *L. micholitzii* is most closely related to *L. dimorpha*, which was recovered as sister to *L. micholitzii* in a phenetic and phylogenetic analysis (Lee *et al.*, submitted). However, *L. dimorpha* is easily separated from *L. micholitzii* by the autoicous plant, the glistening-homogeneous, *Massula*-type oil bodies and the peculiar caducous branches (= cladia) with numerous hyaline rhizoids on leaf margins and large, reniform underleaves. Such caducous branches are never produced in *L. micholitzii*.

*Lejeunea micholitzii* varies particularly in the size and shape of the underleaves, which are rather large, 0.30-0.33 mm long, 0.35-0.40 mm wide and somewhat ovate in the type material. Variation is also observed in the apices of the leaf lobes, which may be broadly to narrowly rounded on the same shoot.

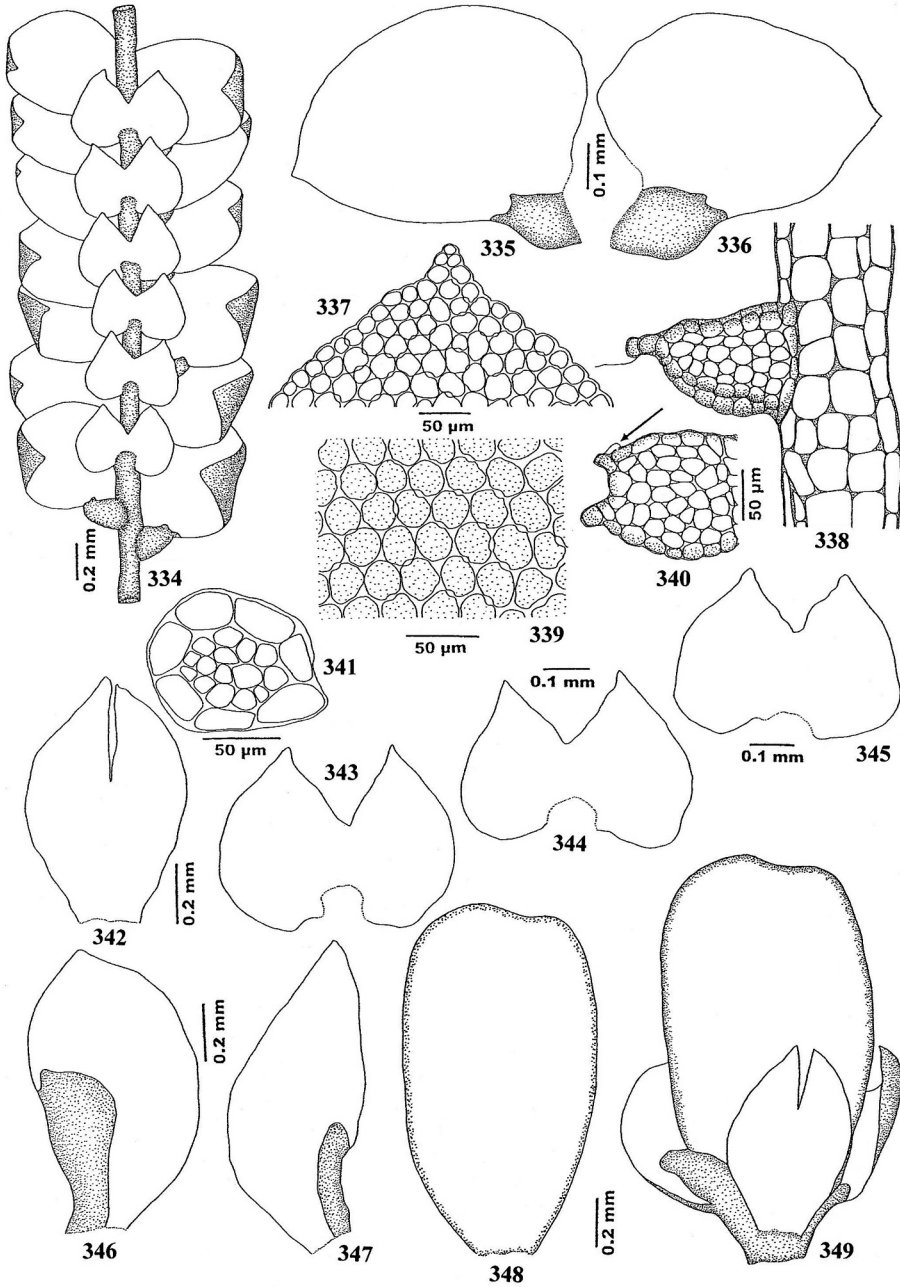
### 19. *Lejeunea microloba* Taylor, *London J. Bot.* 5: 399 (1846)

**Figs 334-349**

≡ *Hygrolejeunea microloba* (Tayl.) Steph., in Rechinger, *Denkschr. Kais. Akad. Wiss. Math. Nat. Klasse Wien* 81: 294 (1908). TYPE: South Sea Isles, *Nightingale s.n.* (holotype: FH!; isotype: BM!)

= *Hygrolejeunea chalmersii* Steph., *Sp. Hepat.* 5: 558 (1914), [*Hygrolejeunea chalmersii* Steph., *Hedwigia* 28: 171 (1889), nom. inval.] ≡ *Lejeunea chalmersii* (Steph.) Mizut., *J. Hattori Bot. Lab.* 33: 249 (1970). TYPE: Papua New Guinea, near South Cape, Cloudy Mts. 1884, *Chalmers s.n.* (holotype: G!), syn. *fide* Grolle (1979).

For further synonyms see Grolle (1979).



Figs 334-349. *Lejeunea microloba* Taylor. 334. Part of plant in ventral view; 335, 336. Leaves; 337. Apical cells of leaf lobe; 338. Stem portion and leaf lobule; 339. Median cells of leaf lobe; 340. Upper part of leaf lobule when flattened (hyaline papilla shown by arrow); 341. Cross-section of stem; 342. Female bracteole; 343-345. Underleaves; 346, 347. Female bracts; 348. Perianth; 349. Perianth with bracts and bracteole. All figures drawn from *T. Kodama 40783* (NICH).

**Plants** dioicous, relatively large, 1.0-1.4 mm wide, light brown when dry, irregularly and loosely branched, branches erect-spreading to spreading, collar with three small lobes. **Stems** 0.10-0.15 mm in diameter, about 6 cells high in cross-section, epidermal cells 7, 37-50  $\mu\text{m}$  wide, medullary cells 15-19, 12-20  $\mu\text{m}$  wide. **Leaves** closely imbricate, recurved when dry, spreading and recurved when moist. **Leaf lobes** 0.6-0.8 mm long, 0.5-0.6 mm wide (when flattened), ovate-rectangular; leaf apex apiculate, recurved; leaf margin weakly crenulate; the ventral margin forming an angle of  $140^\circ$ - $150^\circ$  with the keel when flattened; insertion line about 10 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregularly rounded to rectangular towards the leaf margin; apical cells 18-25  $\mu\text{m}$  long and 18-25  $\mu\text{m}$  wide, median cells 30-38  $\mu\text{m}$  long and 18-23  $\mu\text{m}$  wide, basal cells 43-50  $\mu\text{m}$  long and 25-30  $\mu\text{m}$  wide; cell walls hyaline, with well-developed trigones and conspicuous intermediate thickenings, 1-3 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies not seen. **Leaf lobules** sometimes reduced, 0.15-0.2 mm long, 0.10-0.15 mm wide, to 1/4-1/3 the length of the lobe, at an angle of  $60^\circ$ - $70^\circ$  to the stem, ovate, inflated along the keel; apex obliquely truncate; keel curved free margin incurved fully; apical tooth 22-24  $\mu\text{m}$  long, oblong, erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 20-23  $\mu\text{m}$  long and 17-20  $\mu\text{m}$  wide. **Underleaves** 0.4-0.6 mm long, (0.35) 0.6-0.85 mm wide, to 4-5 times wider than the stem, imbricate to contiguous, reniform (wider than long), covering the lobules; bilobed, lobes to 1/2 of underleaf length, about 11 cells wide, triangular, distant; sinus broad, acute, V-shaped; underleaf margin weakly crenulate; base cordate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.5-1.2 mm long, 0.3-0.5 mm wide with bracts, on short lateral branches, occasionally on the main shoots. Male bracts in 4-10 pairs, entire without wing, apex acute to obtuse, keels inflated. Male bracteoles 1-2, smaller than the underleaf, margin entire. Antheridia not seen. **Gynoecea** on short branches, sometimes on main shoots, female bracts loosely arranged, with one innovation, usually with one gynoeceum in a lateral position. Female bracts smaller than the leaf, erect-spreading when moist, not enveloping the perianth. Lobes 0.5-0.6 mm long, 0.2-0.25 mm wide, ovate to obovate, apex acute, margin weakly crenulate. Lobules 0.2-0.4 mm long, 0.04-0.07 mm wide, 1/2-1/4 the width and 1/3-1/2 the length of the lobe, oblong, apex acute to obtuse, sometimes obliquely truncate, keels straight and smooth, 0.2-0.3 mm long. Female bracteoles 0.6-0.8 mm long, 0.35-0.50 mm wide, 1/2 of the perianth length, ovate with tips acute, lobes to 1/2 of female bracteole length, sinus narrow, acute, margin weakly crenulate. Perianths 1.0-1.4 mm long, 0.5-0.8 mm wide, emergent to 1/2 of the perianth length, oblong, without keel and beak; apex truncate; cells of the perianth smooth; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined.** **MALAYSIA.** *Sabah:* Mt. Kinabalu, between Tenompok Pass and Ulu Damaian, 1463-1500 m, 1963, *M. Mizutani* 3230, 3267 as *Lejeunea chalmersii* (NICH); Kinabalu National Park, near Mamut Mine, 1300 m, 1970, *T. Kodama* 40783 as *L. chalmersii* (NICH). **INDONESIA.** *Seram:* Manusela National Park, 750-1290 m, 1985, *H. Akiyama* 8699, 8716 (NICH). **PAPUA NEW GUINEA.** Southern Highlands Province, 6 km SE of Ialibu, 1850 m, 1982, *H. Streimann* 26430 (NICH).

**Distribution and habitat in Malaysia:** Sabah; on tree trunks and leaves, rarely terrestrial, at 750-1500 m.

**General distribution:** Malesia.

**Discussion:** *Lejeunea microloba* is characterized by 1) strongly recurved leaves with apiculate apex, 2) leaf cells with well-developed trigones and intermediate

thickenings, 3) reniform underleaves with cordate base, and 4) eplicate perianth. By its perianth, underleaf and leaf lobule, *L. microloba* resembles *L. umbilicata*, from which it differs essentially by the apiculate leaf apex. In a phenetic analysis (Lee *et al.*, submitted), the two species are clustered by high similarity. *Lejeunea microloba* is similar to *L. contracta* in the shape of the underleaf but the 5-keeled perianth and the leaf cells without intermediate thickenings in *L. contracta* separate this species from *L. microloba*. The relationships between these two species are distant (Lee *et al.*, submitted).

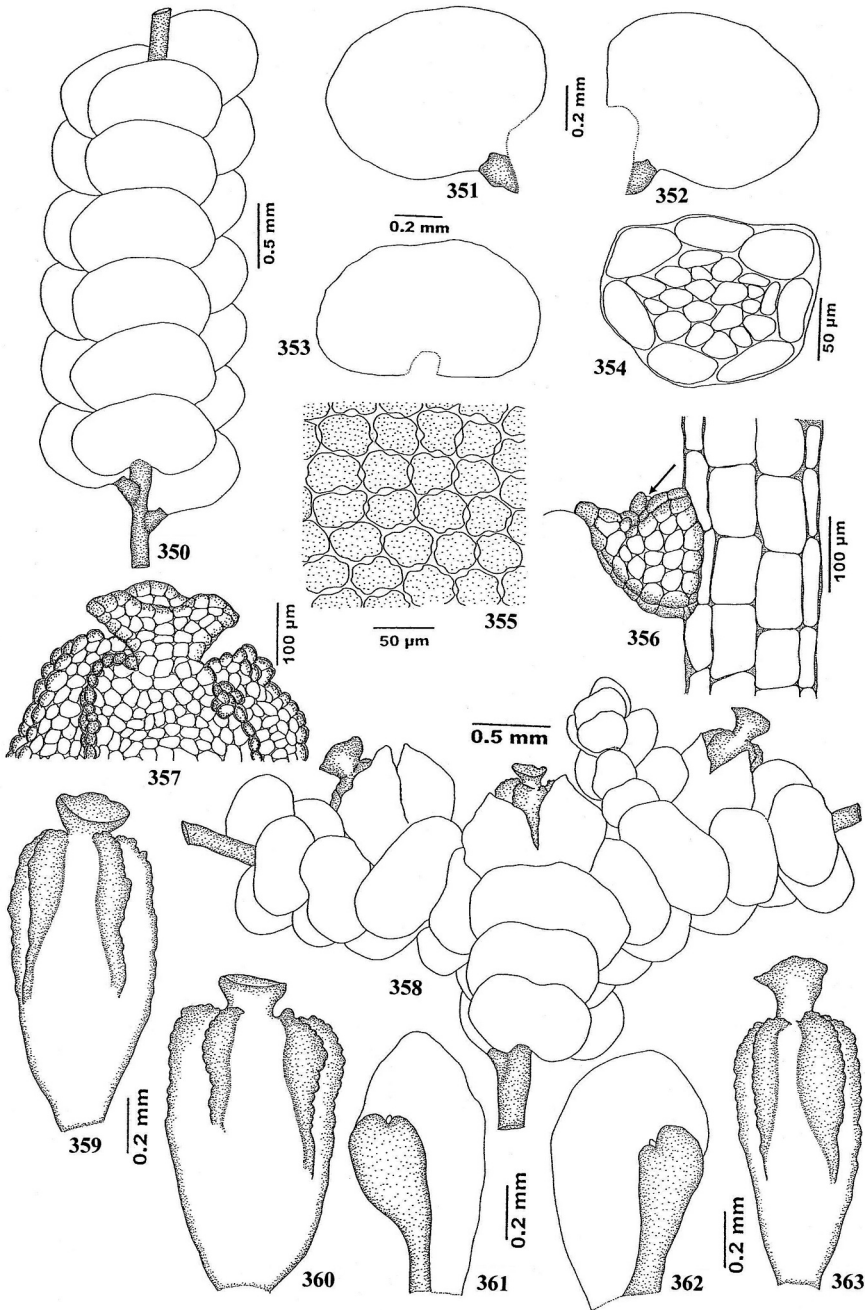
Specimens from Seram (Indonesia) differ slightly from those of Sabah by less imbricate leaves, stronger crenulation of leaf margins, frequently reduced leaf lobules and more distant underleaves. According to Mizutani (1972) the leaf margins are always strongly crenulate and the underleaf bases strongly cordate-auriculate, but these characters may vary and crenulation may sometimes be weak and auricles absent. Underleaves are smaller in the type of *Hygrolejeunea microloba* than in the type of *H. chalmersii*.

**20. *Lejeunea mimula* Hürl., *Bauhinia* 11: 12 (1993)**

**Figs 350-363**

≡ *Hygrolejeunea luteola* Steph., *Sp. Hepat.* 5: 553 (1914) ≡ *Taxilejeunea luteola* (Steph.) Eifrig, *Ann. Bryol.* 9: 104 (1936) ≡ *Lejeunea luteola* (Steph.) Mizut., *J. Hattori. Bot. Lab.* 33: 243 (1970), *nom. illeg. (non Lejeunea luteola* Spruce).  
 TYPE: Java, Tjibodas, *Nyman s.n.* (holotype: G!).

**Plants** dioicous, relatively large, 1.0-1.5 mm wide, yellowish green when fresh to dark brown when dry, irregularly and slightly branched, sometimes pinnately branched, branches erect-spreading to spreading, collar with three small (sometimes reduced) lobes. **Stems** 0.10-0.15 mm in diameter, about 7 cells high in cross-section, epidermal cells 7, 50-65 µm wide, medullary cells 20-23, 15-35 µm wide. **Leaves** imbricate, rarely recurved when dry, erect-spreading to spreading and plane when moist. **Leaf lobes** 0.6-0.8mm long and 0.5-0.7 mm wide (when flattened), ovate to ovate-orbicular; leaf apex broadly rounded, sometimes narrowly rounded, always flat; leaf margin entire; the ventral margin forming an angle of 100°-120° with the keel when flattened; insertion line about 12 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, sometimes somewhat quadrate to pentagonal, irregularly quadrate to rectangular towards the leaf margin; apical cell 20-25 µm long and 15-25 µm wide, median cell 30-40 µm long and 17-25 µm wide, basal cell 45-60 µm long and 20-25µm wide; cell walls hyaline, with well-developed trigones and conspicuous intermediate thickenings, 2-4 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies somewhat glistening to faintly opaque-granular, fine *Jungermannia*-type, with minute granules, somewhat rough externally; marginal cells with 3-4 oil bodies per cell, 2-3 µm long and 2-3 µm wide, mostly globose to ovoid; median cells with 5-8 oil bodies per cell, 5-10 µm long and 3-4 µm wide, ovoid to ellipsoid; basal cells with 6-8 oil bodies per cell, 5-14 µm long and 3-4 µm wide, ovoid to ellipsoid. **Leaf lobules** sometimes reduced, 0.12-0.15 mm long and 0.08-0.10 mm wide, to 1/5-1/4 the length of the lobe, at an angle of 40°-50° to the stem, ovate-triangular, inflated along the keel; apex obliquely truncate; keel curved; free margin incurved partially; apical tooth 17-20 µm long, oblong, somewhat erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 30-35 µm long and 25-28 µm wide. **Underleaves** 0.3-0.5 mm long, 0.7-1.0 mm wide, to 5-6 times wider than the stem, imbricate, reniform (wider than long), always covering the lobules; unlobed, apex truncate to weakly retuse; lobes and



Figs 350-363. *Lejeunea mimula* Hürl. 350. Part of plant in ventral view; 351, 352. Leaves; 353. Underleaves; 354. Cross-section of stem; 355. Median cells of leaf lobe; 356. Stem portion and leaf lobule (hyaline papilla shown by arrow); 357. Upper portion of perianth; 358. Part of plant, with perianth-bearing branches; 359, 360, 363. Perianths; 361, 362. Female bracts. 350-356 drawn from *M. Mizutani* 3239 (NICH); 357-363 from *G.E. Lee* 1749 (UKMB).

sinus indistinguishable; underleaf margin entire; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.3-0.4 mm long, 0.2-0.3 mm wide with bracts, on short lateral branches. Male bracts in 1-2 pairs, entire without wing, apex obtuse, keels inflated. Male bracteole 0-1, smaller than underleaf, margin entire. Antheridia not seen. **Gynoecea** terminal on main shoots, on short or long branches, female bracts somewhat crowded, with two innovations, 2-5 gynoecea in a lateral row due to repeatedly fertile innovations. Female bracts smaller than the leaf, erect-spreading when moist, somewhat enveloping the perianth. Lobes 0.8-1.0 mm long, 0.4-0.5 mm wide, obovate to elliptic, apex obtuse, margin entire. Lobules 0.5-0.6 mm long, 0.2-0.3 mm wide, rarely reduced, 1/2 the width and 3/4 the length of the lobe, obovate to oblong, apex obtuse, sometimes forms a sinus with hyaline papilla at lateral side, keels straight, smooth, 0.15-0.25 mm long. Female bracteoles 0.8-0.9 mm long, 0.7-0.8 mm wide, almost as long as perianth length, widely obovate with tips obtuse, lobes to 1/3 of female bracteole length, distant, sinus narrow, acute, margin entire. Perianths 0.8-1.0 mm long, 0.4-0.5 mm wide, emergent to 1/5 of the perianth length, oblong, with 5 keels; beak 4-6 cells long, funnel-shaped; cells of the perianth at the keels mammillose; stalk-like elongation sometimes present, 0.4-0.5 mm long. **Sporophyte**: seta to 0.3 mm long; capsule 0.3-0.4 mm in diameter, valves 0.4 mm long, 0.25 mm wide at middle, scarcely spreading after dehiscence; elaters *ca* 0.2 mm long; spores not seen. **Vegetative propagation** not seen.

