

Notes on the taxonomy and distribution of *Acanthocoleus yoshinaganus* and *Lejeunea papilionacea* (Hepaticae, Lejeuneaceae)

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Received 13 November 2000, accepted 8 December 2000

Zhu, R.-L. & Grolle, R. 2001: Notes on the taxonomy and distribution of *Acanthocoleus yoshinaganus* and *Lejeunea papilionacea* (Hepaticae, Lejeuneaceae). — *Ann. Bot. Fennici* 38: 329–336.

Acanthocoleus yoshinaganus (S. Hatt.) Kruijt, previously known from Japan and Korea, is reported here as a new generic record for the Chinese bryoflora. Both lejeuneoid and pycnolejeuneoid gynoecial innovations occur in *A. yoshinaganus*. The SE Asian *Lejeunea herzogii* Mizut. is synonymized with *L. papilionacea* Steph., which was known from Africa (Cameroun, Comores, Ghana, Madagascar, and Sierra Leone). Detailed descriptions, illustrations, taxonomic notes, and distribution of *A. yoshinaganus* and *L. papilionacea* are provided.

Key words: *Acanthocoleus yoshinaganus*, Hepaticae, *Lejeunea herzogii*, *L. papilionacea*, Lejeuneaceae, taxonomy

Acanthocoleus yoshinaganus (S. Hatt.) Kruijt is the only representative of *Acanthocoleus* R.M. Schust. in East Asia. Liu *et al.* (1993) listed it as *Dicranolejeunea yoshinagana* (S. Hatt.) Mizut. in “Checklist of plants of five provinces and one city in Eastern China” (in Chinese). However, according to D.-K. Li (pers. comm.), Liu *et al.*’s record was based on his uncertain label data on his collection from Fujian Province. Two years ago the voucher specimen (Fujian Province,

Wuyishan Nature Reserve, on tree trunks, associated with mosses, 1200 m, D.-K. Li 13307, SHM) was sent to the first author of the present paper for confirmation. It actually belongs to *Lopholejeunea* sp. rather than to *Dicranolejeunea yoshinagana*. During our studies on Chinese Lejeuneaceae, we have seen specimens of true *Acanthocoleus yoshinaganus* from China.

Lejeunea herzogii Mizut., an epiphyllous liverwort from Borneo (Mizutani 1972), New Guin-

ea (Grolle & Piippo 1984), Papua New Guinea (Pócs *et al.* 1995), Philippines (Mizutani 1978), and Sri Lanka (Onraedt 1981), is readily recognized by the compressed perianth with 2-winged, auriculate lateral keels. Examination of type material of the African *Lejeunea papilionacea* Steph. revealed that it produces similar perianths. All features characteristic of *L. herzogii* are in good accordance with those of *L. papilionacea*. The names should be considered synonyms.

***Acanthocoleus yoshinaganus* (S. Hatt.) Kruijt (Fig. 1)**

Bryophyt. Biblioth. 36: 105. 1988. — *Lopholejeunea subfusca* var. *yoshinagana* S. Hatt., Bot. Mag. (Tokyo) 58: 38. 1944. — *Lopholejeunea yoshinagana* (S. Hatt.) S. Hatt., J. Hattori Bot. Lab. 8: 33. 1952. — *Dicranolejeunea yoshinagana* (S. Hatt.) Mizut., J. Hattori Bot. Lab. 24: 174. 1961. — Type: Japan. Kanagawa Pref. "Prov. Sagami", Miho-mura (nisitanzawa), saxicola, 5.X.1938 Hattori 3118 (holotype TNS-2182!, isotype NICH).

ILLUSTRATIONS: Mizutani 1961: 176 (fig. XII: 1–13, as *Dicranolejeunea yoshinagana*); Choe 1980: 557 (fig. 268, as *D. yoshinagana*); Mizutani 1980: 239 (fig. 2, as *D. yoshinagana*); Kruijt 1988: 106 (fig. 15).