**Further specimens examined.** MALAYSIA. Sabah: Mt. Kinabalu, between Tenompok Pass and Ulu Damaian, 1463-1500 m, 1963, *M. Mizutani 3239, 3258, Z. Iwatsuki 4541b* as *Lejeunea luteola* (NICH); Penampam, Gunung Alab, 1600-1930 m, 1968, *Hotta & Kokawa 1915bis* as *L. luteola* (NICH); Kinabalu Park, trail from Timpohon gate to Kandis Shelter, 1900 m, 2010, *G.E. Lee 1799* (UKMB), trail from Mempening Shelter to Layang-layang Staff Quarters, 2500-2800 m, 2010, *G.E. Lee 1909* (UKMB), Botanical Garden, around Power station road, 1515 m, 2010, *G.E. Lee 1745, 1749* (UKMB). FIJI: Viti Levu, near Tamavuva Waterfalls, 1954, *E. Whitehouse 29923* as *L. luteola* (NICH), forest station at Nandarivatu, 884-1127 m, 1955, *E. Whitehouse 29965a, 29986D* as *L. luteola* (NICH).

**Distribution and habitat in Malaysia:** Sabah; on trees at higher elevations, above 1400 m.

**General distribution:** Malesia.

**Discussion:** *Lejeunea mimula* can be distinguished from its allies by 1) yellowish-green color (when fresh) delicate plant in the field, 2) large, reniform and unlobed underleaves, 3) small leaf lobules with incurved free margin, 4) large and widely obovate female bracteoles, and, especially 5) the large, funnel-shaped beak of the perianth. Underleaves and lobules resemble those in *L. albescens* and *L. sordida*; for differences see under *L. sordida*.

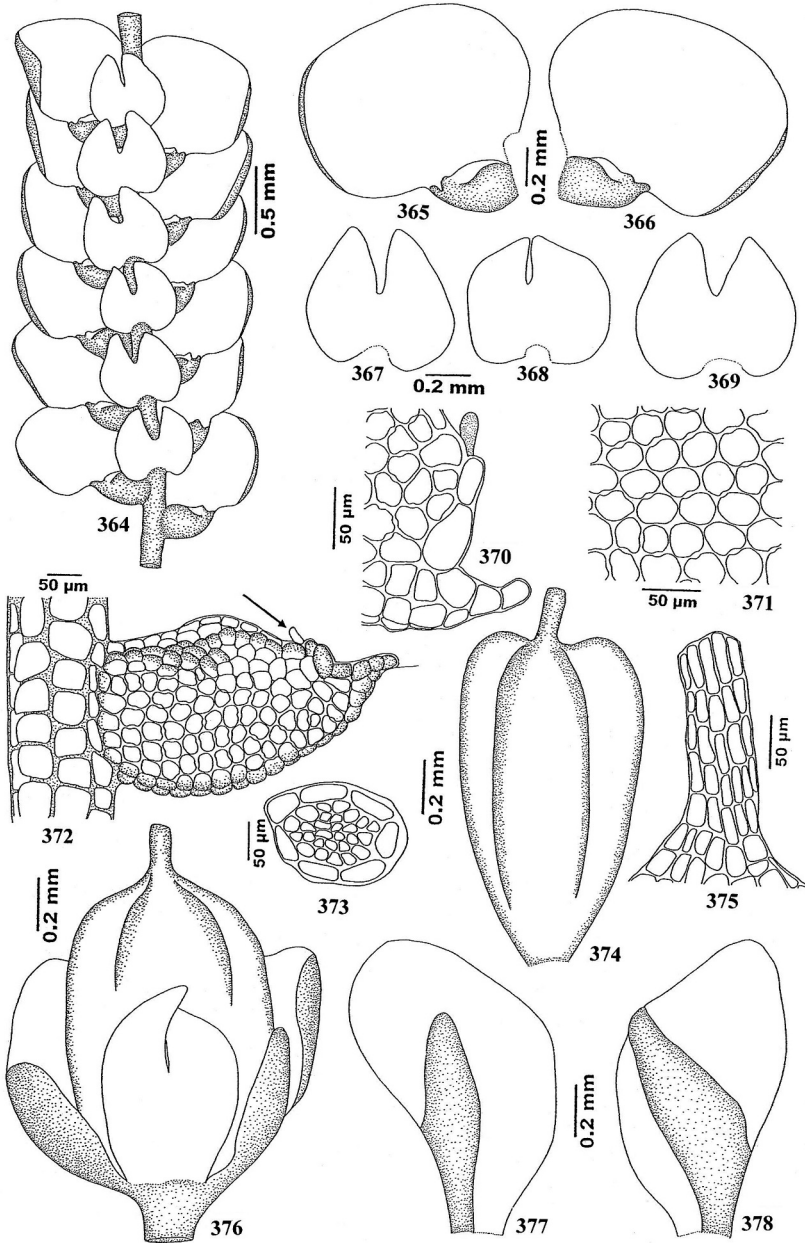
When sterile, *L. mimula* is very similar to *L. leratii*, which has an almost similar habit, leaves and underleaves; the two differ mainly by the funnel-shaped perianth beak and gynoecea with usually two innovations in *L. mimula*. Mizutani (1970) mentioned further differences between these two species, including the arrangement of the leaves (imbricate vs. contiguous), the shape of the underleaf apices (truncate vs. retuse) and the number of medullary cells in cross-section of stem (20 vs. 10). In my study, I could not identify these two species without perianth; therefore, they may not deserve recognition at species level. For the time they are kept as separate species; more collections of *L. leratii* are needed to arrive at a better understanding of the differences between the two species. Eifrig (1937) cited a specimen of *L. leratii* from Malaysia (Mt. Kinabalu, Tenompok, *Clemens 1931/32*, as *Taxilejeunea patersonii*), however, this specimen could not be located in JE nor BM. *Lejeunea leratii* is therefore excluded from this revision.

**21. *Lejeunea mizutanii* Grolle, *J. Hattori Bot. Lab.* 45: 178 (1979) Figs 364-378**

≡ *Cheilolejeunea zollingeri* Steph. *Hedwigia* 34: 245 (1895) ≡ *Pycnolejeunea zollingeri* (Steph.) Mizut., *J. Hattori Bot. Lab.* 30: 179 (1967) ≡ *Lejeunea zollingeri* (Steph.) Mizut., *J. Hattori Bot. Lab.* 33: 242 (1970), *nom. illeg.* (*non Lejeunea zollingeri* Steph.). TYPE: Java, *Zollinger s.n.* (holotype: G!).

**Plants** dioicous, relatively large, 1.0-2.0 mm wide, yellowish green when fresh to light brown when dry, irregularly and loosely branched, branches spreading, collar with three small lobes. **Stems** 0.10-0.15 mm in diameter, about 10 cells high in cross-section, epidermal cells 7, 50-62  $\mu\text{m}$  wide, medullary cells 25-27, 25-38  $\mu\text{m}$  wide. **Leaves** closely imbricate, recurved when dry, spreading and slightly recurved when moist. **Leaf lobes** 0.65-1.25 mm long, 0.5-0.9 mm wide (when flattened), ovate-orbicular; leaf apex broadly rounded, usually slightly recurved; leaf margin entire to weakly crenulate; the ventral margin forming an angle of 110°-140° with the keel when flattened; insertion line about 13 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregularly quadrate to rectangular towards the leaf margin; apical cells 20-25  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide, median cells 30-37.5  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide, basal cells 37.5-45  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide; cell walls hyaline, with well-developed trigones and conspicuous intermediate thickenings, 1-2 per cell, 0-1 between 2 adjacent trigones. Cuticle smooth. Oil bodies not seen. **Leaf lobules** relatively large, rarely reduced, 0.35-0.40 mm long, 0.15-0.25 mm wide, to 1/2 the length of the lobe, at an angle of 70°-80° to the stem, ovate to oblong, inflated along the keel; apex obliquely truncate; keel slightly curved; free margin flat; apical tooth 37-50  $\mu\text{m}$  long, oblong, somewhat erect, apex obtuse; margin between tooth and sinus 3-4 cells long, large disc cell present, cell below the apical tooth 55-95  $\mu\text{m}$  long and 37-45  $\mu\text{m}$  wide. **Underleaves** 0.45-0.6 mm long, 0.3-0.45 mm wide, to 4-5 times wider than the stem, contiguous, sometimes distant, ovate (longer than wide), covering 1/4-1/2 of the lobules; bilobed, lobes to 1/2 of underleaf length, about 10 cells wide, triangular, distant, sometimes connivent to slightly overlapping; sinus narrow, acute, V-shaped; underleaf margin entire to crenulate; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** not seen. **Gynoecea** on short or long lateral branches, occasionally on main shoots, female bracts loosely arranged, with one innovation, usually with one gynoeceum in a lateral position. Female bracts smaller than the leaves, erect spreading when moist, somewhat enveloping the perianth. Lobes 0.8-1.0 mm long, 0.5-0.6 mm wide, elliptic, apex obtuse, margin entire. Lobules 0.7-0.8 mm long, 0.20-0.25 mm wide, rarely reduced, 1/3-1/2 the width and 2/3 the length of the lobe, oblong to lanceolate, apex obtuse, keels straight, smooth, 0.3-0.4 mm long. Female bracteoles 0.7-0.8 mm long, 0.50-0.55 mm wide, 2/3 the length of the perianth, ovate with the tips obtuse, lobes to 1/2 of female bracteole length, overlapping, sinus narrow, acute, margin entire. Perianths 1.0-1.3 mm long, 0.6-0.8 mm wide, emergent to 1/3 of the perianth length, obovoid, with 5 keels, sometimes with 3 sharp keels and 2 indistinct dorsal and ventral keels; beak 6 cells long; cells of the perianth at the keels smooth, rarely mamilliose; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined. MALAYSIA. Sabah:** Mt. Kinabalu, between Kamaranga Radio Station and waterfalls, 2000-2146 m, 1963, *Z. Iwatsuki 438* as *L. zollingeri* (NICH), along Mamut road, 1000-1100 m, 1970, *T. Kodama 41054, 41155* as *L. zollingeri* (NICH), Carson's camp to Radio Station, 2000-2650 m, 1974, *T. Kodama 49700bis* as *L. zollingeri* (NICH), trail from Mempening shelter to Layang-layang Staff Quarters, 2500-2800 m, 2010, *G.E. Lee 2273* (UKMB).



Figs 364-378. *Lejeunea mizutanii* Grolle. **364.** Part of plant in ventral view; **365, 366.** Leaves; **367-369.** Underleaves; **370.** Upper part of leaf lobule when flattened (hyaline papilla shown in gray); **371.** Median cells of leaf lobule; **372.** Stem portion and leaf lobule (hyaline papilla shown by arrow); **373.** Cross-section of stem; **374.** Perianth; **375.** Beak of perianth; **376.** Perianth with bracts and bracteole; **377, 378.** Female bracts. 364-367, 370-373, 376 drawn from *T. Kodama 41155* (NICH); 368 from *Z. Iwatsuki 438* (NICH); 369, 374, 375, 377, 378 from *T. Kodama 41054* (NICH).



**Distribution and habitat in Malaysia:** Sabah; epiphytic at elevations above 1000 m.

**General distribution:** Sabah, Indonesia (Java).

**Discussion:** *Lejeunea mizutanii* resembles *L. discreta*, *L. lumbricoides*, *L. pectinella* and *L. utriculata* in the recurved leaves, relatively large lobules and the presence of a large rectangular disc cell below the apical tooth, but differs from these four species by the usually flat free margin of leaf lobules (sometimes incurved in the proximal half). In the other species the free margin is strongly incurved over its entire length and the apical tooth and rectangular disc cell are invisible without preparation. Further important characters of *L. mizutanii* are 1) ovate-orbicular leaf lobes, 2) large underleaves with obtuse tips, 3) the perianth with keels, to 3/4 of its length, 3) lobes of female bracteole usually overlapping, and 4) perianth with a 6 cells long beak and long keels (to 3/4).

**22. *Lejeunea papilionacea* Steph., *Hedwigia* 31: XVII (1892)**

(+ p. 169 "*Hygrolejeunea*")

**Figs 379-393**

= *Hygrolejeunea papilionacea* (Steph.) Steph., *Sp. Hepat.* 5: 525 (1914). TYPE: W Africa, Cameroon, 330 m, *Dusén* 502 (holotype: G!)

= *Hygrolejeunea diversitexta* (Steph.) Steph., *Sp. Hepat.* 5: 559 (1914) ≡ *Lejeunea diversitexta* (Steph.) Mizut., *J. Hattori Bot. Lab.* 35: 408 (1972). TYPE: Papua New Guinea, Moroka, district Moresby, 1300 m, 1893, *Loria* 103 (holotype: G!).

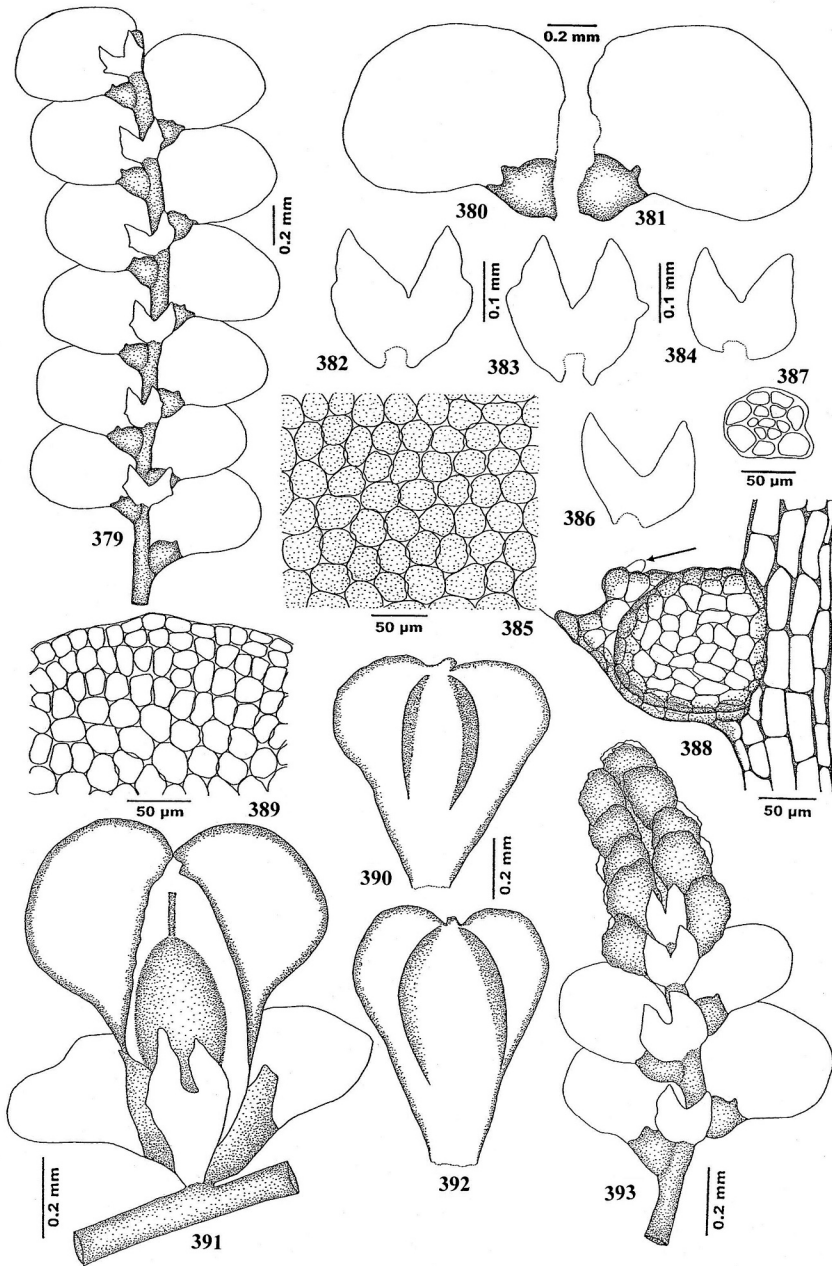
= *Cheilolejeunea pterota* Herz., *Mitt. Inst. Allg. Bot. Hamburg* 7: 210 (1931) = *Lejeunea pterota* (Herz.) Mizut., *J. Hattori Bot. Lab.* 29: 167 (1966) [*non Lejeunea pterota* (Tayl.) Tayl. in Gott., Lindenb & Nees, *Syn. Hepat.*: 367 (1845)] ≡ *Lejeunea herzogii* Mizut., *J. Hattori Bot. Lab.* 30: 180 (1967). TYPE: West Borneo, Sungai Obat, 1925, *Winkler* 3301/a (lectotype, designated by R. Grolle & R.-L. Zhu in sched: JE!, 3 small packets mounted on one sheet); West Borneo, Bukit Titing, 1925, *H. Winkler* 3309 (syntype: JE!).

= *Cardiolejeunea cardiantha* R.M. Schust. et Kachroo, *Hedwigia* 9: 150 (1963). TYPE: Java, *Massart* s.n. (holotype: FH, not seen), syn. *fide* Söderström *et al.* (2010).

= *Eulejeunea infestans* Steph., *Hedwigia* 35: 90 (1896) ≡ *Rectolejeunea infestans* (Steph.) Steph., *Sp. Hepat.* 5: 697 (1914) ≡ *Lejeunea infestans* (Steph.) Mizut., *J. Hattori Bot. Lab.* 27: 143 (1964). TYPE: Vietnam, Tonkin, *Balansa* 1889 (holotype: G!), **syn. nov.**

For further synonyms see Grolle (1981) and Wigginton & Grolle (1996).

**Plants** autoicous, rather minute, 0.7-1.3 mm wide, light green when fresh to dark green when dry, irregularly and densely branched, sometimes with loosely pinnate to bipinnately branched, branches erect-spreading, collar with three small lobes. **Stem** 0.06-0.09 mm in diameter, about 5 cells high in cross-section, epidermal cells 7, 20-30 µm wide, medullary cells 7-10, 10-17 µm wide. **Leaves** contiguous to imbricate, slightly recurved when dry, erect-spreading to spreading and plane when moist. **Leaf lobes** 0.4-0.7 mm long, 0.3-0.5 mm wide (when flattened); oblong-rectangular; leaf apex broadly rounded, flat; leaf margin entire; the ventral margin forming an angle of 130°-150° with the keel when flattened; insertion line about 10 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded to quadrate, 2-3 row of rectangular to quadrate cells on leaf margin; apical cells 14-17 µm long and 8-15 µm wide, median cells 25-38 µm long and 22-25 µm wide, basal cells 31-40 µm long and 25-31 µm wide; cell walls hyaline, with well-developed trigones and occasionally with conspicuous intermediate thickenings, 1-2 per cell, 0-1 between 2 adjacent trigones. Cuticle smooth to slightly rough, covering each cell with



Figs 379-393. *Lejeunea papilionacea* Steph. 379. Part of plant; 380, 381. Leaves; 382-384, 386. Underleaves; 385. Median cells of leaf lobe; 387. Cross-section of stem; 388. Leaf lobule (hyaline papilla shown by arrow); 389. Apical cells of leaf lobe; 390, 392. Perianths; 391. Perianth with bracts and bracteole; 393. Androecial shoot. 379, 385, 390-392 drawn from *A. Damanhuri* 08-3 (UKMB); 380, 381, 387-389, 393 from *A. Damanhuri* 09-6 (UKMB); 382-384 from *G.E. Lee* 1428a (UKMB); 386 from *G.E. Lee & H.Y. Tang* 1444 (UKMB).

minute papillae. Oil bodies not observed. **Leaf lobules** occasionally reduced, 0.12-0.15 mm long and 0.10-0.12 mm wide, up to 1/4 the length of the lobe, at an angle of 60°-70° (80°) to the stem, ovate, inflated along the keel; apex truncate, sometimes curved; keel curved to straight; free margin incurved partially; apical tooth relatively small, 22-25 µm long, oblong, obtuse, somewhat erect, usually upward-pointing, parallel with the stem; margin between tooth and sinus 3 cells long, with a rectangular disc cell below apical tooth, 25-30 µm long, 25-27.5 µm wide. **Underleaves** 0.15-0.30 mm long, 0.15-0.25 mm wide, 2-3 times wider than the stem, distant, orbicular (slightly longer than wide), covering 1/4-1/2 of the lobules; bilobed, lobes up to 1/2-2/3 of underleaf length, about 10-12 cells wide, triangular to lanceolate, oblique, sometimes divaricates; sinus broad, acute to obtuse, U-shaped to V-shaped; underleaf margin entire; base ± cuneate, insertion line curved; the two large basal underleaf cells differentiated; underleaves attached to the stem by 2 superior central cells. **Androecia** 0.4-0.5 (0.8-1.0) mm long, 0.25-0.40 mm wide with bracts, terminal on short or long lateral branches, sometimes on the main shoots. Male bracts in 3-5 (8-10) pairs, crenulate with wing, lobules almost same size as the lobes, apex obtuse, free margin flat, keels inflated. Male bracteoles 0-2, usually larger than the underleaf, margin entire. Antheridia not seen. **Gynoecea** on short or long lateral branches, female bracts loosely arranged, with one innovation, 1-3 gynoecea in a lateral row due to repeatedly fertile innovations. Female bracts smaller than the leaf, erect-spreading when moist, not enveloping the perianth. Lobes 0.30-0.35 mm long, 0.2-0.3 mm wide, oblong to obovate, apex broadly rounded, sometimes obliquely truncate, margin entire. Lobules 0.15-0.25 mm long, 0.05-0.10 mm wide, rarely reduced, 1/4-1/3 the width and 1/2-3/4 the length of the lobe, oblong, apex acute to truncate, keels straight, smooth, 0.10-0.15 mm long. Female bracteoles 0.20-0.25 mm long, 0.15-0.20 mm wide, 1/3 of the perianth length, obovate with tips acute to obtuse, lobes to 1/2 female bracteole length, distant, sinus narrow to broad, acute to obtuse, margin entire. Perianths 0.5-1.0 mm long, 0.35-0.90 mm wide, emergent to 1/3-1/2 of the perianth length, obovoid, with 5 keels, sometimes 4 keels with 1 indistinct dorsal keel; the lateral keels extended above as auricles, 0.15-0.25 mm wide; beak 2 cells long; cells of the perianth at the keels smooth, rarely mammillose; stalk-like elongation sometimes present, 0.3-0.4 mm long. **Sporophyte**: seta to 0.30 mm long; capsule *ca* 0.4 mm in diameter, valves 0.35 mm long, 0.15 mm wide at middle, scarcely spreading after dehiscence; elaters *ca* 0.2 mm long; spores oval-rectangular or irregular-shaped, *ca* 20 µm long and *ca* 10 µm wide. **Vegetative propagation** not seen.

**Further specimens examined.** MALAYSIA. **Pulau Langkawi**: trail to Gunung Jaya, 665 m, 2010, *G.E. Lee 2164, 2165* (UKMB). **Kedah**: Kulim, Sungai Sedim, trail of Sungai Teruna, 50 m, 2009, *G.E. Lee 1410* (UKMB). **Kelantan**: Gua Musang, Gunung Chamah, trail from Kem Abdullah Sani to Kem Barat, 1150 m, 2011, *A. Damanhuri 11-84* (UKMB). **Pahang**: Fraser's Hill, road to Clock Tower and Post Office, 1120 m, 2009, *G.E. Lee 1099a, 1423, 1428a* (UKMB); Genting Highlands, Goh Tong Jaya, near waterfall, 845 m, 2011, *G.E. Lee 2174, 2184* (UKMB); Kenong, trail to Gunung Batu Putih, 160 m, 2009, *A. Damanhuri 09-6, 09-7, 09-8* (UKMB). **Selangor**: Ulu Langat, Sungai Gabai, staircase to the summit, 100 m, 2010, *Daniel 11-9, 11-12* (UKMB). **Sarawak**: Bintulu, Bukit Setiam, 410 m, 2010, *G.E. Lee & H.Y. Tang 1444, 1455, 1458, G.E. Lee 2163, 2166* (UKMB); Lanjak Entimau, Sungai Joh 1, 155 m, 2008, *A. Damanhuri 08-3, 08-4* (UKMB); Lanjak Entimau Wildlife Sanctuary, Nanga Bloh, 100 m, 2008, *M. Suleiman 3256* (BORH). **Sabah**: Mt. Silam, SW of Lahad Datu, 220-250 m, 1963, *Z. Iwatsuki 5609, 5635, 5625, 5626a* as *L. pterota* (NICH); Sosopodon near Kundasang, 1350 m, 1963, *M. Mizutani 242, 250* as *L. infestans* (NICH), 1350-1500 m, 1969, *Shobei Kokawa & Mitsuru Hotta 5207* as *L. diversitexta* (NICH), between Mamut ridge and Ulu Berambang, 1600-1800 m, 1969, *Shobei Kokawa & Mitsuru Hotta 5893* as *L. diversitexta* (NICH), near Mamut Mine, 1300 m, 1970, *T. Kodama 40782* as *L. herzogii* (NICH), Poring

to Langanan Waterfall, 600-1000 m, 1974, *T. Kodama 48349* as *L. diversitexta* (NICH); Kinabalu Park, between Bundu Tuhan View trail and Liwagu trail, 1530 m, 2010, *G.E. Lee 1846* (UKMB), trail from Timpohon gate to Kandis shelter, montane forest, 1900 m, 2010, *G.E. Lee 1777* (UKMB). **CAMEROON**. 1975, *R. Letouzey s.n.* (NICH). **INDIA**. Sikkim: Dalapchand, ca 1650 m, 2006, *D. Singh 39604* (CAL). **SINGAPORE**. Upper Peirce Canal, 2007, *R.L. Zhu 20070124-11A* (SING); Bukit Timah, Waterfall, 2007, *R.L. Zhu 20070203-13* (SING); Bukit Timah, Fern Valley, 2007, *R.L. Zhu 20070203-14* (SING); Nee Soon Swamp, 2007, *R.L. Zhu 20070124-6C* (SING). **INDONESIA**. Kalimantan: Balikpapan, Kutei peak, *W. Meijer B1554e* (BO); Nunukan north of Tarakan, 1953, *W. Meijer B5014* (BO); Sulawesi: Lore Lindu National Park, Toro, 900-1100 m, 2005, *N.S. Ariyanti B2/Sp2/S4/2* (BIOT).

**Distribution and habitat in Malaysia:** Pulau Langkawi\*, Kedah\*, Kelantan\*, Pahang\*, Selangor\*, Sarawak, Sabah; epiphytic at wide elevational range, from sea level to 1900 m.

**General distribution:** Africa, tropical Asia.

**Discussion:** The prominently auriculate perianths instantly set *L. papilionacea* apart from other species in the genus. Other distinguishing characters include 1) the oblong-rectangular leaf lobes, 2) 2-3 rows of quadrate to rectangular cells on leaf margins, 3) androecia terminal on main shoots or branches, and 4) male bracts often winged. *Lejeunea papilionacea* is somewhat similar to *L. anisophylla* (Mizutani, 1972) but is readily distinguished from the latter by the oblong-rectangular leaf lobes, leaf cells with well-developed trigones and intermediate thickenings and the auriculate perianth.

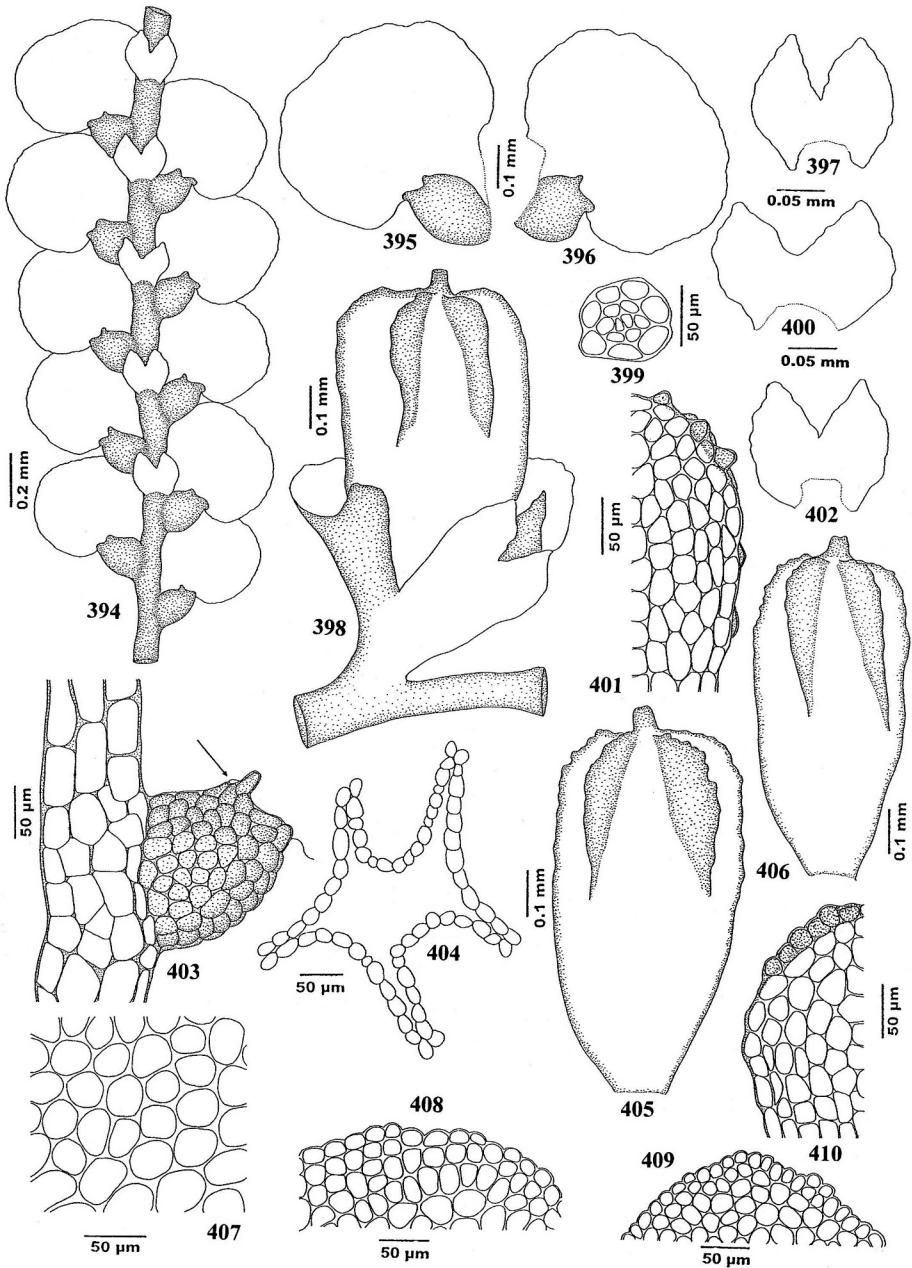
*Lejeunea papilionacea* varies in the size of the perianth auricles. Only well-developed perianths display this special feature and at times, perianths without or with slight auricles are found on the same plant (see also Mizutani, 1972). Specimens from Borneo are epiphylls and usually have larger auricles than the Peninsular Malaysian or Singaporean specimens which were mostly collected on branches and shrubs. Variation is also observed in the position of the perianths and the underleaf margins. Large perianths (0.6-0.7 mm long) are emergent to 1/3-1/2 whereas small perianths (0.3-0.4 mm long) are usually more or less submerged between the bracts. Large, 0.20-0.25 mm long underleaves differ from smaller ones in having a blunt angle on the outer margins.

According to Mizutani (1964) and Zhu & So (2001), *L. infestans* is very similar to *L. anisophylla*. However, the former species differs clearly from *L. anisophylla* by having leaf cells with well-developed trigones and occasional intermediate thickenings, and an obovoid perianth with small auricles. By these characters *L. infestans* is similar to *L. papilionacea*. Although *L. infestans* has ribbon-like regenerants at leaf margins and the perianth auricles are rather small, these characters are insufficient to separate *L. infestans* from *L. papilionacea* at the species level and the former species is therefore treated here as a synonym of *L. papilionacea*.

### 23. *Lejeunea patersonii* (Steph.) Steph., *Sp. Hepat.* 5: 784 (1915) **Figs 394-410**

Basionym: *Eulejeunea patersonii* Steph., *Hedwigia* 35: 92 (1896). TYPE: Java, *Paterson s.n.* (holotype: G, not seen).

**Plants** dioicous, relatively small, 0.8-1.0 mm wide, green to dark green when fresh to brown when dry, irregularly and slightly branched, branches erect-spreading, collar with three small lobes. **Stems** 0.07-0.10 mm in diameter, about 5-6 cells high in cross-section, epidermal cells 7, 25-38  $\mu$ m wide, medullary cells (8)10-12, 13-20  $\mu$ m wide. **Leaves** contiguous to imbricate, slightly recurved when dry, erect-spreading and plane when moist. **Leaf lobes** 0.4-0.6 mm long, 0.4-0.5 mm wide (when flattened), orbicular; leaf apex broadly rounded, flat,



Figs 394-410. *Lejeunea patersonii* (Steph.) Steph. 394. Part of plant in ventral view; 395, 396. Leaves; 397, 400, 402. Underleaves; 398. Perianth with bracts and bracteole; 399. Cross-section of stem; 401, 410. Cells of wings at lateral keel of perianth; 403. Stem portion and leaf lobule (hyaline papilla shown by arrow); 404. Cross-section of perianth; 405, 406. Perianths; 407. Median cells of leaf lobe; 408. Marginal cells of leaf lobe; 409. Apical cells of leaf lobe. All figures drawn from A. Damanhuri 11-465 (UKMB).

rarely recurved; leaf margin strongly crenulate due to projecting cells; the ventral margin forming an angle of  $70^{\circ}$ - $90^{\circ}$  with the keel when flattened; insertion line about 12 lobe cells long. **Leaf cells** somewhat differentiated from base to middle and gradually become smaller from the middle to the apex of the leaf, basal cells more or less elongated, usually rounded at the middle, irregular quadrate to rectangular towards the leaf margin; apical cells 20-25  $\mu\text{m}$  long and 13-20  $\mu\text{m}$  wide, median cells 25-45  $\mu\text{m}$  long and 25-33  $\mu\text{m}$  wide, basal cells 38-50  $\mu\text{m}$  long and 25-33  $\mu\text{m}$  wide; cell walls hyaline, with well-developed trigones and without intermediate thickenings. Cuticle smooth. Oil bodies not seen. **Leaf lobules** sometimes reduced, 0.15-0.20 mm long and 0.12-0.15 mm wide, to  $1/3$  the length of the lobe, at an angle of about  $70^{\circ}$  to the stem, ovate, inflated along the keel; apex obliquely truncate; keel curved; free margin flat; apical tooth 30-38  $\mu\text{m}$  long, oblong, erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 25-30  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide. **Underleaves** ca 0.1 mm long and wide, to 2 times wider than the stem, distant, suborbicular, sometimes reniform (wider than long), not covering the lobules; bilobed, lobes to  $1/2$ - $2/3$  of underleaf length, about 5 cells wide, somewhat triangular, oblique, distant; sinus broad, acute to slightly obtuse, widely V-shaped; underleaf margin crenulate; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.4-1.0 mm long, 0.4-0.5 mm wide with bracts, on short or long lateral branches. Male bracts in 3-7 (9) pairs, crenulate without wing, apex obtuse, keels strongly inflated. Male bracteoles 1-2, smaller than underleaf, margin crenulate. Antheridia not seen. **Gynoecia** on short or long branches, female bracts somewhat crowded, with one innovation, usually with one gynoecium in a lateral position. Female bracts smaller than the leaf, erect-spreading when moist, slightly enveloping the perianth. Lobes 0.5-0.6 mm long, 0.25-0.3 mm wide, ovate, apex obtuse to acute, margin crenulate. Lobules 0.35-0.4 mm long, ca 0.1 mm wide, rarely reduced,  $1/3$ - $1/2$  the width and  $4/5$  the length of the lobe, ovate, apex acute to obtuse, keels straight, smooth, ca 0.2 mm long. Female bracteoles 0.4-0.5 mm long, 0.2-0.3 mm wide,  $1/2$  of the perianth length, ovate with tips acute, lobes to  $1/3$  of female bracteole length, distant, sinus narrow, acute, margin crenulate. Perianths 0.75-1.0 mm long, 0.4-0.45 mm wide, emergent to  $1/2$  of the perianth length, oblong, with 5 keels, the keels slightly 2-winged, wings 1-2 cells wide, beak 2-3 cells long; cells of the perianth at the keels sometimes mammillose; stalk-like elongation sometimes present, ca 0.5 mm long. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined.** MALAYSIA. **Kelantan:** Gunung Chamah, Dakota trail, 775 m, 2011, *A. Damanhuri* 11-465 (UKMB). **Pahang:** Genting Highlands, Goh Tong Raya, near waterfall, 845 m, 2011, *G. E. Lee* 2170, 2171 (UKMB). **Kuala Lumpur:** along waterfall, Templer Park, 150-300 m, 1965, *Hiroshi Inoue* 11192, 11193 (TNS). **Johor:** G. Sumalayang, 330 m, 1971, *S. C. Chin* 691, 704, 706, 732 (SING).

**Distribution and habitat in Malaysia:** Kelantan\*, Pahang\*, Kuala Lumpur, Johor; terrestrial on humus or soil covering rock at elevations below 1000 m.