Plants brown in dry condition, 10–35 mm long. Shoots 1.4–2.2 mm wide, irregularly and scarcely branched, branching of *Lejeunea*-type, rarely of *Frullania*-type, leaf sequence of lateral branch lejeuneoid. Stem 160–220 µm in diameter, transverse section consisting of 9–14 cortical cells and 18–25 medullary cells, cortical cells ± rectangular, 32–60 × 22–36 µm, walls thickened, trigones small, medullary cells isodiametric to rectangular, 12–30 × 11–29 µm, walls thickened, trigones small. Ventral merophytes of stem (2–)3–4 cells wide. Rhizoids few, tufted, often brown, at base of underleaves, rhizoid disc absent. Leaves imbricate, diverging from stem at an angle of 45–60°. Leaf lobes ovate, 0.7–1.0 mm long, 0.5–1.0 mm wide, usually somewhat falcate, apex rounded, obtuse or acute, margin entire, rarely slightly dentate near apex, dorsal margin strongly arched. Leaf cells thin to thickened, trigones small to large, triangular, intermediate thickenings usually frequent, 1 per cell wall. Marginal cells of leaf lobe subquadrate, 18–30 × 12–22 µm, median cells isodia-

metric, 24–40 × 18–30 µm, basal cells similar to median ones in shape, 32–54 × 30–38 µm, dorsal cuticle smooth. Ocelli and vitta absent. Oil bodies homogeneous (Mizutani 1961). Leaf lobules ovate, usually inflated, ca. 1/3 as long as leaf lobes, free lateral margin slightly incurved, apex obliquely truncate, free margin with 2 blunt teeth, first tooth 2 cells long, 1 cell wide at base, hyaline papilla on inner surface of base of first tooth, second tooth unicellular, sometimes indistinct, keel arched, smooth. Stylus not seen. Underleaves distant to contiguous, subtransversely or sometimes sinuately inserted, suborbicular, 0.28–0.40(–0.54) mm long, 0.30–0.45(–0.56) mm wide, usually slightly wider than long, 3–4 times as wide as stem, entire. Androecia not seen. Gynoecia usually on main shoots, with 1–2 athecal innovations, leaf sequence of innovation pycnolejeuneoid, rarely lejeuneoid, bract lobe ovate-oblong, 0.9–1.1 mm long, 0.6–0.7 mm wide, apex usually acute, ventral margin entire, dorsal one usually slightly dentate near apex, bract lobule strongly reduced, narrowly oblong, ca. 0.24 × 0.07 mm, composed of 12–20 cells, with 1 tooth (1–2 cells long), keel slightly arched, smooth, bracteole broadly spatulate, ca. 0.85 mm long, 0.74 mm wide, entire. Perianth emergent, obovate, 0.84–1.0 mm long, 0.6–0.85 mm wide, with 3–4 ± ciliate keels (2 lateral and 1–2 ventral), lateral keel usually winged, ventral ones low, cilia 2–6 cells long, beak 3–5 cells long. Capsule spherical, ca. 0.48 mm in diameter. Elaters linear, ca. 16 µm wide, with a single light brown spiral band of thickenings. Spores isodiametric or irregularly oblong in shape, 40–120 × 24–44 µm, surface densely minutely papillose, rosettes not seen. Asexual reproductive organs not seen.

According to Thiers (1985), Kruijt (1988), and Gradstein (1994), the gynoecial innovation of *Acanthocoleus* and *Dicranolejeunea* is pycnolejeuneoid, except for *A. javanicus* (Steph.) Kruijt, which has a lejeuneoid one. The gynoecial innovation of *A. yoshinaganus* has been described or illustrated as pycnolejeuneoid (Mizutani 1961, 1980), Thiers (1985), Kruijt (1988), and Gradstein (1994). In the Chinese material of this species, however, both pycnolejeuneoid and lejeuneoid gynoecial innovations were found, even on the same plant (Fig. 1). Also in the