**General distribution:** Malesia.

**Discussion:** *Lejeunea patersonii* is mainly characterized by 1) dark green color when fresh, 2) orbicular leaves with strongly crenulate margins, 3) lobules with flat free margin, 4) small, distant underleaves (margins crenulate), and 5) the oblong and often winged perianths. *Lejeunea patersonii* is morphologically very similar to *L. tuberculosa* (SL 0.73) and was resolved as sister to *L. tuberculosa* in phenetic and phylogenetic analysis. However, *L. patersonii* differs from *L. tuberculosa* by having leaf margins strongly crenulate, a smooth cuticle, and a flat free margin of

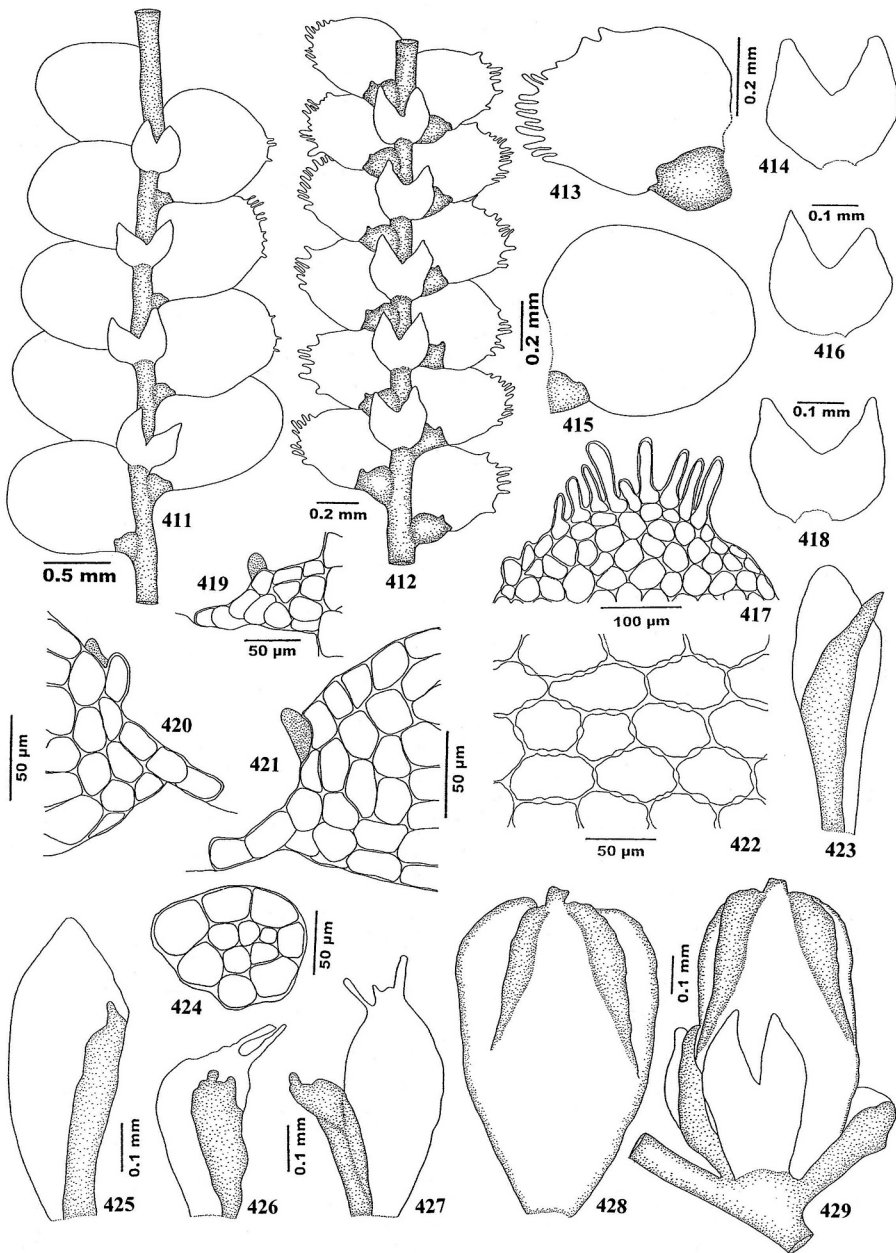
leaf lobule. Superficially, *L. patersonii* can be confused with *L. tamaspocsii* in the oblong perianth with 2-winged keels and a short, 2-3 cells long beak. The latter species clearly differs however, by having asymmetrical leaf lobes with a narrowly rounded apex (lobes symmetrical and with broadly rounded apex in *L. patersonii*). The relationships between the two species are distant (Lee *et al.*, submitted).

*Lejeunea patersonii* varies in the wings of the perianth keels, which are sometimes not developed; a similar variation is seen in *L. papilionacea*. I did not have the opportunity to examine the type of *L. patersonii*. According to Stephani's illustration of the holotype (Icones Ined. nr. 2705) the perianth is short cylindrical and weakly 5-keeled in the upper half, with low and smooth keels. The winged keels are not visible in the illustration nor mentioned in the description.

**24. *Lejeunea patriciae* Schäf.-Verw., *Candollea* 56: 64-67 (2001) Figs 411-429**

≡ *Lejeunea pilifera* Tixier, *Gard. Bull. Singapore* 25: 344, 351 (1971), *nom. illeg.* (non *Lejeunea pilifera* Spruce). TYPE: Peninsular Malaysia, Fraser's Hill, 1969, Tixier 4811 (holotype: PC!).

**Plants** dioicous, rather minute, fragile, 0.7-1.0 mm wide, usually light green to yellowish green when fresh to dark brown when dry, irregularly and densely branched, branches erect-spreading to spreading, collar with three small lobes. **Stem** 0.07-0.08 mm in diameter, about 5 cells high in cross-section, epidermal cells 7, 29-45  $\mu$ m wide, medullary cells 5-8, 12-25  $\mu$ m wide. **Leaves** contiguous to distant, somewhat crisped and plane to slightly recurved when dry,  $\pm$  erect-spreading and plane when moist. **Leaf lobes** 0.4-0.5 mm long, 0.3-0.4 mm wide (when flattened), ovate to orbicular; leaf apex narrowly to broadly rounded; leaf margin entire to weakly crenulate; marginal rhizoids present at the apex with 5-10 projecting cells; the ventral margin forming an angle of 140°-160° with the keel when flattened; insertion line 10-11 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregularly quadrate to rectangular towards the leaf margin; apical cell 18-36  $\mu$ m long and 10-32  $\mu$ m wide, median cell 33-50  $\mu$ m long and 25-38  $\mu$ m wide, basal cell 43-65  $\mu$ m long and 30-38  $\mu$ m wide; cell walls hyaline, with well-developed trigones and conspicuous intermediate thickenings, 2-6 per cell, 0-1 (2) between 2 adjacent trigones. Cuticle smooth. Oil bodies somewhat glistening to faintly opaque-granular, fine *Jungermannia*-type, with minute granules, somewhat rough externally; marginal cells with 7-11 oil bodies per cell, 4-7  $\mu$ m long and 3-4  $\mu$ m wide, mostly globose and ovoid; median cells with 12-16 oil bodies per cell, 5-10  $\mu$ m long and 3-5  $\mu$ m ovoid and ellipsoid; basal cells with 13-18 oil bodies per cell, 5-10  $\mu$ m long and 3-5  $\mu$ m wide, mostly ellipsoid. **Leaf lobules** usually reduced, 0.13-0.15 mm long, 0.08-0.10 mm wide, to 1/5-1/3 the length of the lobe, at an angle of 70°-90° to the stem, ovate, inflated along the keel; apex obliquely truncate; keel curved; free margin flat; apical tooth 15-20  $\mu$ m long, oblong, somewhat erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 25-28  $\mu$ m long and 10-12  $\mu$ m wide. **Underleaves** 0.20-0.25 mm long, 0.2-0.3 mm wide, to 3 times wider than the stem, distant, orbicular (slightly wider than long), covering 1/2-1/4 of the lobules; bilobed, lobes to 1/2-3/5 underleaf length, about 4-6 cells wide, triangular; sinus broad, V-shaped to U-shaped; underleaf margin slightly crenulate; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 2 superior central cells. **Androecia** 0.4-0.5 mm long, 0.3-0.4 mm wide with bracts, on short or long lateral branches. Male bracts in 3-5 pairs, crenulate with wing, apex obtuse, keels inflated. Male bracteoles 1,



Figs 411-429. *Lejeunea patriciae* Schäf.-Verw. **411, 412.** Part of plant in ventral view; **413, 415.** Leaves; **414, 416, 418.** Underleaves; **417.** Apical cells of leaf lobe with marginal rhizoids; **419.** Stem portion and reduced leaf lobule (hyaline papilla shown in gray); **420, 421.** Upper part of leaf lobule (hyaline papilla shown in gray); **422.** Basal cells of leaf lobe; **423, 425-427.** Female bracts; **424.** Cross-section of stem; **428.** Perianth; **429.** Perianth with bracts and bracteole. 411, 415, 428 drawn from *G.E. Lee 2204* (UKMB); 412-414, 416-422, 424 from *G.E. Lee 1099* (UKMB); 423, 425 from the holotype, *Tixier 4811* (PC); 426, 427, 429 from *G.E. Lee 2180* (UKMB).



smaller than underleaf, margin entire. Antheridia not seen. **Gynoecea** on short or long branches, female bracts loosely arranged, sometimes somewhat crowded, with one innovation, usually with one gynoeceium in a lateral position. Female bracts smaller than the leaves, erect spreading when moist, somewhat enveloping the perianth. Lobes 0.35-0.45 mm long, 0.20-0.25 mm wide, elliptic to obovate, apex acute to obtuse, sometimes marginal rhizoids present at the apex, margin entire. Lobules 0.25-0.30 mm long, 0.08-0.10 mm wide, rarely reduced, 1/3-2/3 the width and 2/3-5/6 the length of the lobe, sometimes almost as long as the lobe, oblong to obovate, apex obtuse, sometimes with marginal rhizoids at the apex, keels straight, smooth, 0.2-0.3 mm long. Female bracteoles 0.3-0.4 mm long, 0.15-0.30 mm wide, 1/3 of the perianth length, ovate with the tips acute, lobes to 1/2-2/3 of female bracteole length, distant, sinus narrow, acute, margin crenulate. Perianths (0.55) 0.70-0.75 mm long, 0.3-0.4 mm wide, emergent to 1/2 the perianth length, obovoid to oblong, with 5 keels; beak 2 cells long; cells of the perianth at the keels smooth to mammillose; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** by means of young plantlets at leaf margins or leafy propagules.

**Further specimens examined.** MALAYSIA. **Kelantan:** Gua Musang, foot of Gunung Chamah, Dakota trail, 770 m, 2011, A. *Damanhuri* 11-395 (UKMB). **Pulau Pinang:** Penang Hill, 'broken staircase' trail, 750 m, 2008, G.E. *Lee* 1095 (UKMB); Highland trail, 1300 m, 2008, G.E. *Lee* 1205 (UKMB). **Perak:** Maxwell Hill, 1000-1100 m, 2004, A. *L. Ilkiu-Borges et al.* 2990, 3005 (GOET). **Pahang:** Fraser's Hill, road to Clock Tower and Post Office, 1120 m, 2008-2009, G.E. *Lee* 1099, 1099a, 1423, 1426 (UKMB); Genting Highlands, Goh Tong Jaya, near waterfall, 845 m, 2011, G.E. *Lee* 2167, 2168, 2169, 2172, 2173, 2175, 2177, 2179, 2180, 2182, 2183, 2186, 2187, 2188, 2189, 2196, 2197, 2199, 2202, 2204, 2205, 2207, 2209, 2210, 2211, 2212, 2214 (UKMB); along stream near pumping plant, ca 1200 m, 1996, N. *Ohnishi* 2804, 2840 (HIRO); Cameron Highlands, tea plantation area, 1500 m, 2009, G.E. *Lee* 2332 (UKMB).

**Distribution and habitat in Malaysia:** Kelantan\*, Pulau Pinang\*, Perak, Pahang; epiphytic in open areas at 700-1300 m.

**General distribution:** Peninsular Malaysia, Indonesia: Sumatra (Schäfer-Verwimp, 2006).

**Discussion:** This species, previously regarded as a Peninsular Malaysian endemic, is now known to occur in Indonesia as well (Schäfer-Verwimp, 2006). The distinguishing characters of *L. patriciae* are the development of marginal rhizoids at the leaf apex with 5-10 projecting cells and the presence of two intermediate thickenings in the basal leaf cells between adjacent trigones. Furthermore, the species is characterized by 1) rather minute and fragile plant, often with fragmented shoots, 2) leaf cells with well-developed trigones and intermediate thickenings, and 3) orbicular, distant underleaves with rounded to acute tips (the tips sometimes ending in 2 cells). Without the presence of the marginal rhizoids, *L. patriciae* is very similar to the widespread *L. papilionacea* and *L. anisophylla* but differs from these two species by the presence of two intermediate thickenings between adjacent trigones in basal laminal cells and the crenulate underleaf margins.

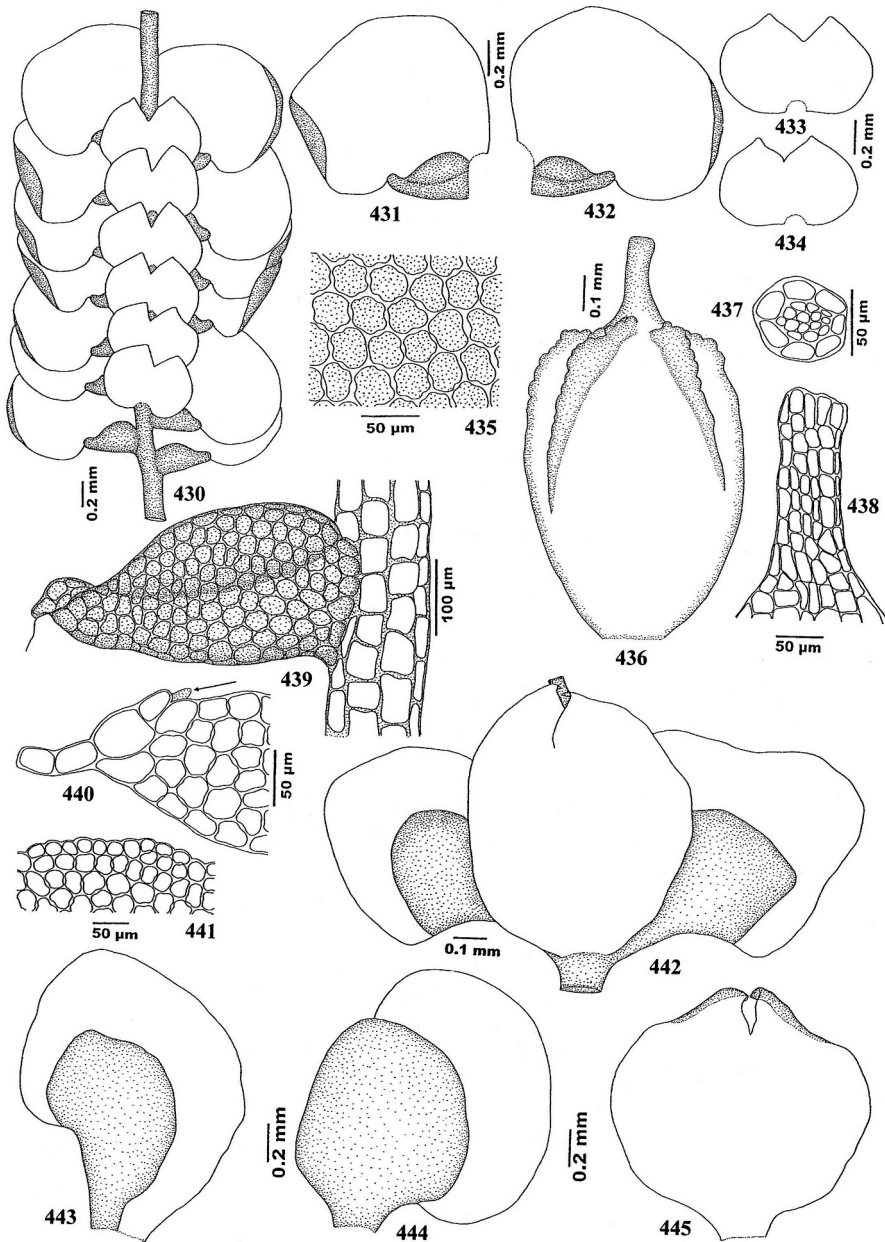
*Lejeunea patriciae* varies considerably in plant size, leaf structure, lobules, length of underleaf lobes and in the number and length of the marginal rhizoids. The plants are usually small; rather large plants occur at 800-1000 m elevation on Maxwell Hill, Perak and Genting Highlands, Pahang. These larger plants usually have imbricate and orbiculate leaves, the apices of the leaves are somewhat recurved when dry and also produce fewer and shorter marginal rhizoids; sometimes they are without marginal rhizoids. Small plants, in contrast, have ovate, contiguous to distantly arranged leaves and the apices of the leaves

are always plane and with abundant and longer marginal rhizoids. In the type material the leaf lobule is strongly reduced. However, well-developed lobules are also seen on single plants in some of the collections. The apical tooth of the lobules is usually prominent; however, at times the apical tooth is very low or obsolete. The length of the underleaf varies even within the same shoot of plant. Large underleaves (0.2 mm long) are bifid to 3/5 and have tips 2 cells long while smaller underleaves (0.15 mm long) are less deeply bifid (to 2/5) and the tips consist of only 1 cell.

**25. *Lejeunea pectinella* Mizut., *J. Hattori Bot. Lab.* 33: 239 (1970) Figs 430-445**

TYPE: Malaysia, Sabah, between Tenompok Pass and Kamaranga Radio Station, south slope of Mt. Kinabalu, 1400-1900 m, 1963, *Mizutani 2103a* (holotype: NICH!).

**Plants** dioicous, comparatively large, 1.5-2.0 mm wide, dark green when fresh to dark brown when dry, irregular and densely branched, branches spreading, collar with three small lobes. **Stem** *ca* 0.1 mm in diameter, about 6 cells high in cross-section, epidermal cells 7, 38-72  $\mu$ m wide, medullary cells 10-15, 12-25  $\mu$ m wide. **Leaves** closely imbricate, recurved when dry, spreading and recurved when moist. **Leaf lobes** 0.8-1.0 mm long, 0.6-0.9 mm wide (when flattened), ovate-orbicular; leaf apex broadly rounded, recurved; leaf margin slightly crenulate; the ventral margin forming an angle of 90°-100° with the keel when flattened; insertion line about 11 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregular quadrate, rectangular towards the leaf margin; apical cell 20-30  $\mu$ m long and 20-30  $\mu$ m wide, median cell 38-50  $\mu$ m long and 30-38  $\mu$ m wide, basal cell 50-63  $\mu$ m long and 25-38  $\mu$ m wide; cell walls yellowish, with well-developed trigones and conspicuous intermediate thickenings, 1-4 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies not seen. **Leaf lobules** rarely reduced, 0.3-0.4 mm long and *ca* 0.2 mm wide, to 1/3-1/2 the length of the lobe, at an angle of about 90° to the stem, ovate-oblong, inflated along the keel; apex obliquely truncate; keel straight, sometimes curved; free margin incurved fully; apical tooth 40-50  $\mu$ m long, oblong, erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell present, cell below the apical tooth 75  $\mu$ m long and 20  $\mu$ m wide. **Underleaves** 0.35-0.40 mm long, 0.6-0.8 mm wide, to 5-6 times as wide as the stem, imbricate, reniform (wider than long), covering 3/5-4/5 of the lobules; bilobed, lobes to 1/3 of underleaf length, about 10 cells wide, triangular, distant; sinus narrow, acute, V-shaped; underleaf margin crenulate; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells lacking; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.4-0.55 mm long, 0.4-0.5 mm wide with bracts, on main shoots. Male bracts in 2-4 pairs, entire without wing, apex truncate, keels inflated. Male bracteoles 0-1, smaller than the underleaf, margin entire. Anteridia not seen. **Gynoecia** on short or long branches, occasionally terminal on main shoots, female bracts somewhat crowded, with one innovation, 1-2 gynoecia in a lateral row due to repeatedly fertile innovations. Female bracts usually larger than the leaves, subislobous, erect-spreading when moist, enveloping the perianth. Lobes 1.0-1.4 mm long, 0.8-1.0 mm wide, obovate, apex broadly rounded, margin crenulate. Lobules 0.8-1.0 mm long, 0.5-0.6 mm wide, rarely reduced, 1/2 the width and 3/4 the length of the lobe, widely obovate, apex broadly rounded, keels straight, smooth, 0.5-0.6 mm long. Female bracteoles 1.0-1.5 mm long, 1.0-1.3 mm wide, almost as long as perianth length, orbicular to widely ovate with the tips acute, lobes to 1/5



Figs 430-445. *Lejeunea pectinella* Mizut. **430**. Part of plant in ventral view; **431**, **432**. Leaves; **433**, **434**. Underleaves; **435**. Median cells of leaf lobe; **436**. Perianth; **437**. Cross-section of stem; **438**. Beak of perianth; **439**. Stem portion and leaf lobule; **440**. Upper part of leaf lobule when flattened (hyaline papilla shown by arrow); **441**. Apical cells of leaf lobe; **442**. Perianth with bracts and bracteole; **443**, **444**. Female bracts; **445**. Female bracteole. All figures drawn from the holotype, *M. Mizutani 2103a* (NICH).

of the female bracteole length, connivent, sinus narrow, acute, margin crenulate. Perianth 1.0-1.3 mm long, 0.5-0.6 mm wide, submerged between the bracts, oblong, with 5 keels, sometimes 4 keels with 1 indistinct dorsal keel, the keels often with 2-3 small teeth above; beak 8-10 cells long; cells of the perianth at the keels mammillose; stalk-like elongation sometimes present, 0.2-0.3 mm long.

**Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined.** MALAYSIA. Sabah: Mt. Kinabalu, between Tenompok Pass and Kamaranga Radio Station, 1400-1900 m, 1963, *M. Mizutani* 3252 (NICH); Kinabalu National Park, between Power station and Kamarangoh Telecoms station, 1800-2200 m, 1974, *T. Kodama* 48731 (NICH); trail from Lowii Shelter to Mempening Shelter, montane forest, 2300-2500 m, 2010, *G.E. Lee* 1672 (UMKB); trail from Kandis shelter to Ubah shelter, montane forest, 2000 m, 2010, *G.E. Lee* 2009 (UKMB); trail from Mempening shelter to Layang-layang Staff Quarters, montane forest, 2500-2800 m, 2010, *G.E. Lee* 1902, 1904 (UKMB).

**Distribution and habitat in Malaysia:** Sabah (Mt. Kinabalu); epiphytic at 1400-2800 m.

**General distribution:** only known from Mt. Kinabalu.

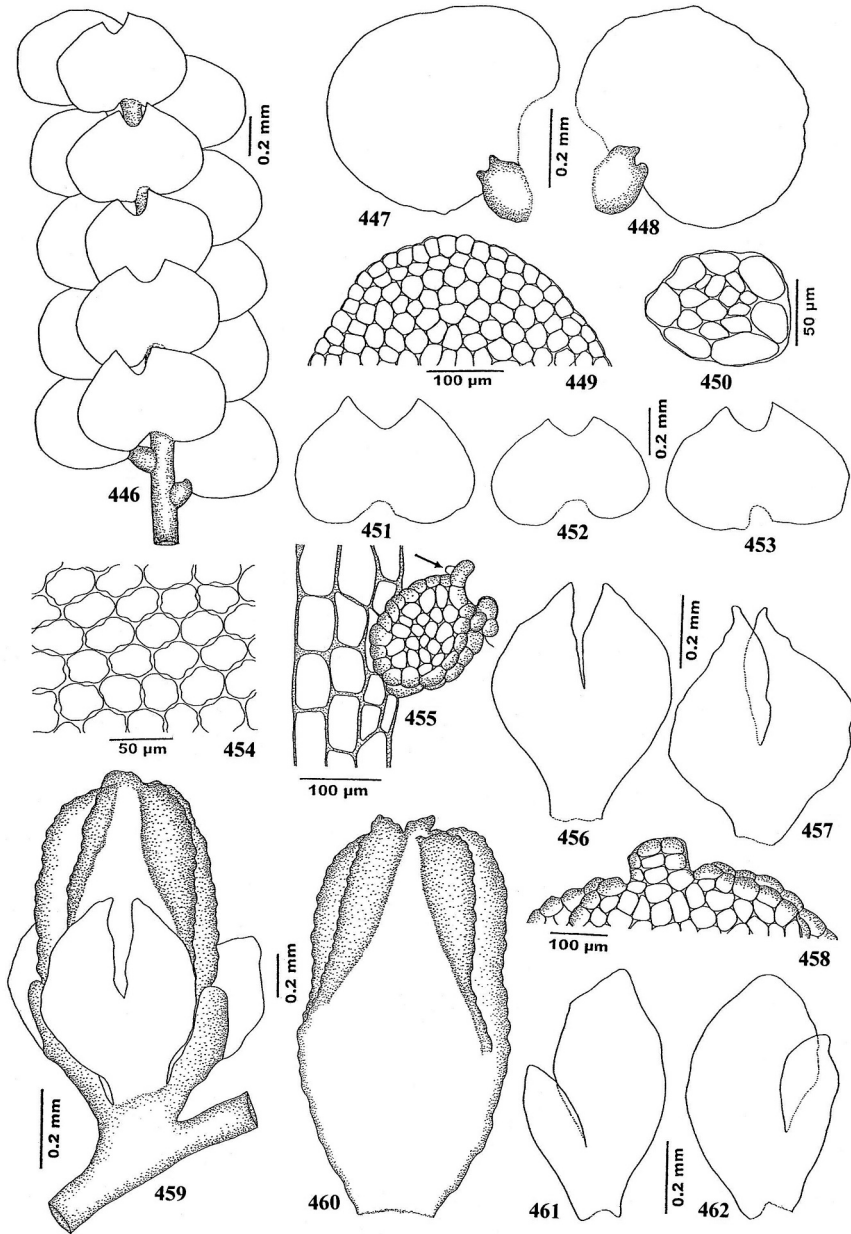
**Discussion:** The characters of *L. pectinella* include 1) ovate-orbicular leaves with broadly rounded apex, 2) large, rarely reduced leaf lobules with fully incurved free margin, 3) leaf cells with distinct trigones and intermediate thickenings, 4) large, reniform underleaves, 5) large subisobolous female bracts, and 6) oblong perianths with toothed keels and a 8-10 cells long beak. The species resembles *L. fleischeri* most closely; differences between the two are discussed under the latter species. A similar lobule occurs in *Lejeunea discreta*, *L. fleischeri*, *L. stephaniana* and *L. utriculata*, but perianth keels in these species are smooth, never toothed and the underleaves of *L. pectinella* are always reniform.

## 26. *Lejeunea sordida* (Nees) Nees, *Nat. Eur. Leberm.* 3: 278 (1838) **Figs 446-462**

Basionym: *Jungermannia sordida* Nees, *Enum. Pl. Crypt. Jav.*: 41 (1830) ≡ *Hygrolejeunea sordida* (Nees) Schiffn., in Engler & Prantl, *Nat. Pflanzenfam.* 1, 3: 125 (1893) ≡ *Taxilejeunea sordida* (Nees) Eifrig, *Ann. Bryol.* 9: 101 (1937). TYPE: Indonesia, Java "in tumulis Baduorum sanctis", *Blume s.n.* (holotype: STR!).

For further synonyms see Eifrig (1937), Mizutani (1970) and Grolle (1981).

**Plants** dioicous, relatively large, 1.0-1.3 mm wide, glossy light green to pale green when fresh, dark brown when dry, irregularly and loosely pinnate, branches erect spreading, collar with three small lobes. **Stems** 0.10-0.13 mm in diameter, about 6 cells high in cross-section, epidermal cells 7, 23-46 µm wide, medullary cells 11-12, 13-20 µm wide. **Leaves** imbricate to somewhat contiguous, rarely recurved when dry, erect-spreading to spreading and plane when moist. **Leaf lobes** 0.6-0.7 mm long, 0.5-0.6 mm wide (when flattened), orbicular; leaf apex broadly rounded, always flat; leaf margin entire, sometimes slightly crenulate with projecting cells; the ventral margin forming an angle of 60°-90° with the keel when flattened; insertion line about 13 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually quadrate to pentagonal, sometimes somewhat rounded, irregularly quadrate to rectangular towards the leaf margin; apical cells 20-27 µm long and 13-27 µm wide, median cells 33-40 µm long and 26-33 µm wide, basal cells 53-80 µm long and 26-53 µm wide; cell walls hyaline, with well-developed trigones and occasionally with conspicuous intermediate thickenings, 1-2 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies glistening-botryoidal, *Calypogeia*-type, made up of large granules, faintly rough externally; marginal cells with 3-5 oil bodies per cell, 3-5 µm long and 2-3 µm wide, globose



Figs 446-462. *Lejeunea sordida* (Nees) Nees. 446. Part of plant in ventral view; 447, 448. Leaves; 449. Apical cells of leaf lobe; 450. Cross-section of stem; 451-453. Underleaves; 454. Median cells of leaf lobe; 455. Stem portion and leaf lobule (hyaline papilla shown by arrow); 456, 457. Female bracteoles; 458. Upper portion of perianth; 459. Perianth with bracts and bracteole; 460. Perianth; 461, 462. Female bracts. 446, 449-453, 455 drawn from *Z. Iwatzuki* 5722 (NICH); 447, 448 from *G.E. Lee* 1154 (UKMB); 454, 456-462 from *G.E. Lee* 1159 (UKMB).

and ovoid; median cells with 5-14 oil bodies per cell, 5-13  $\mu\text{m}$  long and 3-5  $\mu\text{m}$  wide, globose to somewhat ellipsoid; basal cells 6-14 oil bodies per cell, 8-15  $\mu\text{m}$  long and 3-5  $\mu\text{m}$  wide, mostly ellipsoid. **Leaf lobules** rarely reduced, 0.1-0.2 mm long, 0.13-0.16 mm wide, to 1/3 the length of the lobe, at an angle of 50°-60° to the stem, ovate, inflated along the keel; apex obliquely truncate, U-shaped; keel curved; free margin incurved partially; apical tooth 20-25  $\mu\text{m}$  long, oblong, somewhat curved, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 33  $\mu\text{m}$  long and 20  $\mu\text{m}$  wide. **Underleaves** 0.4-0.5 mm long, 0.6-0.7 mm wide, to 7 times wider than the stem, contiguous to subimbricate, reniform (wider than long), always covering the lobules; bilobed, lobes to 1/3 of underleaf length, about 10 cells wide, very shallowly triangular; sinus broad, rounded to obtuse, U-shaped to V-shaped; underleaf margin entire; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells lacking; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.5-0.7 mm long, 0.3-0.4 mm wide with bracts, terminal on short or long branches, occasionally along the main shoots. Male bracts in 3-5 pairs, entire without wing, apex obtuse, keels inflated. Male bracteole 1, smaller than the underleaf, margin entire. Antheridia 2 per bract, 100-120  $\mu\text{m}$  in diameter, hyaline, with a long and hyaline stalk, 70-160  $\mu\text{m}$  in length. **Gynoecia** on short branches, female bracts loosely arranged to somewhat crowded, with one innovation, 1-2 gynoecia in a lateral row due to repeatedly fertile innovations. Female bracts slightly smaller than the leaf, erect spreading when moist, not enveloping the perianth. Lobes 0.6-0.7 mm long, 0.3-0.4 mm wide, elliptic, apex obtuse, margin entire. Lobules 0.4-0.5 mm long, 0.1-0.2 mm wide, rarely reduced, 1/3 the width and 2/3 the length of the lobe, oblong, apex obtuse, keel straight, slightly sinuate, 0.2-0.4 mm long. Female bracteoles 0.6-0.7 mm long, 0.4-0.5 mm wide, 1/2 of the perianth length, ovate with the tips acute, lobes to 1/2 of female bracteole length, distant to overlapping, sinus acute, margin entire. Perianths 1.0 mm long, 0.5 mm wide, emergent to 1/3-1/2 of the perianth length, obovoid to ellipsoid, with 5 keels; beak 2-3 cells long; cells of the perianth at the keels mammillose; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** by means of plantlet regeneration at leaf margins or by leafy propagules.

**Further specimens examined.** **MALAYSIA.** **Perlis:** Bukit Ayer recreational forest, 150 m, 2011, *Daniel 11-28* (UKMB). **Pulau Langkawi:** Lubuk Semilang, 60 m, 2010, *G.E. Lee 1460* (UKMB); Gunung Jaya, 690 m, 2010, *G.E. Lee 1461, 1462* (UKMB). **Kedah:** Kulim, Sungai Sedim recreational park, 50 m, 2009, *G.E. Lee 1413, 1416, 1384, 1386* (UKMB); Hutan Lipur Ulu Paip, 80 m, 2010, *A. Damanhuri s.n.* (UKMB); trail of Sungai Teruna, 50 m, 2009, *G.E. Lee 1388* (UKMB). **Pulau Pinang:** Bukit Panchor, river trail, 2008, *G.E. Lee 1054a* (UKMB); Penang Hill, 'broken staircase' trail, 750 m, 2008, *G.E. Lee 1088, 1095, 1182* (UKMB), trail to cave, 30 m, 2008, *A. Damanhuri 08-7* (UKMB). **Kelantan:** Gunung Chamah, Dakota trail, 770-780 m, 2011, *A. Damanhuri 11-4, 11-369, 11-384* (UKMB). **Perak:** Pulau Lalang, 1925, *E. Seimund 20996, 20997* (SING). **Selangor:** Ulu Langat, Sungai Congkak, trail to Sungai Congkak waterfall, 30 m, 2009, *G.E. Lee & H.Y. Tang 1179* (UKMB); Pangsoon, trail to Pangsoon waterfall, 100 m, 2011, *A. Damanhuri 11-1, 11-2* (UKMB). **Pahang:** Fraser's Hill, main entrance, 820 m, 2008, *G.E. Lee 1154* (UKMB); Genting Highlands, road to the Noah Mosque, 1650 m, 2009, *G.E. Lee 1195* (UKMB); Goh Tong Jaya, near waterfall, 845 m, 2011, *G.E. Lee 2209* (UKMB); Krau Wildlife Reserve, Perlok, 205 m, 2009, *A. Damanhuri 09-5* (UKMB); trail to Lata Bujang, 135 m, 2009, *A. Damanhuri 09-10* (UKMB). **Johor:** Kluang, Gunung Belumut Expedition base camp, 80 m, 2009, *G.E. Lee 1231, 1232* (UKMB); Expedition trail no. 4, 80 m, 2009, *G.E. Lee 1233* (UKMB); Tangkai, trail to summit of Gunung Ledang, 200 m, 2009, *G.E. Lee 1203, 1204* (UKMB). **Sarawak:** Kuching, Sungai Lalang, road to Bau, 30 m, 2009, *G.E. Lee 1159* (UKMB); Bintulu, Bukit Setiam, 445 m, 2010, *G.E. Lee & H.Y. Tang 1442* (UKMB). **Sabah:**

Ranau, North of Jesselton, 1963, *M. Mizutani* 6078 (NICH); Madai Cave, SW of Lahad Datu, 60-100 m, 1963, *Z. Iwatzuki* 5722 (NICH); 60 km W of Sandakan, Labuk & Sugut, along Kolapis road, 1968, *S. Kokawa & M. Hotta* 49bis (NICH); Kinabalu National Park, around Poring Hot Spring, 600 m, 1971, *T. Narita* 4539 (NICH). **INDONESIA.** Kalimantan: Bukit Condong Bentuang Karimun, 1997, *H. Sujadmiko* 142 (BO); Balikpapan, Kutei peak, 1952, *W. Meijer* B2164 (BO); Ambon: 1965, *D. Balázs* com. *T. Pócs* 91-92j (NICH); W Java: Cibodas Botanical Garden, 2001, *S.R. Gradstein* 51 (GOET); Bogor Botanical Garden, 2011, *G.E. Lee* 2308, 2309, 2311, 2312, 2317, 2318, 2322 (UKMB); Sulawesi: Lore Lindu National Park, Toro, 800-900 m, Cacao plantation, 2005, *N.S. Ariyanti* D1/P6/Q3/0-50/E/4 (BIOT). **THAILAND.** Peninsular: Khao Chong, *Ch. Charoenphol et al.* 3546 (NICH), Pang-nga, to Ru-sisawan cave, 1980, *T. Boonkerd* 15 (NICH). **SINGAPORE.** Botanical Garden, 20 m, 1930, *F. Verdoorn* 251 (SING). **PHILIPPINES.** Luzon: Barrio Calminoe, Louisiana Laguna, 1984, *B.C. Tan* 84-040 (NICH). **JAPAN.** Ogasawara Archipelago, Chichijima Is., 2008, *T. Yamaguchi* 29848 (HIRO). **PAPUA NEW GUINEA.** Milne Bay Prov., Woodlark I., 5 m, 1984, *R. Kumei* 94 (NICH); East Sepik Prov., Kairuru Island, 1979, *J. Clay* 8 (NICH). **NEW CALEDONIA.** Mé Aoui, 500 m, 1951, *Guillaumin & Baumann-B.* 10180, 10253 (GOET).

**Distribution and habitat in Malaysia:** Perlis\*, Pulau Langkawi\*, Kedah, Pulau Pinang, Kelantan\*, Perak\*, Selangor, Pahang, Johor, Sarawak, Sabah; epiphytic, occasionally terrestrial on rocks at wide elevational range from sea level to 2000 m.

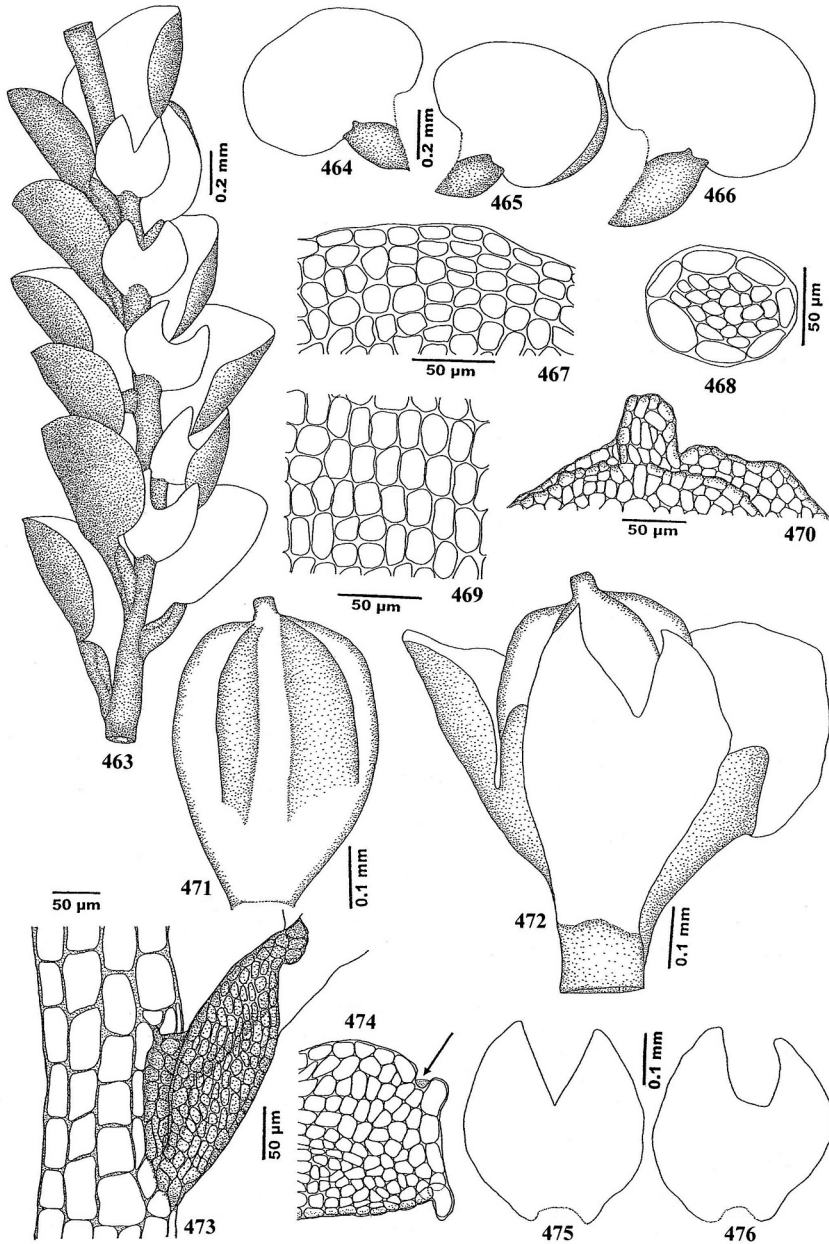
**General distribution:** Malesia, northern Australia (Queensland), New Caledonia.

**Discussion:** *Lejeunea sordida* is the most common species of the genus *Lejeunea* in Malaysia and is widespread throughout the country. The species is easily recognized by 1) the glossy green to yellowish green color of the plants in the field, usually growing abundantly in big patches on tree trunks, 2) large, reniform underleaves which always cover the lobule, 3) small leaf lobules, 4) leaf cells with well-developed trigones and intermediate thickenings, and 5) perianth with long mammilose keels which may extend to the base of the perianth. *Lejeunea sordida* may be confused with *L. tuberculosa*, especially in the field, but is readily separated from the latter by the large, reniform underleaves and a small leaf lobule. In a phenetic analysis (Lee *et al.*, submitted), *L. sordida* was most closely related to *L. kinabalensis* at a similarity level of 0.80. The latter species differs from *L. sordida* by the strongly crenulate margin of leaf lobe, leaf lobule, underleaf, female bract and bracteole, and by the suborbicular underleaves with a cordate base.