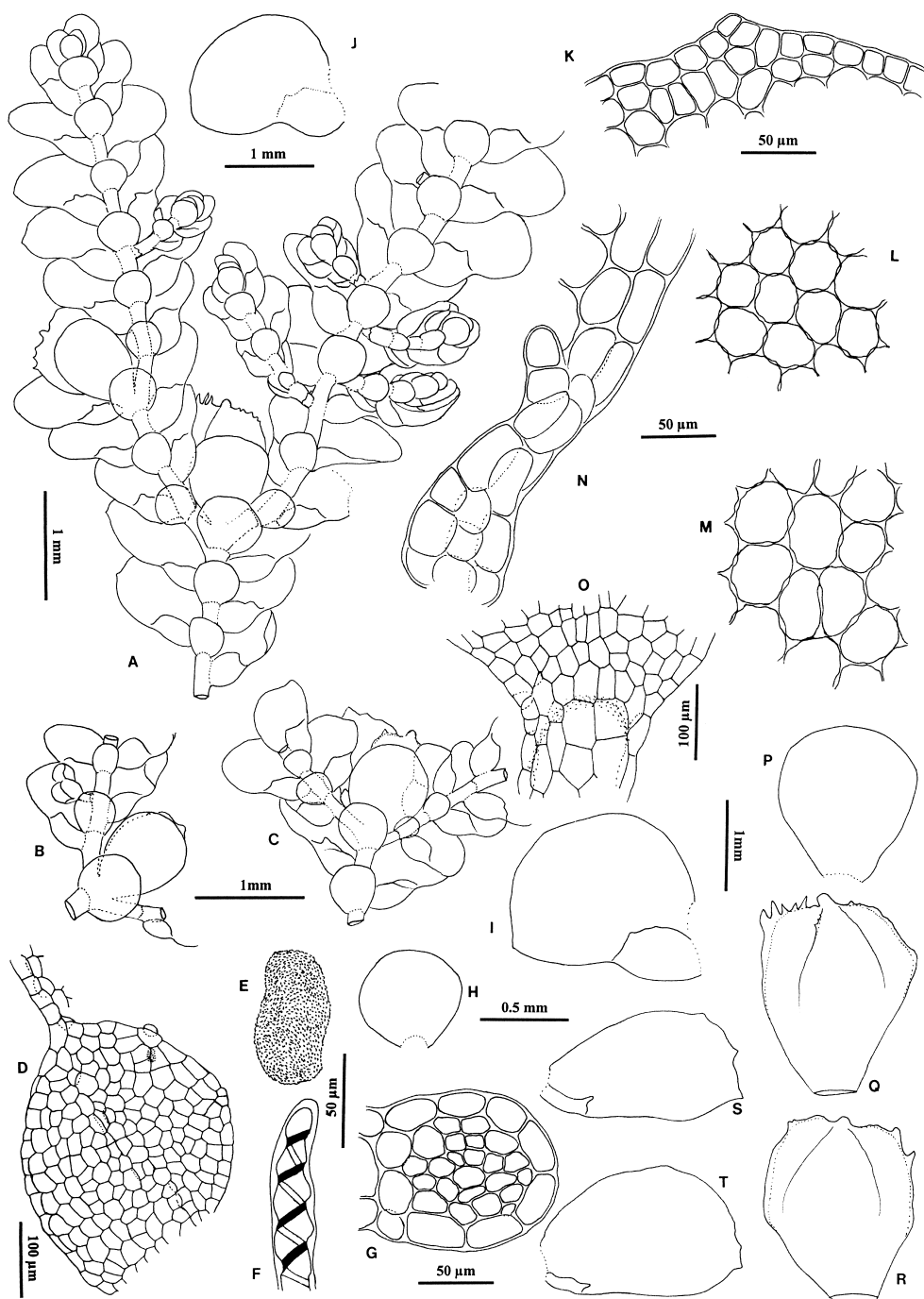


Fig. 1. *Acanthocoleus yoshinaganus* (S. Hatt.) Kruijt (from Zheng 917, HSNU). — **A**: Portion of plant showing pycnolejeuneoid gynoecial innovations, ventral view. — **B** and **C**: Portions of plants showing lejeuneoid gynoecial innovations, ventral view. — **D**: Leaf lobule. — **E**: Spore. — **F**: Portion of elater. — **G**: Transverse section of stem. — **H**: Underleaf. — **I** and **J**: Leaves (**I** ventral view, **J** dorsal view). — **K**: Apex of leaf lobe. — **L**: Median cells of leaf lobe. — **M**: Basal cells of leaf lobe. — **N**: Female bract lobule. — **O**: underleaf base and portion of stem showing insertion of underleaf on stem, ventral view. — **P**: Female bracteole. — **Q** and **R**: Perianths, ventral view.