**27. *Lejeunea stephaniana* Mizut., *J. Hattori Bot. Lab.* 27: 143 (1964) Figs 463-476**

≡ *Strepsilejeunea heterophylla* Steph., *Sp. Hepat.* 6: 395 (1923) (*cf. Lejeunea heterophylla* Sande Lac.). TYPE: Indonesia, Java, *Nyman s.n.* (holotype: G!).

**Plants** dioicous, relatively large, 1.7-2.0 mm wide, light green when fresh, light brown when dry, irregularly and densely branched, branches erect-spreading, collar with three small lobes. **Stems** 0.12-0.16 mm in diameter, about 7 cells high in cross-section, epidermal cells 7, 27-38  $\mu$ m wide, medullary cells 12-21, 10-24  $\mu$ m wide. **Leaves** closely imbricate, recurved when dry, erect-spreading to spreading and recurved when moist. **Leaf lobes** 0.7-0.8 mm long, 0.6-0.7 mm wide (when flattened), ovate; leaf apex broadly rounded, usually recurved; leaf margin entire, irregularly sinuate; the ventral margin forming an angle of 90°-100° with the keel when flattened; insertion line about 15 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded to quadrate, irregularly rectangular towards the leaf margin; apical cells 16-20  $\mu$ m long and 10-12  $\mu$ m wide, median cells 20-30  $\mu$ m long and 10-16  $\mu$ m wide, basal cells 32-50  $\mu$ m long and 12-24  $\mu$ m wide; cell walls hyaline, with small or indistinct trigones and without intermediate thickenings. Cuticle smooth. Oil bodies not



Figs 463-476. *Lejeunea stephaniana* Mizut. **463.** Part of plant in ventral view; **464-466.** Leaves; **467.** Apical cells of leaf lobe; **468.** Cross-section of stem; **469.** Median cells of leaf lobe; **470.** Upper portion of perianth; **471.** Perianth; **472.** Perianth with bracts and bracteole; **473.** Stem portion and leaf lobule; **474.** Upper part of leaf lobule when flattened (hyaline papilla shown by arrow); **475, 476.** Underleaves. 463-467, 473-476 drawn from *M. Mizutani* 2752 (NICH); 471, 472 from the holotype, *Nyman s.n.* (G).



seen. **Leaf lobules** rarely reduced, 0.2-0.3 mm long, 0.09-1.10 mm wide, to 1/3-1/2 the length of the lobe, at an angle of 30°-40° to the stem, ovate-oblong, inflated along the keel, apex truncate, keel curved, free margin incurved fully, apical tooth 26-30 µm long, oblong, somewhat erect, apex obtuse, margin between tooth and sinus 4-5 cells long, large disc cell lacking, cell below the apical tooth 27-30 µm long and 16-18 µm wide. **Underleaves** 0.3-0.4 mm long, 0.3-0.35 mm wide, to 2 times wider than the stem, distant, sometimes contiguous, orbicular to ovate, covering half of the lobules; bilobed, lobes to 1/2 of underleaf length, about 10 cells wide, triangular to lanceolate; sinus broad, rounded to acute, U-shaped to V-shaped; underleaf margin entire; base ± cuneate, insertion line curved; two large basal underleaf cells lacking; underleaves attached to the stem by 4 superior central cells. **Androecia** not seen. **Gynoecea** on short or long branches, female bracts loosely arranged, with one innovation, 1-2 gynoecea in a lateral row due to repeatedly fertile innovations. Female bracts smaller than the leaf, erect-spreading when moist, somewhat enveloping the perianth. Lobes 0.4-0.5 mm long, 0.2-0.3 mm wide, elliptic to obovate, apex subacute to obtuse, margin slightly sinuate. Lobules 0.3-0.4 mm long, 0.10-0.15 mm wide, rarely reduced, 1/2 the width and 3/4 the length of the lobe, obovate to oblong, apex obtuse to truncate, keels straight to slightly curved, smooth, 0.16-0.20 mm long. Female bracteoles 0.43-0.50 mm long, 0.30-0.35 mm wide, almost of the perianth length, obovate with tips obtuse, lobes to 1/3 of female bracteole length, distant, sinus slightly narrow, obtuse, margin slightly sinuate. Perianths 0.45 mm long, 0.30 mm wide, emergent to 3/4 of the perianth length, obovoid, with 5 keels; beak 3-4 cells long; cells of perianth at the keels smooth, rarely mammillose; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined.** MALAYSIA. Sabah: Mt. Kinabalu, below Paca Cave, 2500-2800 m, 1963, *M. Mizutani* 2752, *Z. Iwatzuki* 784 (NICH); Paca cave, trail between Villosa shelter and Laban Rata rest house, 2900-3050 m, 2010, *G.E. Lee* 1515 (UKMB); trail from Mempoing shelter to Layang-layang Staff Quarters, 2500-2800 m, 2010, *G.E. Lee* 1671 (UKMB); trail from Timpohon gate to Kandis shelter, 1900 m, 2010, *G.E. Lee* 2142 (UKMB).

**Distribution and habitat in Malaysia:** Sabah; epiphytic, occasionally terrestrial in upper montane forest, 2500-2800 m.

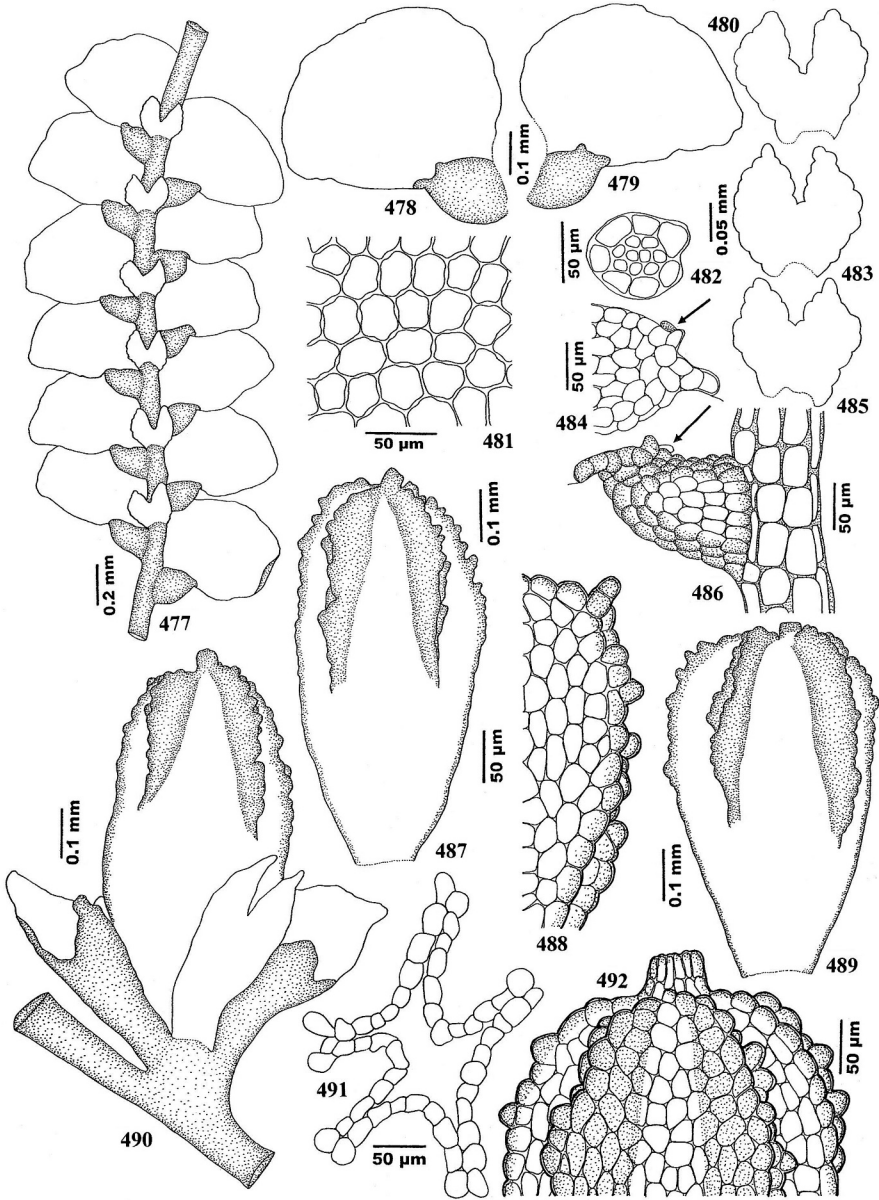
**General distribution:** Sabah, Indonesia (Java).

**Discussion:** *Lejeunea stephaniana* is characterized by 1) the recurved and occasionally crisped leaves when dry, 2) large lobules (1/2 of the length of the lobe), 3) absence of a large disc cell below the apical tooth, 4) leaf cells with small or indistinct trigones and without intermediate thickenings, 5) lobules with fully incurved free margins, and 6) obovoid perianths with a 3-4 cells long beak. *Lejeunea stephaniana* is a rare species and is known only from from Java (type) and Sabah (Mt. Kinabalu). The species is closely related to *L. pectinella*, *L. lumbricoides* and *L. compacta* but differs by its laminal cells with small or indistinct trigones and no intermediate thickenings (trigones and intermediate thickenings conspicuous in *L. pectinella*, *L. lumbricoides* and *L. compacta*).

**28. *Lejeunea tamaspocsii* G.E. Lee, *Polish J. Bot.* 58(1): 69 (2013) Figs 477-492**

TYPE: Peninsular Malaysia, Pahang, Genting Highlands, Goh Tong Jaya, area around the waterfall, 845 m, 3 March 2011, *G.E. Lee* 2194 (holotype: UKMB!; isotype: EGR!).

**Plants** autoicous, relatively small, 0.8-1.0 mm wide, light green when fresh to brown when dry, irregularly and slightly branched, branches erect-spreading, collar with three small lobes. **Stems** 0.07-0.10 mm in diameter, about



Figs 477-492. *Lejeunea tamaspocsi* G.E. Lee. **477.** Part of plant in ventral view; **478, 479.** Leaves; **480, 483, 485.** Underleaves; **481.** Median cells of leaf lobe; **482.** Cross-section of stem; **484.** Upper part of leaf lobule when flattened (hyaline papilla shown by arrow); **486.** Stem portion and leaf lobules (hyaline papilla shown by arrow); **487, 489.** Perianths; **488.** Cells of perianth keel; **490.** Perianth with bracts and bracteole; **491.** Cross-section of perianth; **492.** Upper portion of perianth. All figures drawn from the holotype, *G.E. Lee 2194* (UKMB).

5-6 cells high in cross-section, epidermal cells 7, 25-38  $\mu\text{m}$  wide, medullary cells 4-5, 13-18  $\mu\text{m}$  wide. **Leaves** distant to contiguous,  $\pm$  erect-spreading, convex when moist. **Leaf lobes** 0.5-0.6 mm long, 0.4-0.5 mm wide (when flattened), ovate, asymmetrical with strongly arched dorsal margin and straight to slightly curved ventral margin; leaf apex narrowly rounded, flat, sometimes recurved; leaf margin crenulate due to slightly projecting marginal cells; the ventral margin forming an angle of  $100^\circ$ - $150^\circ$  with the keel when flattened; insertion about 13 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually quadrate to pentagonal, irregularly quadrate to rectangular towards the leaf margin; apical cells 25-30  $\mu\text{m}$  long and 13-25  $\mu\text{m}$  wide, median cells 25-38  $\mu\text{m}$  long and 18-25  $\mu\text{m}$  wide, basal cells 38-50  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide; cell walls hyaline, with well-developed trigones and occasionally with intermediate thickenings, 1-2 per cell, 0-1 (2) between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies not seen. **Leaf lobules** relatively large, rarely reduced, 0.15-0.20 mm long and 0.12-0.15 mm wide, to 1/3 the length of the lobe, at an angle of about  $60^\circ$  to the stem, ovate, inflated along the keel; apex obliquely truncate; keel curved; free margin flat, sometimes incurved fully; apical tooth 20-25  $\mu\text{m}$  long, oblong, erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell lacking, cell below the apical tooth 30  $\mu\text{m}$  long and 25  $\mu\text{m}$  wide. **Underleaves** *ca* 0.1 mm long, 0.15 mm wide, to 2 times wider than the stem, distant, suborbicular to wider than long, not covering the lobules; bilobed, lobes to 1/2 of underleaf length, about 4 cells wide, somewhat triangular, distant; sinus narrow to broad, acute to slightly obtuse, widely V-shaped; underleaf margin strongly crenulate; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 2 superior central cells. **Androecia** 0.2-0.3 mm long, *ca* 0.3 mm wide with bracts, usually on main shoots, rarely on short or long lateral branches. Male bracts in 2-3 pairs, entire to somewhat crenulate without wing, apex obtuse, keels inflated. Male bracteoles 1, smaller than underleaf, margin crenulate. Antheridia not seen. **Gynoeceia** usually on main shoots, occasionally on short or long branches, female bracts loosely arranged, with one innovation, usually with one gynoeceium in a lateral position. Female bracts slightly smaller than the leaf, erect-spreading when moist, not enveloping the perianth. Lobes 0.4-0.5 mm long, *ca* 0.2 mm wide, oblong to obovate, apex acute, margin crenulate. Lobules *ca* 0.3 mm long, 0.07-0.09 mm wide, rarely reduced, 1/2 the width and 2/3-3/4 the length of the lobe, oblong, apex obtuse, keels straight, smooth, 0.25-0.30 mm long. Female bracteoles 0.4-0.5 mm long, 0.15-0.20 mm wide, 1/2 the length of the perianth length, oblong with tips acute, lobes to 1/4 of female bracteole length, sinus narrow, acute, margin crenulate. Perianths 0.75 mm long, 0.3 mm wide, emergent to 1/2 of the perianth length, oblong, with 5 keels, the keels 2-winged, wings 1-2 cells wide, lateral keels sometimes with 1-3 celled cilia; beak 2-3 cells long; cells of the perianth at the keels sometimes bulging on surface; stalk-like elongation lacking. **Sporophyte**: seta to 0.7 mm long; capsule *ca* 0.4 mm in diameter, valves 0.3 mm long, 0.2 mm wide at middle, widely spreading after dehiscence; elaters *ca* 0.15-0.25 mm long; spores rectangular to irregular-shaped, 38-50  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide. **Vegetative propagation** not seen.

**Further specimens examined.** **MALAYSIA. Kelantan:** Gua Musang, foot of Gunung Chamah, Dakota trail, 770 m, 2011, A. *Damanhuri* 11-466 (UKMB). **Pahang:** Fraser's Hill, road to the Clock Tower and Post Office, 1120 m, 2009, G.E. *Lee* 1423 (UKMB); Cameron Highlands, Robinson Waterfall, 1340 m, 2009, G.E. *Lee* 2274 (UKMB); Mentigi trail, 1365 m, 2009, G.E. *Lee* 2275 (UKMB). **Sabah:** roadside from Headquarters to Timpohon gate, 1530 m, 2010, G.E. *Lee* 1732 (UKMB).

**Distribution and habitat in Malaysia:** Kelantan\*, Pahang\*, Sabah\*; on tree trunks and rotten stumps in open areas and shady slopes, 800-1600 m.

**General distribution:** only known from Malaysia (Peninsular Malaysia, Sabah).

**Discussion:** Characteristic features of *L. tamaspocsii* are: 1) the asymmetrical leaf lobes with arched dorsal margin and straight to slightly curved ventral margin and with a narrowly rounded apex; 2) the small, distant underleaves with coarsely crenulate margins; 3) the rough cuticle covered by minute papillae; and 4) the perianths with 2-winged keels, the wings sometimes with 2-celled cilia. Two-winged perianth keels have previously been recorded from some Neotropical members of the genus *Crossotolejeunea*, a genus now included in *Lejeunea* (Reiner-Drehwald & Goda, 2000), but are rare among Malaysian *Lejeuneas* where 2-winged perianth keels were only observed in *L. tamaspocsii* and *L. dipterota* (Eifrig) G.E. Lee. The latter species differs from *L. tamaspocsii* by numerous features and relationships between the two taxa are distant (Lee *et al.*, submitted).

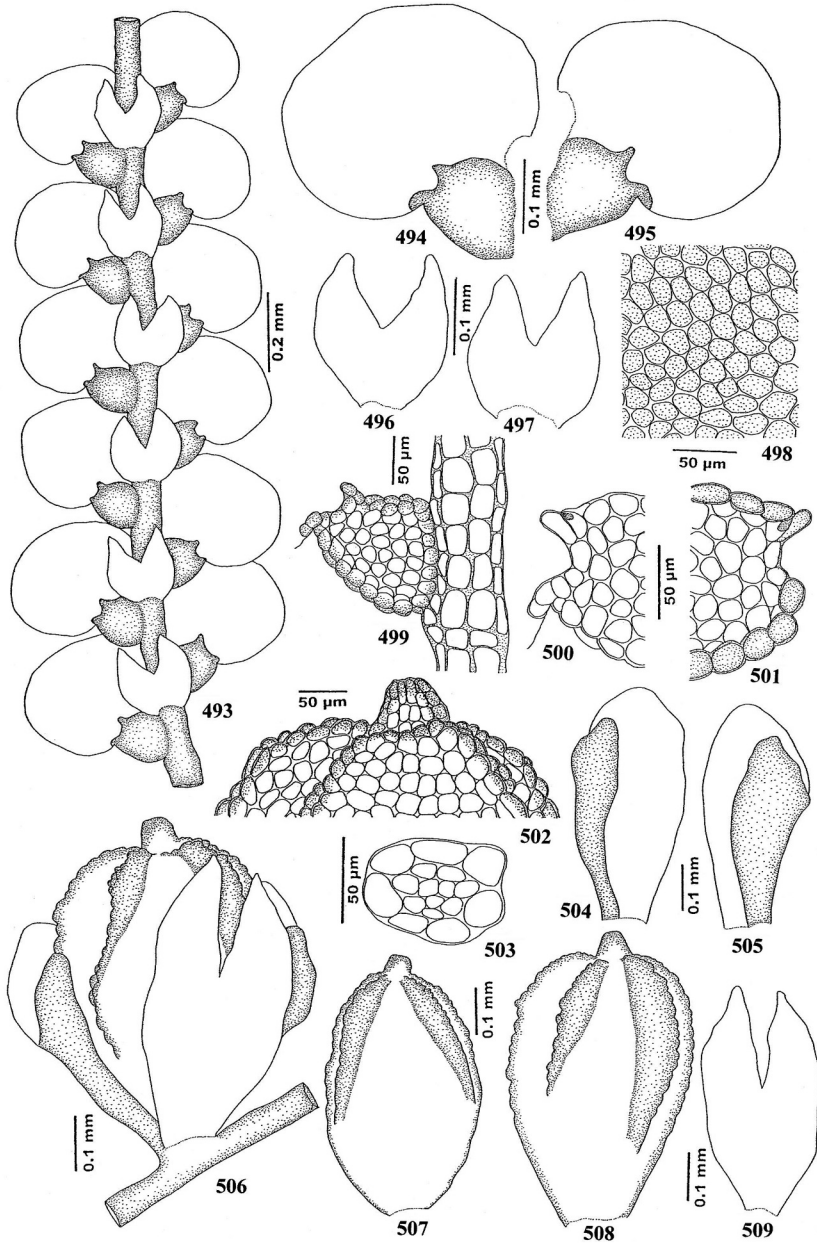
Among the Malaysian *Lejeuneas*, *L. tamaspocsii* is most closely related to *L. apiculata*, which was recovered as sister to *L. tamaspocsii* in a phenetic and phylogenetic analysis (Lee *et al.*, submitted). *Lejeunea apiculata* is easily recognized from *L. tamaspocsii*, however, by having more symmetrical leaf lobes with long apiculate apices ending in a row of (2-)3-4 cells, and by the underleaves being more deeply bifid (to 2/3 of length) and having narrow lanceolate lobes and hardly crenulate margins.