Japanese material (*Kitagawa 15462*) lejeuneoid gynoecial innovations occasionally occur. The frequency of lejeuneoid gynoecial innovations is, however, rather low. We counted 80 gynoecial innovations in the Chinese material, only five of which were lejeuneoid. Moreover, lejeuneoid gynoecial innovations occur only when the gynoecium bears two innovations: one lejeuneoid and one pycnolejeuneoid or two, both pycnolejeuneoid (Fig. 1C).

Leaf sequence of gynoecial innovations has considerable importance for the taxonomy of the Lejeuneaceae at various ranks. It proved to be useful for delimitation of species e.g. in *Cheilolejeunea* (Spruce) Schiffn., of subgenera in *Archilejeunea* (Spruce) Schiffn. and of many genera of the Lejeuneoideae and Ptychanthoideae. More or less instability of the type of gynoecial innovation, however, also occurs in some species. Different gynoecial innovations on the same plant were reported by Thiers (1985) for *Fulfordianthus evansii* (Fulford) Gradst. and *Tuzi-beanthus chinensis* (Steph.) Mizut. The observation in the former species may have been erroneous, however (B. M. Thiers in pers. comm. to Gradstein 1994: 7). In any case *Acanthocoleus yoshinaganus* is an example with both pycnolejeuneoid and lejeuneoid gynoecial innovations on the same plant.

Mizutani (1961) indicated that the holotype of *Lopholejeunea subfusca* var. *yoshinagana* S. Hatt. was deposited in TI. Mizutani (1980) and Kruijt (1988) failed to indicate the holotype's herbarium in their monographic work. The holotype is in fact in TNS.

Acanthocoleus yoshinaganus is rather similar to several species of *Lopholejeunea* (Spruce) Schiffn. (e.g., *L. subfusca* Nees, *L. gradsteinii* Udar *et al.*, and *L. javanica* Steph.) in (1) lejeuneoid branching type of vegetative branches, (2) entire leaves, underleaves, and female bracteoles, (3) isodiametric leaf cells with triangular trigones, and (4) homogeneous oil bodies. The latter species, however, are distinguished from the former by (1) absence of athecal gynoecial innovations, (2) presence of darkish-brownish secondary pigmentation of cell walls, (3) single lobular tooth, and (4) hypostatic male bracts.

Seven species were recognized in Kruijt's

(1988) monograph of *Acanthocoleus*. Afterwards Gradstein (1992) added one more neotropical species, *A. trigonus* (Nees & Mont.) Gradst., and one new variety from tropical America (*A. aberrans* var. *laevis* Gradst.; Gradstein 1994). Therefore *Acanthocoleus* now comprises nine taxa (Table 1).

REPRESENTATIVE SPECIMENS EXAMINED: **China.** Anhui, Shexian, Qingliangfeng, *Zheng 917* (HSNU-013745). **Japan.** Pref. Miyazaki, Mt. Mukabaki, 1952 *Amakawa s. n.* (Hattori, Hepat. Jap. Ser. 8, 1956); Pref. Mie, Tachimado-dani, Shimowake, Kiho-cho, Minamimuro-gun, 200–400 m, 1976 *Kitagawa 15462* (HSNU).

HABITAT: On moist rocks and soils at elevations of 200–900 m.

DISTRIBUTION: As 2: China (Anhui), Japan, and Korea (Hattori *et al.* 1962, Hong 1998, and Yamada & Choe 1997 as *Dicranolejeunea yoshinagana*). Mizutani (1980) and Kruijt (1988) did not cite any material from Korea, and the present authors also failed to receive any Korean material for further study from several herbaria where it might be kept.

Lejeunea papilionacea Steph. (Fig. 2)

Hedwigia 31: XVII (+ p. 169 “*Hygrolejeunea*”). 1892. — *Hygrolejeunea papilionacea* (Steph.) Steph., Sp. Hepat. 5: 525. 1914. — *Cardiolejeunea papilionacea* (Steph.) R.M. Schust., Hepat. Anthocer. N. Amer. 4: 1026. 1980. — Type: Cameroon. Etome, 330 m, *Dusen 502 p. p.* (holotype G-11813, isotypes JE!, BM).

Prionolejeunea exarmata Steph., Sp. Hepat. 5: 201. 1914. — Type: Cameroon. Zenker (holotype G-17859!).

Prionolejeunea aberrans Steph., Sp. Hepat. 6: 387. 1923. — Type: Madagascar. Hildebrandt (holotype G!).

Lejeunea herzogii Mizut., J. Hattori Bot. Lab. 30: 180. 1967, *syn. nov.* — *Lejeunea pterota* (Herzog) Mizut., J. Hattori Bot. Lab. 29: 167. 1966. (*hom. illeg., non Lejeunea pterota* (Taylor) Gottsche *et al.* 1845). — *Cheilolejeunea pterota* Herzog, Mitt. Inst. Allg. Bot. Hamburg 7: 210. 1931. — Type: Indonesia. West-Borneo. Am Sungei Obat, um 100 m, 30.I.1925 *Winkler 3301a p. p.* (syntype HBG!, isosyntype JE!).

Lejeunea diversitexta (Steph.) Mizut., J. Hattori Bot. Lab. 35: 408. 1972. (*non Lejeunea diversitexta* Hampe & Gottsche 1853). — *Hygrolejeunea diversitexta* Steph., Sp. Hepat. 5: 559. 1914. — Type: Papua New Guinea. Moroka, Distr. Moresby, 1300 m, 1893 *Loria s. n.* (holotype G!).

ILLUSTRATIONS: Stephani 1892: 169 (tab. XI, fig. 8–

11); Herzog 1931: 209 (fig. b, as *Cheilolejeunea pterota* Herzog); Jones 1972: 41 (fig. 8g–k), 43 (fig. 9b and c); Mizutani 1972: 409 (fig. V, as *Lejeunea diversitexta* (Steph.) Mizut.).

Autoicous. Plants pale brown in dry condition, 4–12 mm long. Shoots 0.58–1.2(–1.4) mm wide, densely irregularly branched, branching of *Lejeunea* type, leaf sequence of lateral branches lejeuneoid. Stem 55–90 µm in diameter, transverse section consisting of 7(–8) cortical cells and 9–11 medullary cells, cortical cells quadrate to rectangular, 20–34 × 9–25 µm, medullary cells ± subisodiametric, 8–18 × 8–14 µm. Ventral merophytes of stem 2 cells wide. Rhizoids numerous, at base of underleaves, tufted, usually hyaline, rhizoid disc absent. Leaves imbricate, sometimes contiguous, diverging from stem at an angle of 45–80°. Leaf lobes oblong-rectangular, rarely ovate, usually somewhat or not falcate, 0.40–0.70 mm long, 0.30–0.45 mm wide, apex rounded or rounded-truncate, flat, margin entire or slightly crenulate, dorsal margin ± slightly arched. Leaf

cells thin-walled to moderately thickened, trigones small to large, intermediate thickenings usually frequent. Marginal cells of leaf lobe quadrate to rectangular, 10–20(–30) × 8–18 µm, median cells ± isodiametric, 24–36 × 18–32 µm, basal cells isodiametric to rectangular, 32–48 × 20–38 µm, dorsal cuticle smooth to slightly finely punctate. Vitta and ocelli absent. Oil bodies not seen. Leaf lobules triangular-subquadrate, strongly inflated, 1/6–1/5 as long as leaf lobes (usually strongly reduced), lateral free margin incurved, bordered by 3–5(–6) subquadrate to rectangular cells, apex obliquely truncate, usually not constricted, with a unicellular apical tooth towards stem apex, keel almost straight to arched, smooth, hyaline papilla oblong, ca. 16–20 × 8–12 µm, situated at proximal side of apical tooth. Underleaves remote, usually slightly longer than wide, 1.5–2.5 times as wide as stem, bilobed to 1/2–2/3 underleaf length, sinus U- or V-shaped, lobes narrowly triangular, acute at apex, 6–7 cells long, 4–6 cells wide at base, margin entire or

Table 1. Taxa and distribution of *Acanthocoleus*.