**29. *Lejeunea tuberculosa* Steph., Spec. Hepat. 5: 790 (1915)**

**Figs 493-509**

TYPE: Sikkim, Ryang Valley, 5000 ft., 8 Febr 1898, *Gammie 11551* (holotype: G!).

**Plants** dioicous, 0.5-0.9 mm wide, yellowish green to light green when fresh to light brown when dry, irregularly and slightly branched, sometimes bipinnately branched, branches erect-spreading to spreading, collar with three small lobes. **Stem** 0.05-0.07 mm in diameter, about 6 cells high in cross-section, epidermal cells 7, 25-38  $\mu\text{m}$  wide, medullary cells 9-12, 13-15  $\mu\text{m}$  wide. **Leaves** contiguous to distant, rarely recurved when dry, erect-spreading and rarely recurved when moist. **Leaf lobes** 0.3-0.4 mm long and 0.2-0.3 mm wide (when flattened), ovate-orbicular; leaf apex broadly rounded, always flat; leaf margin entire; the ventral margin forming an angle of 90°-100° with the keel when flattened; insertion about 11 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually pentagonal to hexagonal, sometimes rounded, irregularly quadrate to rectangular towards the leaf margin; apical cell 12.5-25.0  $\mu\text{m}$  long and 12.5-17.5  $\mu\text{m}$  wide, median cell 15-25  $\mu\text{m}$  long and 12.5-20.0  $\mu\text{m}$  wide, basal cell 25.0-32.5  $\mu\text{m}$  long and 15-25  $\mu\text{m}$  wide; cell walls hyaline, with somewhat distinct to scarce trigones and intermediate thickenings. Cuticle rough by numerous minute papillae. Oil bodies somewhat glistening to faintly opaque-granular, fine *Jungermannia*-type, with minute granules, somewhat rough externally; marginal cells with 2-3 oil bodies per cell, 3-4  $\mu\text{m}$  long and 3-4  $\mu\text{m}$  wide, mostly globose to ovoid; median cells with 3-5 oil bodies per cell, 5-10  $\mu\text{m}$  long and 3-5  $\mu\text{m}$  wide, globose, ovoid to somewhat ellipsoid; basal cells with 3-5 oil bodies per cell, 5-13  $\mu\text{m}$  long and 4-5  $\mu\text{m}$  wide, globose, ovoid to ellipsoid. **Leaf lobules** rarely reduced, 0.11-0.13 mm long and *ca* 0.10 mm wide, to 1/3-1/2 the length of the lobe, at an angle of 60°-70° to the stem, ovate, inflated along the keel; apex obliquely truncate; keel curved; free margin incurved partially; apical tooth 18-23  $\mu\text{m}$  long, oblong, erect, apex obtuse; margin between tooth and sinus 3-4 cells long, large disc cell lacking, cell below the apical tooth 17.5-20.0  $\mu\text{m}$  long and 12.5-15.0  $\mu\text{m}$  wide. **Underleaves** 0.15-0.18 mm long,



Figs 493-509. *Lejeunea tuberculosa* Steph. 493. Part of plant in ventral view; 494, 495. Leaves; 496, 497. Underleaves; 498. Median cells of leaf lobe; 499. Stem portion and leaf lobule; 500. Upper part of leaf lobule when flattened (hyaline papilla shown in gray); 501. Upper part of leaf lobule in dorsal view; 502. Upper portion of perianth; 503. Cross-section of stem; 504, 505. Female bracts; 506. Perianth with bracts and bracteole; 507, 508. Perianths; 509. Female bracteole. 493-498, 503, 507 drawn from *G.E. Lee 1183* (UKMB); 499-501 from *G.E. Lee 1786* (UKMB); 502, 504, 505, 506, 508, 509 from *G.E. Lee 1700* (UKMB).

0.12-0.17 mm wide, to 2-3 times wider than the stem, very distant, orbicular (slightly longer than wide), covering half of the lobules; bilobed, lobes to 1/2 of underleaf length, about 6 cells wide, triangular, slightly oblique; sinus broad, obtuse, U-shaped to V-shaped; underleaf margin entire; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells lacking; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.50-0.85 mm long, 0.40-0.45 mm wide with bracts, on short or long lateral branches. Male bracts in 3-6 pairs, crenulate without wing, apex broadly rounded, keels inflated. Male bracteoles 0-2, smaller than underleaf, margin entire. Antheridia not seen. **Gynoecia** on short or long branches, occasionally on main shoots, female bracts somewhat crowded, with one innovation, usually with one gynoeium in a lateral position. Female bracts slightly smaller than the leaves, erect-spreading when moist, somewhat enveloping the perianth. Lobes 0.4-0.5 mm long, 0.2-0.3 mm wide, obovate to oblong, apex obtuse, margin entire. Lobules 0.3-0.4 mm long, 0.10-0.15 mm wide, rarely reduced, 2/3 the width and 4/5 the length of the lobe, oblanceolate, apex obtuse, keels straight, smooth, 0.20-0.25 mm long. Female bracteoles 0.4-0.5 mm long, 0.20-0.25 mm wide, almost of the perianth length, obovate to oblong with tips acute to obtuse, lobes to 1/2 of female bracteole length, sinus acute, margin entire. Perianths 0.4-0.5 mm long, 0.30-0.35 mm wide, emergent to 1/3-3/4 of the perianth length, obovoid, with 5 keels; beak short, to 3 cells long; cells of the perianth at the keels mammillose; stalk-like elongation lacking. **Sporophyte**: seta to 0.3 mm long; capsule *ca* 0.3 mm in diameter, valves 0.3 mm long, 0.15 mm wide at middle, slightly spreading after dehiscence; elaters and spores not seen. **Vegetative propagation** by means of plantlet regeneration from leaf margins or leafy propagules.

**Further specimens examined.** **MALAYSIA.** **Kedah:** Sungai Sedim recreational park, 50 m, *G.E. Lee* 1413, 1419 (UKMB). **Pulau Pinang:** Penang Hill, "broken staircase trail", 750 m, 2008, *G.E. Lee* 1093 (UKMB). **Perak:** Kinta Valley, trail to Gunung Korbu, 410 m, 2008, *A. Damanhuri* 08-8 (UKMB). **Pahang:** Cameron Highlands, Robinson Waterfalls, 1340 m, 2009, *G.E. Lee* 1165, 1167, 1172, 1174, 1175 (UKMB); near gate of Cool Point Hotel, 1300 m, 2009, *G.E. Lee* 2280, 2281 (UKMB); Mentigi trail, 1365 m, 2009, *G.E. Lee* 1164, 1183, 2286, 2292, 2293, 2294, 2337 (UKMB); Parit Waterfalls, 1340 m, 2009, *G.E. Lee* 1173, 2160, 2329, 2330, 2333, 2335, 2336 (UKMB); Gunung Brinchang, 1600 m, 2008, *A. Damanhuri* 08-1 (UKMB); Genting Highlands, Theme Park, 1650 m, *G.E. Lee* 1187, 1188 (UKMB); Goh Tong Jaya, near waterfall, 845 m, 2011, *G.E. Lee* 2176, 2186, 2188, 2191, 2193, 2198, 2201, 2203, 2206a, 2210, 2212, 2213 (UKMB). **Selangor:** road to Bukit Tabor, 135 m, 2008, *Khairil s.n.* (UKMB); Klang gates, 165 m, 2008, *Khairil s.n.* (UKMB); Ulu Langat, Sungai Tekala, Hutan Lipur Sungai Tekala, 30 m, 2008, *G.E. Lee* 1150 (UKMB); Sungai Gabai, staircase to the summit, 100 m, 2010, *Daniel* 11-12, *G.E. Lee* 2275 (UKMB); Gunung Nuang, trail to summit, 295 m, 2009, *A. Damanhuri* 09-9 (UKMB). **Sabah:** Kinabalu Park, trail from Timpohon gate to Kandis shelter, 1900 m, 2010, *G.E. Lee* 1771, 1772, 1775, 1776, 1780, 1781, 1785, 1786, 1788, 1790, 1793, 1796, 1798, 1799, 1800, 1811, 1818 (UKMB); between Bundu Tuhan View trail and Liwagu trail, 1530 m, 2010, *G.E. Lee* 1531, 1633 (2 packets), 1679, 1689, 1700, 1703, 1716, 1729, 1830, 1834, 1835, 1837, 1838, 1839, 1840, 1844, 1847, 1849, 1850, 1851, 1853, 2123 (UKMB); trail from Kandis shelter to Ubah shelter, 2000 m, 2010, *G.E. Lee* 1561 (UKMB), Botanical Garden, around Power station road, 1515 m, 2010, *G.E. Lee* 1739, 1743, 1745, 1747, 2022, 2025, 2027, 2028, 2031, 2033, 2036, 2039, 2041, 2043, 2046, 2047, 2048, 2052, 2053, 2054, 2055, 2056, 2060, 2062, 2064, 2068, 2069, 2071, 2075, 2078, 2079, 2080, 2082, 2084 (UKMB); trail from Ubah shelter to Lowii shelter, 2000 m, 2010, *G.E. Lee* 1621 (UKMB); trail from Lowii shelter to Mempoening shelter, 2300-2500 m, 2010, *G.E. Lee* 2003 (UKMB); road from Headquarters to Timpohon gate, 1530 m, 2010, *G.E. Lee* 1705, 1824 (UKMB), Kota Kinabalu, Inanam, Kionsom Waterfall, 200 m, 2010, *G.E. Lee* 2144, 2148, 2150, 2151 (UKMB); Tawau district, Tawau Hills Park, Headquarters to KM 10, 400 m, 2008, *M. Suleiman & D.P. Masundang* 2892 (BORH). **INDIA.** Kumaun Himalaya, Naini Tal, 1981, *S.D. Tewari s.n.* (NICH). **SRI LANKA.** Mt. Vernon, 1954, *F. Schmid* 10188, 10202 (NICH). **THAILAND.** Payap, Mt. Inthanon, 1750-1800 m alt, 1965,

*A. Touw* 9921 (NICH); (Mt.) Chiengdao, 1650-1750 m, *A. Touw* 9242 (NICH); Phuket, Mt. Nang Hong between Pungah and Krabi, 170-320 m, 1966, *A. Touw* 11306 (NICH). **INDONESIA.** Java: Bogor Botanical Garden, *G.E. Lee* 2310, 2313, 2314, 2315, 2316, 2319, 2320, 2321 (UKMB); Halimun Salak Mt. National Park, 1080 m, 2005, *Radhiah Zakaria* 249c (BIOT). **PHILIPPINES.** Luzon: Laguna, Mt. Makiling, 1977, *Tan & Alvarez Jr.* 0-77817, 77817 (NICH); Benguet Prov., Mt. Santo Tomas, 1550-2350 m, 1984, *M. Onraedt* 10979 (NICH); Baguio, 1500 m, 1984, *M. Onraedt* 10822 (NICH).

**Distribution and habitat in Malaysia:** Kedah\*, Pulau Pinang\*, Perak\*, Pahang\*, Selangor\*, Sabah; on various substrates but especially on trees, 100-2500 m.

**General distribution:** Africa, tropical Asia, Pacific region.

**Discussion:** The distinctive characters of *L. tuberculosa* include 1) the very plane leaves both in dry and moist condition, 2) ovate leaf lobes with the ventral margin making a sharp angle with the keel, 3) large, rarely reduced leaf lobules, 4) distant underleaves, and 5) opaque perianths with mammillose-crenulate keels. *Lejeunea tuberculosa* is closely related to *L. patersonii*; both species have identical leaves and leaf lobules and cluster with high similarity (SL 0.73) (Lee et al., submitted). Differences are discussed under the latter species. *Lejeunea tuberculosa* superficially resembles *L. sordida* but the latter differs by having large, reniform and more contiguous underleaves.

*Lejeunea tuberculosa* varies particularly in the shape of the leaf cells and the presence of trigones and intermediate thickenings. The cells are usually rounded and with distinct trigones and occasionally with intermediate thickenings. However, quadrate to pentagonal cells without distinct trigones and intermediate thickenings are also found, sometimes in leaves of the same shoot. Sometimes these differences are found between leaf cells on branches and on main shoots.

### 30. *Lejeunea umbilicata* (Nees) Nees, *Nova Acta Acad. Caes. Leop. Carol.*

*German. Nat. Cur.* 19: 472 (1843)

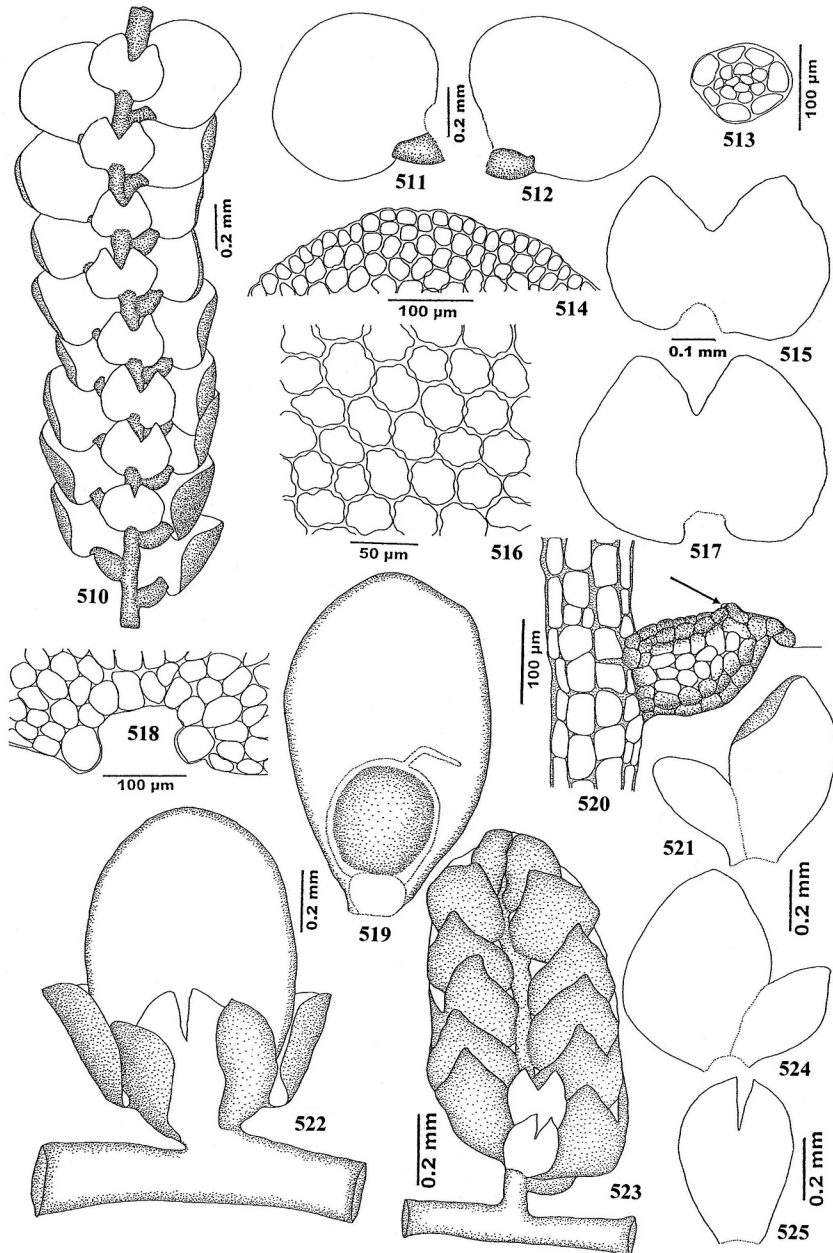
**Figs 510-525**

Basionym: *Jungermannia umbilicata* Nees, *Enum. Pl. Crypt. Jav.*: 42 (1830). TYPE: Indonesia, Java, *Blume s.n.* (isotype: STR!).

= *Taxilejeunea cuculliflora* Steph., *Hedwigia* 35: 133 (1896) ≡ *Lejeunea cuculliflora* (Steph.) Mizut., *J. Hattori Bot. Lab.* 33: 236 (1970). TYPE: Fiji, Ovalau, 1864, *Graeffe s.n.* (Herb. Jack no. 321) (holotype: G!), **syn. nov.**

For further synonyms see Mizutani (1961, 1970).

**Plants** dioicous, relatively large, 1.0-1.6 mm wide, usually light green to slightly yellowish green when fresh to dark brown when dry, irregularly and densely pinnate to bipinnate, branches erect-spreading to spreading, collar with three small (sometimes reduced) lobes. **Stem** 0.08-0.12 mm in diameter, about 6 cells high in cross-section, epidermal cells 7, 21-50 µm wide, medullary cells 10-18, 12-22 µm wide. **Leaves** contiguous to imbricate, slightly recurved when dry, spreading and slightly recurved when moist. **Leaf lobes** 0.4-0.8 mm long, 0.4-0.6 mm wide (when flattened), orbicular to ovate; leaf apex broadly rounded, slightly recurved; leaf margin entire to crenulate due to projecting cells; the ventral margin forming an angle of 130°-150° with the keel when flattened; insertion line about 12 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded to quadrate, irregular rounded to rectangular towards the leaf margin; apical cells 15-29 µm long and 13-23 µm wide, median cells 25-48 µm long and 21-35 µm wide, basal cells 48-69 µm long and 28-45 µm wide; cell walls hyaline, with well-developed trigones and conspicuous intermediate thickenings, 2-4 per cell, 0-1 between 2 adjacent trigones. Cuticle smooth, sometimes weakly rough. Oil bodies somewhat glistening to faintly opaque-granular, fine *Jungermannia*-type, with minute



Figs 510-525. *Lejeunea umbilicata* (Nees) Nees. 510. Part of plant in ventral view; 511, 512. Leaves; 513. Cross-section of stem; 514. Apical cells of leaf lobe; 515, 517. Underleaves; 516. Median cells of leaf lobe; 518. Basal cells of underleaf; 519. Perianth; 520. Stem portion and leaf lobule (hyaline papilla shown by arrow); 521, 524. Female bracts; 522. Perianth with bracts and bracteole; 523. Androecial shoot; 525. Female bracteole. All figures drawn from *M. Mizutani* 3769 (NICH).



granules, somewhat rough externally; marginal cells with 5-7 oil bodies per cell, 2-3  $\mu\text{m}$  long and 2-3  $\mu\text{m}$  wide, mostly globose; median cells with 7-10 oil bodies per cell, 5-8  $\mu\text{m}$  long and 3-4  $\mu\text{m}$  wide, globose and ovoid; basal cells with 8-12 oil bodies per cell, 5-10  $\mu\text{m}$  long and 3-4  $\mu\text{m}$  wide, globose, ovoid and ellipsoid. **Leaf lobules** sometimes reduced, 0.1-0.2 mm long and 0.07-0.1 mm wide, to 1/4-1/3 the length of the lobe, at an angle of 50°-60° to the stem, oblong, inflated along the keel; apex obliquely truncate, U-shaped when flattened; keel curved; free margin incurved fully, apical tooth 20-30  $\mu\text{m}$  long, rectangular to oblong, erect, apex obtuse; margin between tooth and sinus 3-4 cells long, large disc cell lacking, cell below the apical tooth 25-30  $\mu\text{m}$  long and 15-20  $\mu\text{m}$  wide. **Underleaves** 0.1-0.3 (0.45) mm long, 0.2-0.45 (0.6) mm wide, to 3 times wider than the stem, contiguous to distant, uniform (wider than long), covering half of the lobules; bilobed, lobes to 1/2 of underleaf length, about 10 cells wide, triangular to shallowly triangular; sinus narrow to broad, acute to obtuse, V-shaped to U-shaped; underleaf margin weakly to strongly crenulate; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells differentiated; underleaves attached to the stem by 4 superior central cells. **Androecia** 0.7-0.8 mm long, 0.4-0.5 mm wide with bracts, on short branches. Male bracts in 3-6 pairs, crenulate without wing, apex obtuse to truncate, keels inflated. Male bracteoles 2, smaller than the underleaf, margin entire. Antheridia 2 per bract, 100-120  $\mu\text{m}$  in diameter, somewhat yellowish with a short and hyaline stalk, 125-130  $\mu\text{m}$  in length. **Gynoecia** on short or long branches, female bracts loosely arranged, with one innovation, 2 gynoecia in a lateral row due to repeatedly fertile innovations. Female bracts smaller than the leaf, erect-spreading when moist, somewhat enveloping the perianth. Lobes 0.6-0.7 mm long, 0.3-0.4 mm wide, elliptic to obovate, apex obtuse, margin slightly crenulate. Lobules 0.4-0.5 mm long, 0.12-0.17 mm wide, 1/2-1/3 the width and 3/4 the length of the lobe, sometimes longer than the lobe, elliptic to oblong, apex acute to obtuse, keels straight and smooth, 0.20-0.25 mm long. Female bracteoles 0.5-0.6 mm long, 0.3-0.4 mm wide, 1/2 of the perianth length, ovate to obovate with tips acute to obtuse, lobes to 1/2 of female bracteole length, sinus narrow, acute, margin crenulate. Perianths 0.8-1.2 mm long, 0.4-0.5 mm wide, emergent to 1/2 of the perianth length, obovoid, without keels and beak; apex somewhat truncate; cells of perianth at the keels smooth, rarely mammillose; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** by means of plantlet regeneration from leaf margins or leafy propagules.