Taxa	Distribution	Sources
<i>A. aberrans</i> (Lindenb. & Gottsche) Kruijt var. <i>aberrans</i>	Costa Rica, Dominica, French Guiana, Guatemala, Jamaica, Mexico	Gradstein (1994)
<i>A. aberrans</i> var. <i>laevis</i> Gradst.	Widely distributed in tropical America and Africa	Kruijt (1988), Gradstein (1994)
<i>A. chrysophyllus</i> (Lehm.) Kruijt	Cameroon, Kenya, Nigeria, South Africa, Rwanda, Tanzania, Uganda, Zambia, Zimbabwe	Wigginton & Grolle (1996)
<i>A. gilvus</i> (Gottsche) Kruijt	Bhutan, India, Nepal, Sri Lanka	Long & Grolle (1990), Onraedt (1985), Kruijt (1988)
<i>A. javanicus</i> (Steph.) Kruijt	Indonesia (Java, Sumatra, West Irian), Papua New Guinea	Mizutani (1980), Kruijt (1988)
<i>A. juddii</i> Kruijt	Cuba, Haiti, Mexico	Gradstein (1994)
<i>A. madagascariensis</i> (Steph.) Kruijt	Burundi, Comores, Guinea, Madagascar, Mauritius, Réunion, Rwanda, Sierra Leone, South Africa, Tanzania, Zimbabwe	Grolle (1995), Wigginton & Grolle (1996)
<i>A. trigonus</i> (Nees & Mont.) Gradst.	Argentina, Bolivia, Brazil, Peru	Gradstein (1994)
<i>A. yoshinaganus</i> (S. Hatt.) Kruijt	China, Japan, Korea	Kruijt (1988), present study

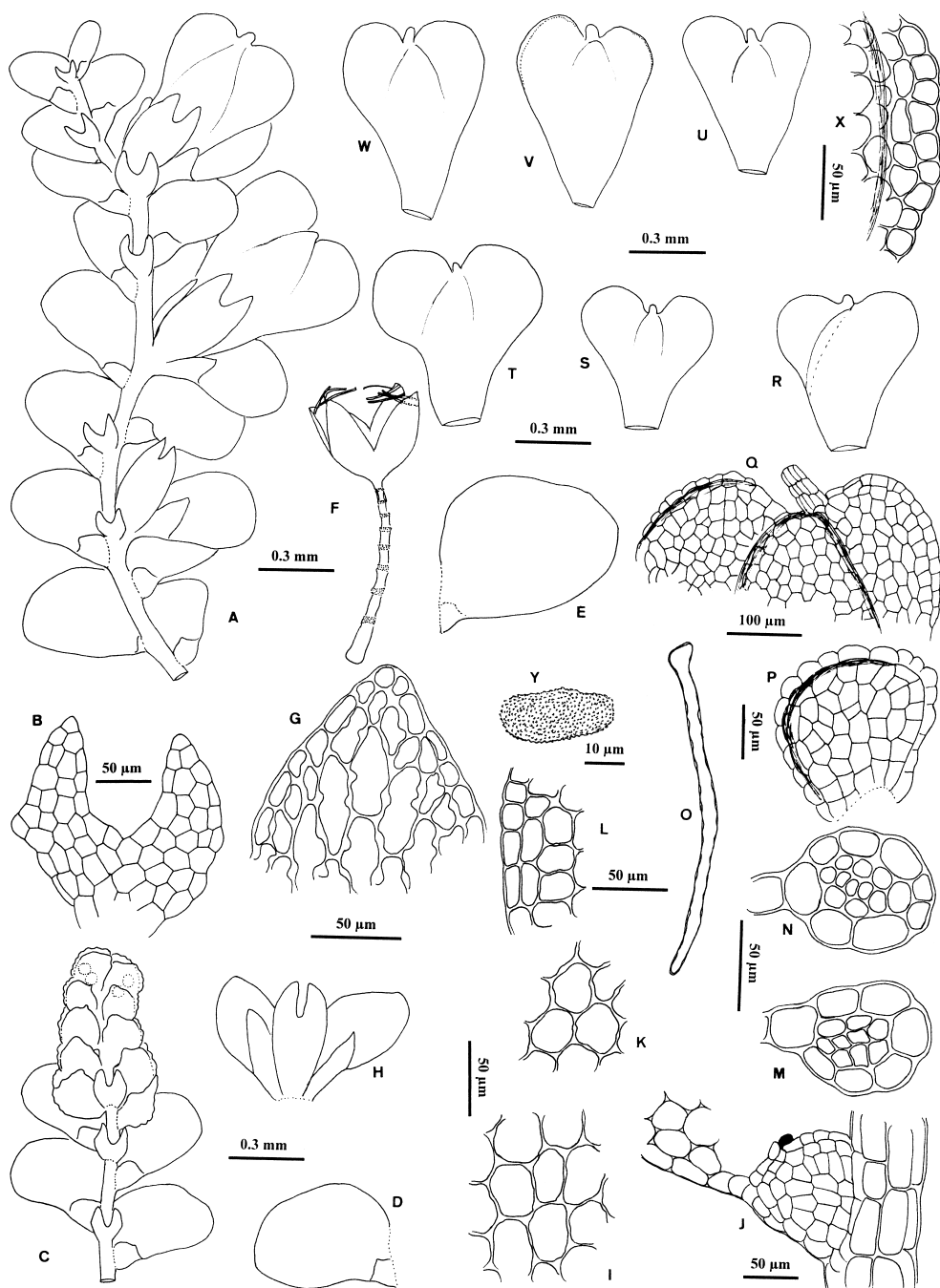


Fig. 2. *Lejeunea papilionacea* Steph. (R–T from *Iwatsuki 5626a*, NICH, the others from isotype). — **A**: Portion of plant, ventral view. — **B**: Underleaf. — **C**: Androecium, ventral view. — **D** and **E**: Leaves (**D** ventral view, **E** dorsal view). — **F**: Sporophyte showing articulate seta. — **G**: Outer layer of capsule valve. — **H**: Female bracts and bracteole, ventral view. — **I**: Basal cells of leaf lobe. — **J**: Leaf lobule and portion of stem, showing free lateral margin of leaf lobule and a hyaline papilla. — **K**: Median cells of leaf lobe. — **L**: Marginal cells of leaf lobe. — **M** and **N**: Transverse sections of stem. — **O**: Elater. — **P**: Male bract, ventral view. — **Q**: Apex of perianth, ventral view. — **R–W**: Perianths, ventral view. — **X**: Well developed wing of perianth keel. — **Y**: Spore.

slightly crenulate, outer lateral margin usually with a blunt tooth, insertion transverse, base never cordate. Androecia usually on elongate branches or on main shoots, terminal, bracts 2–15 pairs, hypostatic, 0.22–0.30 mm long, 0.13–0.25 mm wide, apex rounded, bract lobule almost as large as bract lobe, keel rounded, usually with a distinct wing formed of one row of projecting, hyaline cells towards apex, antheridia 2 per bract, 70–90 μ m in diameter, bracteoles 1(–2), borne only at base of androecium. Gynoecia on short or long branches, with one lejeuneoid innovation, innovation usually again bearing an innovation, bracts obovate or oblong-ovate, 0.35–0.62 mm long, 0.24–0.40 mm wide, margin entire, apex rounded, bract lobule oblong or lingulate, 1/4–4/5 as long as bract lobe, keel 1/3–2/3 as long as bract lobule, apex obtuse or acute, bracteole oblong-ovate, 1/5–1/3(–1/2) as long as perianth, 0.24–0.40 mm long, 0.15–0.27 mm wide, bilobed to 1/3–2/3 its length at apex, margin entire or slightly crenulate, lobes narrowly triangular or lanceolate, apex acute, sinus acute. Perianth emergent, obcordate, 0.60–0.90 mm long, 0.50–0.85 mm wide at apex, compressed dorsiventrally above, with 2 auriculate lateral keels and 1–2 ventral keels, lateral keels sometimes with a wing 1–4 cells wide, beak 1–3 cells long. Capsule spherical, valves ca. 0.34 mm long, 0.16 mm wide at middle, capsule wall smooth on surface, consisting of 2 layers of cells, wall cells with trigones and irregular sinuate thickenings, seta articulate, ca. 0.7 mm long, with 8 articulations, 12 outer cells surrounding 4 inner cells in transverse section. Elaters linear, 160–220 μ m long, 6–12 μ m wide, wall slightly sinuately thickened. Spores irregular in shape, 24–50 \times 13–23 μ m, surface minutely papillose, rosettes absent. Asexual reproductive organs not seen.