**Further specimens examined.** **MALAYSIA.** **Kelantan:** Gunung Chamah, trail from Kem Abdullah Sani to Kem Barat, 1075 m, 2011, *A. Damanhuri 11-51* (UKMB). **Perak:** Kampar, Kuala Dipang, Sungai Salu waterfall, along the trail at the recreation park, 50 m, 2011, *Daniel 11-26* (UKMB). **Pahang:** Cameron Highlands, Gunung Brinchang, tropical mossy forest, 1965, *Hiroshi Inoue 11202* as *Taxilejeunea cuculliflora* (TNS); Gunung Jasar, near Tanah Rata, 1965, *Hiroshi Inoue 11236* as *Taxilejeunea cuculliflora* (TNS); near the front gate of Cool Point Hotel, 1300 m, 2009, *G.E. Lee 2281* (UKMB); Fraser's Hill, Bishop's trail, 1995, *S.C. Chin et al. 4532* (SING); roadside to Clock Tower, 1120 m, 2009, *G.E. Lee 1424* (UKMB); Genting Highlands, on top of mountain, disturbed area, 1830 m, 1974, *P.Y. Wong with Kim Wong 1604* (NICH). **Selangor:** Langat Basin, Gunung Nuang, at foot of G. Nuang, trail to campsite, ca 350 m, 1997, *Noorlaila Abdullah 18* (UKMB). **Johor:** Kluang, Gg. Belulut, 900 m, 1923, *R.E. Holttum 10814* (SING). **Sarawak:** Bukit Setiam, 410-445 m, 2010, *G.E. Lee & H.Y. Tang 1441, 1456, 2159, 2160* (UKMB). **Sabah:** Mt. Kinabalu, between Kamaranga Radio Station and Water Falls, 2146-2000 m, 1963, *M. Mizutani 2324* (NICH); in a virgin forest near Forest Dept. Bungalow, Sosopodon, Kundasang, Kinabalu area, 1350 m, 1963, *M. Mizutani 6147* (NICH); mossy forest between Tenompok Pass and Ulu Damaian, south slope of Mt. Kinabalu, 1463-1500 m, 1963, *M. Mizutani 3230, 3248, Z. Iwatsuki 4541a* (NICH); between Sosopodon and S. Kelinggen, foot of Mt. Kinabalu, 1350-1400 m, 1963, *M. Mizutani 3769* (NICH); en route from Radio Station to Carson's

Camp, 2200-2700 m, *T. Kodama 40375* (NICH); Kinabalu National Park, along Mamut road, east of Mamut camp, 900-1400 m, 1969, *Shokei Kokawa & Mitsuru Hotta 5978* (NICH); along Mamut Road, 1000-1100 m, 1970, *T. Kodama 41054* (NICH); near Mamut Mine, 1300 m, 1970, *T. Kodama 40867* as *L. chalmersii* (NICH); Kinabalu Park, trail from Lowii Shelter to Mempening Shelter, montane forest, 2300-2500 m, 2010, *G.E. Lee 1982, 1985, 1992, 2004, 2006* (UKMB); trail from Timponon gate to Kandis Shelter, montane forest, 1900 m, 2010, *G.E. Lee 1799, 1800* (UKMB); trail from Ubah Shelter to Lowii Shelter, montane forest, 2000 m, 2010, *G.E. Lee 1618, 2115, 2116* (UKMB); trail from Mempening Shelter to Layang-layang Staff Quarters, montane forest, 2500-2800 m, 2010, *G.E. Lee 2086, 2102* (UKMB); Botanical Garden, around Power station road, 1515 m, 2010, *G.E. Lee 1741, 2049, 2065, 2071, 2072, 2084* (UKMB); between Bundu Tuhan View trail and Liwagu trail, 1530 m, 2010, *G.E. Lee 1689* (UKMB); Tawau, Luasong camp of N. B. T., about 60 km northwest of Tawau, 100 m, 1968, *Shokei Kokawa & Mitsuru Hotta 809* (NICH). **INDONESIA.** Kalimantan: Bentuang Karimun, 1997, *H. Sujadmiko 89, 142* (BO); Balikpapan, Kutei Peak, 1952, *W. Meijer B1928b* (BO); Java: Pagilaran Tea Plantation, 2000 m, 1972, *J. V. Pancho 4007, 4012* (NICH); Cibodas Botanical Garden, 1400 m, 2003, *S.R. Gradstein 10204* (GOET).

**Distribution and habitat in Malaysia:** Kelantan\*, Perak\*, Pahang, Selangor\*, Johor, Sarawak\*, Sabah; epiphytic, occasionally terrestrial on soil, from sea level to 2800 m.

**General distribution:** Malesia.

**Discussion:** Characteristic features of *L. umbilicata* are 1) the recurved leaves; 2) the fully incurved free margin of leaf lobules; 3) the cells with well-developed trigones and intermediate thickenings; 4) the fine *Jungermannia*-type of oil bodies; 5) the reniform underleaves; and 6) the eplicate perianths. *Lejeunea umbilicata* is very similar to *L. microloba*. The two species clustered at a very high similarity level (0.84) in a phenetic analysis and were resolved as sister species in a phylogenetic analysis (Lee *et al.*, submitted). Both species have oblong leaf lobules with obliquely truncate apex and fully incurved free margin, leaf cells are with well-developed trigones and intermediate thickenings, and eplicate perianths without beak. However, *L. microloba* is easily distinguished from *L. umbilicata* by the apiculate leaves. *Lejeunea umbilicata* superficially resembles *L. contracta* but the latter is separated by the 5-keeled perianth, the flat free margin of the lobules, and the leaf cells without trigones and intermediate thickenings.

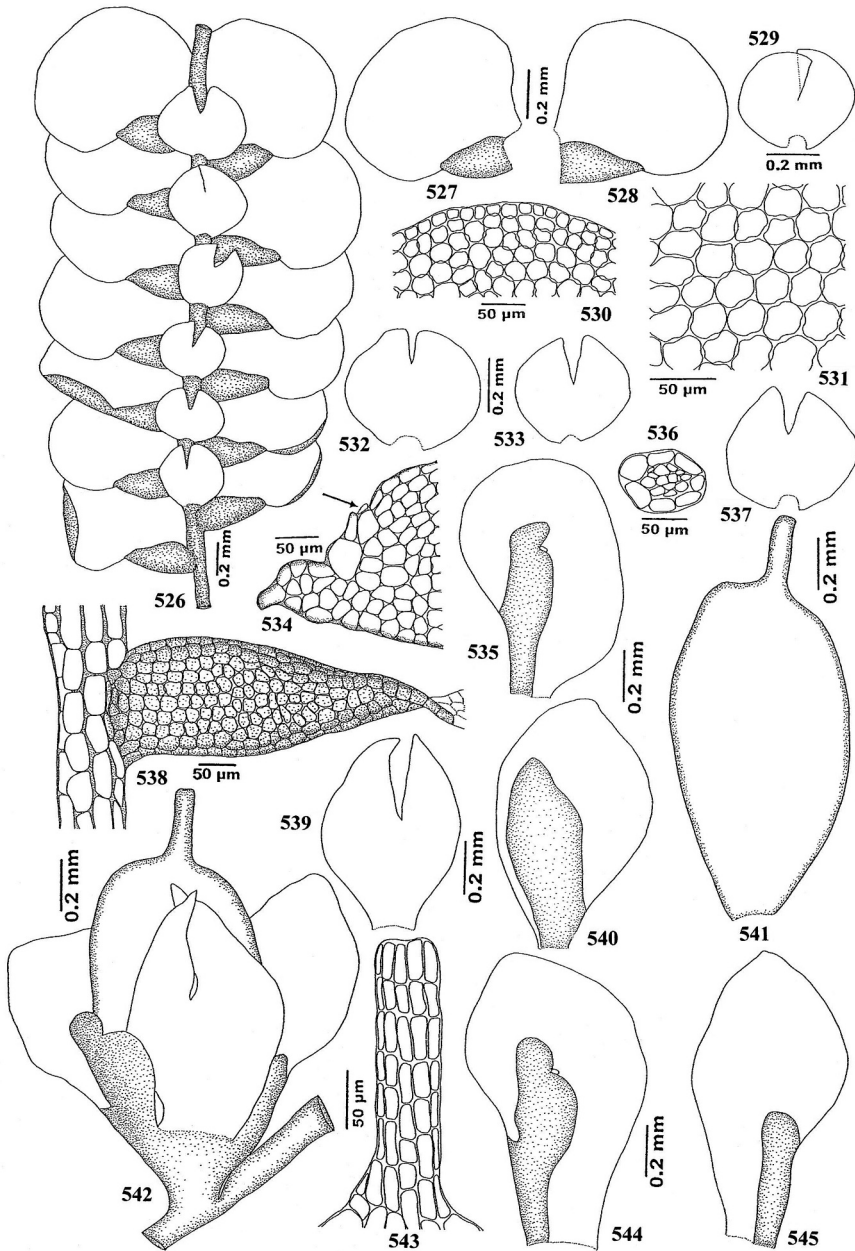
*Lejeunea umbilicata* is a very variable species, most notably in the size of the underleaves. In the type material the underleaves are smaller and more distant than in other collections. Furthermore, variation is also observed in the size of the leaves, in the apices of the underleaves, in the recurvature of leaves, and in the crenulation of the margin of leaves and underleaves. The apex of the underleaves varies, even within the same plant, from acute or somewhat apiculate to obtuse. A terrestrial specimen from Fraser's Hill (*G.E. Lee 1424*) had more strongly crenulated margins than epiphytic plants. *Lejeunea cuculliflora* is very close to *L. umbilicata* and is treated here as a synonym. Mizutani (1970, 1977) mentioned several times the proximity between these two taxa. According to Mizutani (1970), the two might be separated by the underleaf lobes (obtuse vs acute) and the perianth; however the differences mentioned appeared to be very unstable and variable even within the same plant.

**31. *Lejeunea utriculata* (Steph.) Mizut., *J. Hattori Bot. Lab.* 33: 242 (1970)**

**Figs 526-545**

Basionym: *Pycnolejeunea utriculata* Steph. *Hedwigia* 35: 126 (1896). TYPE: Indonesia, Java, *Stahl 34* (holotype: G!).

**Plants** dioicous, relatively large, 1.3-2.0 mm wide, light green when fresh to light brown when dry, irregularly and loosely branched, branches spreading,



Figs 526-545. *Lejeunea utriculata* (Steph.) Mizut. 526. Part of plant in ventral view; 527, 528. Leaves; 529, 532, 533, 537. Underleaves; 530. Apical cells of leaf lobe; 531. Median cells of leaf lobe; 534. Upper part of leaf lobule when flattened (hyaline papilla shown by arrow); 535, 540, 544, 545. Female bracts; 536. Cross-section of stem; 538. Stem portion and leaf lobule; 539. Female bracteole; 541. Perianth; 542. Perianth with bracts and bracteole; 543. Beak of perianth. 526-534, 536-538 drawn from *M. Mizutani 3631* (NICH); 541-545 from the holotype, *Stahl 34* (G); 535, 539, 540 from *G.E. Lee 1851* (UKMB).

collar with three small lobes. **Stems** 0.10-0.12 mm in diameter, about 10 cells high in cross-section, epidermal cells 7, 20-30  $\mu\text{m}$  wide, medullary cells 12-15, 10-17  $\mu\text{m}$  wide. **Leaves** closely imbricate, slightly recurved when dry, erect-spreading to spreading and slightly recurved when moist. **Leaf lobes** 0.75-1.0 mm long, 0.5-0.9 mm wide (when flattened), ovate-orbicular; leaf apex broadly rounded, flat to slightly recurved; leaf margin entire; the ventral margin forming an angle of  $150^\circ$ - $180^\circ$  with the keel when flattened; insertion line about 10 lobe cells long. **Leaf cells** rather uniform, gradually becoming smaller towards the leaf margin, usually rounded, irregularly quadrate to rectangular towards the leaf margin; apical cells 20-25  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide, median cells 30-37.5  $\mu\text{m}$  long and 20-25  $\mu\text{m}$  wide, basal cells 37.5-45  $\mu\text{m}$  long; cell walls hyaline, with well-developed trigones and conspicuous intermediate thickenings, 1-2 per cell, 0-1 between 2 adjacent trigones. Cuticle rough by numerous minute papillae. Oil bodies not seen. **Leaf lobules** rarely reduced, 0.3-0.5 mm long and 0.15-0.20 mm wide, to  $1/2$ - $2/3$  the length of the lobe, at an angle of  $70^\circ$ - $90^\circ$  to the stem, ovate, inflated along the keel; apex obliquely truncate; keel straight to slightly curved; free margin incurved fully; apical tooth 30  $\mu\text{m}$  long, oblong, somewhat erect, apex obtuse; margin between tooth and sinus 3 cells long, large disc cell present, cell below the apical tooth 50  $\mu\text{m}$  long and 43  $\mu\text{m}$  wide. **Underleaves** 0.2-0.3 mm long, 0.3-0.4 mm wide, to 3-4 times wider than the stem, contiguous to distant, ovate (slightly wider than long), covering  $1/4$ - $1/3$  of the lobules; bilobed, lobes to  $1/3$ - $1/2$  of underleaf length, about 10 cells wide, triangular, oblique, sometimes slightly connivent to overlapping, sinus narrow, acute, V-shaped; underleaf margin entire; base  $\pm$  cuneate, insertion line curved; two large basal underleaf cells lacking; underleaves attached to the stem by 4 superior central cells. **Androecia** not seen. **Gynoecia** on short branches, female bracts loosely arranged, with one innovation, usually with one gynoeceum in a lateral position. Female bracts larger than the leaf, erect-spreading when moist, somewhat enveloping the perianth. Lobes 1.0 mm long, 0.5 mm wide, obovate, apex obtuse, margin entire. Lobules 0.4-0.8 mm long, 0.1-0.2 mm wide, rarely reduced,  $1/5$ - $1/3$  the width and  $1/3$ - $2/3$  the length of the lobe, obovate to oblong, apex obtuse, a sinus with hyaline papilla present on the free margin of one of the two bracts, keel straight, smooth, 0.4 mm long. Female bracteoles 1.2 mm long, 5.5 mm wide, almost as long as the perianth, ovate with the tips acute, lobes to  $1/3$  of female bracteole length, overlapping, sinus narrow, acute, margin entire. Perianths 1.1 mm long, 0.6 mm wide, emergent to  $1/5$ - $1/4$  of the perianth length, sometimes somewhat submerged between the female bracts, obovoid, with 5 weak keels, sometimes 3 keels with 2 indistinct dorsal and ventral keel; beak 7-8 cells long; cells of the perianth at the keels smooth, rarely mammillose; stalk-like elongation lacking. **Sporophyte** not seen. **Vegetative propagation** not seen.

**Further specimens examined. Malaysia. Sabah:** Mt. Kinabalu, Ulu Liwagu, 2500-2450 m, 1963, *M. Mizutani 3631* (NICH); Kinabalu Park, trail from Timphohon gate to Kandis shelter, 1900 m, 2010, *G.E. Lee 1777* (UKMB); between Bundu Tuhan View trail and Liwagu trail, 1530 m, 2010, *G.E. Lee 1851* (UKMB); trail from Mempening shelter to Layang-layang Staff Quarters, 2500-2800 m, 2010, *G.E. Lee 1902* (UKMB); road from Headquarters to Timphohon gate, 1530 m, 2010, *G.E. Lee 1641* (UKMB). **INDONESIA.** Java: Mt. Pahuta SW of Bandung, 2000-2100 m, 2009, *Kornochalert S. 1401* (BIOT ex UKMB).

**Distribution and habitat in Malaysia:** Sabah; epiphyte at elevations above 1500 m.

**General distribution:** Sabah, Indonesia (Java).

**Discussion:** *Lejeunea utriculata* is most similar to *L. pectinella* in the broadly rounded leaf apex, long leaf lobules with incurved free margin and large disc cell, the long beak of the perianth, leaf cells with distinct trigones and intermediate

Table 4. Characters of gynoecia in *L. discreta*, *L. pectinella* and *L. utriculata*

Characters	<i>L. discreta</i>	<i>L. pectinella</i>	<i>L. utriculata</i>
Perianth keels	Strongly 5-keeled	Weakly 3-4-keeled	Weakly 3-keeled
Keels above	Smooth	Crenulate with 2-3 teeth	Smooth
Beak	Trumpet-shaped, 3-4(-6) cells long	Cylindrical, 8-10 cells long	Cylindrical, 7-8 cells long
Lobule of female bract	not dimorphic	not dimorphic	dimorphic

thickenings, and the perianth with a long beak (Mizutani, 1970). However, the latter species is distinguished from *L. utriculata* by its large and reniform underleaves and the toothed perianth keels. *Lejeunea discreta* may also be confused with *L. utriculata* but the former differs in the more narrowly rounded leaf apex, the strongly 5-keeled perianth (keels lacking or weak in *L. utriculata*) with keels extending to 2/3 the length of the perianth. Furthermore, the perianth of *L. discreta* is 3-4 (-6) cells long and trumpet-shaped beak (straight and 7-8 cells long in *L. utriculata*). These three species are closely related to each other (Mizutani, 1970) and sterile material may be misidentified. They are readily separated by the characters of the gynoecia (Table 4).

*Lejeunea utriculata* varies in the size of the underleaves, in the apex of leaf lobes, in the recurvature of free margin of the leaf lobules, and in the size and shape of female bracts and bracteoles. The type material has smaller underleaves than in other collections. Some of the epiphyllous as well as corticolous plants have larger underleaves. The typical *L. utriculata* has broadly rounded leaf lobe, however, narrowly rounded leaf lobe is also found on the same stem in the collection from Borneo (*G.E. Lee 1851*). Some of the branch leaves or young shoots have narrowly rounded leaf lobe. In the type specimen, the size of the female bracts and bracteoles are considerably larger than other specimens examined. Furthermore, one of two female bracts has a distinct sinus (with a hyaline papilla) on the lobule, resulting in dimorphic lobules. This character seems to be constantly present throughout the range of the species (Java, Borneo). In an abundantly fertile specimen from Java ten gynoecia were examined and it was found that the sinus on one of the female bract lobules was constant throughout. This character may therefore be used to distinguish this species from closely related Malaysian *Lejeunea* such as *L. fleischeri* and *L. pectinella*. The occurrence, and possible taxonomic value, of this character in other species needs further study.

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