Lejeunea papilionacea is readily separated from other members of *Lejeunea* by the obcordate perianth with 2-winged, auriculate lateral keels, pale brown color of dry plants, large leaf cells usually with large trigones, androecia usually on elongate branches, and male bracts usually with a winged keel. As commented by Jones (1972), *Lejeunea dipteroarpa* E.W. Jones, known from Cameroon and Nigeria (Jones 1972,

1985), is closely related to, and easily confused with, *L. papilionacea* when sterile. The former, however, differs in its triangular-obcordate perianth with 2 winged oblong (not auriculate) keels. The Asiatic and Oceanic *Lejeunea anisophylla* Mont. and the African and American *L. caespitosa* Lindenb. are also readily confused with *L. papilionacea*, but differ in having strongly inflated perianths without winged lateral keels.

Lejeunea papilionacea shows distinct variations in several features. The ventral margin of the leaf lobe is usually straight or almost so in the type of *Lejeunea papilionacea* (Fig. 2E), but sometimes sinuate in some material from SE Asia. In the African collections the beak of the perianth is usually 3 cells long (Fig. 2Q), but 1–2 cells long in some SE Asian material. The wing at the lateral keel of the perianth is sometimes well developed (up to 4 cells wide), as shown in Fig. 2X, but sometimes almost absent. Female bracteoles are rather small, usually only 1/5–1/3 as long as perianths. Mizutani's (1972) description (0.6–0.8 mm long, 0.35–0.5 mm wide) may be erroneous.

REPRESENTATIVE SPECIMENS EXAMINED: **Guinea.** Distr. Macenta, montes Ziam, prope collem Sérédou, 900 m, 1962 *Lisowski s. n.* (JE-H2294). **Indonesia.** West-Borneo, Am Sungei Malang, 1925 *Winkler 3290 p. p.* (syn-type of *Cheilolejeunea pterota* Herzog, HBG). **Malaysia** (Borneo). E. Kutei, peak of Balkpapan, Tegumbit, few m, 1952 *Meijer B1254/c* (JE ex L); ultrabasic area (serpentine) by a stream below mining camp, Mt. Silam, SW of Lahad Datu, East Coast, 220–250 m, 1963 *Iwatsuki 5626a* (NICH-255626a). **New Guinea.** Distr. Moresby, in montosis Mo-roka, 1300 m, 1893 *Loria s. n.* (Hb. Levier no. 122/a, JE ex FI). **Réunion.** Plaine des Cafres, sur rameaux de *Sambucus* sp. introduit, 1570 m, 1974 *Jimalac 74.R.8386* (JE). **Sierra Leone.** Bambawo, Kam-bui Hill, 1966 *Hannington 440* (JE).

HABITAT: Epiphyllous, very rarely epiphytic. The known altitudinal range of the species is from several to 1930 m.

DISTRIBUTION: Afr 2: Cameroon, Ghana (Jones & Harrington 1983), Guinea, Sierra Leone; Afr 3: Comores (Pócs 1993 as *Cardiolejeunea papilionacea*), Réunion, Madagascar (Jones & Harrington 1983); As 3: Sri Lanka (Onraedt 1981 as *Lejeunea herzogii*); As 4: Borneo, Papua New Guinea, Philippines (Mizutani 1978 as *L. herzogii*).

Acknowledgements

We are grateful to M. Higuchi (TNS), P. Geissler (G), D.-K. Li and Z.-K. Bai (SHM), M. Mizutani (NICH), J. Snider and Kwok Leung Yip (CINC), and D. G. Long (E) for the loans of specimens including some types. We also thank D. G. Long for a linguistic check of the manuscript, and S. R. Gradstein for providing valuable suggestions about *Acanthocoleus*.

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