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Taxonomy and distribution of *Lejeunea exilis* (Lejeuneaceae, Hepaticae)

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Drepanolejeunea subacuta (Horik.) H.A. Mill. *et al*. and *Lejeunea lancistipula* (Steph.) H.A. Mill. *et al*., previously known only from Taiwan and New Guinea, respectively, are proposed as synonyms of *Lejeunea exilis* (Reinw. *et al*.) Grolle. *Lejeunea exilis* is a highly variable species and its diagnostic characteristics include (1) dimorphic underleaves (bilobed and subulate-ovate), (2) very small size of plants, (3) eplicate perianths always strongly emergent, (4) highly variable shape of leaves, (5) acute to apiculate leaf apex of the leaf in well developed plants, and (6) asexual reproduction usually by means of ribbon-like marginal regenerants. *Lejeunea exilis* is reported for the first time for China. A detailed description and illustrations of *Lejeunea exilis* are provided. The occurrence of ribbon-like marginal regenerants in the Lejeuneaceae is discussed.

Key words: distribution, Hepaticae, *Lejeunea exilis*, Lejeuneaceae, taxonomy

Introduction

Microlejeunea subacuta Horik. was first described by Horikawa (1934), based on an epiphyllous collection from Taiwan. Its systematic position has been debated. Miller *et al*. (1963) moved it to *Drepanolejeunea* due to its deeply bilobed underleaves and somewhat acute apex of leaf lobe, while Zhu and So (2001) thought that it could be very closely related to *Lejeunea punctiformis* Taylor. *Microlejeunea lancistipula* Steph. from New Guinea, described by Stephani (1915), was known only from the type (Grolle & Piippo 1984). Miller *et al*. (1967) transferred it to *Lejeunea*. *Lejeunea exilis* (Reinw. *et al*.) Grolle was known from Borneo, Carolines, Japan, Java, New Guinea, Philippines, and Seram (cf. Grolle 1979, Mizutani 1986, Pócs *et al*. 1994, Furuki 1998). Our studies show that *L. exilis* is a very variable taxon, and that *Microlejeunea subacuta* is its weak expression. *Microlejeunea lancistipula* is also conspecific with *Lejeunea exilis*. The present paper aims to present the total range, a thorough description, and detailed illustrations of *Lejeunea exilis*.

Lejeunea exilis (Reinw. *et al.*) Grolle (Figs. 1 and 2)

J. Hattori Bot. Lab. 46: 353. 1979. — *Jungermannia exilis* Reinw. *et al.*, Nova Acta Caes. Leop. Nat. Cur. 12: 227. 1825. — *Jungermannia cucullata* var. β *exilis* (Reinw. *et al.*) Nees, Enumer. Pl. Crypt. Jav. Hepat.: 57. 1830. — *Lejeunea cucullata* var. β *exilis* (Reinw. *et al.*) Gottsche *et al.*, Syn. Hepat.: 390. 1845. — *Eulejeunea cucullata* var. β *exilis* (Reinw. *et al.*) Schiffn., Consp. Hepat. Arch. Ind.: 254. 1898. — *Microlejeunea exilis* (Reinw. *et al.*) Bischl. *et al.*, Nova Hedwigia 3: 452. 1962. — Type: Indonesia. Java (holotype STR; isotypes PC, S, W!).

Microlejeunea lancistipula Steph., Sp. Hepat. 5: 830. 1915. — *Lejeunea lancistipula* (Steph.) H.A. Mill. *et al.*, Nova Hedwigia 14: 66. 1967; *syn. nov.* — Type: New Guinea. Stephanson, Aug. 1883 *Kärnbach 1023* (holotype G-14864!).

Microlejeunea subacuta Horik., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 2: 275. 1934. — *Drepanolejeunea subacuta* (Horik.) H.A. Mill. *et al.*, Nova Hedwigia 4: 560. 1963 "1962"; *syn. nov.* — Type: China. Taiwan "Formosa". Taito, Mt. Chipon, epiphyllous, 30.XII.1932 *Y. Horikawa 10478* (holotype HIRO!).

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 Renauld & Cardot, Rev. Bryol. 18: 57. 1891]. — *Microlejeunea abnormis* (Herzog) Inoue & H.A.Mill., Bull. Nat. Sci. Mus. Tokyo 11: 9. 1968. — *Lejeunea byssiformis* Grolle & Mizut. *in* Mizutani, J. Hattori Bot. Lab. 43: 131. 1978 "1977". — Type: Indonesia. Java, Pangerango prope Tjibodas, 1 330 m, *Schiffner 2676 p.p.* (holotype JE!).

Dioicous. Plants yellowish, pale yellowish or pale brown in dry condition. Stem to 11 mm long, (26–)40–70(–90) μm in diameter, (0.20–)0.26–0.60(–0.80) mm wide with leaves, scarcely irregularly branched, branching of *Lejeunea* type, leaf sequence of lateral branches lejeuneoid, transverse section of stem with 7 cortical cells and 3–6 medullary cells, cortical cells quadrate to rectangular, 12–25(–38) × 12–22(–28) μm, medullary cells ± subisodiametric, 7.5–17 × 7.5–14 μm. Ventral merophytes of stem usually 2 cells wide. Rhizoids at base of underleaves, numerous, tufted, usually hyaline, rhizoid disc absent. Leaves remote, sometimes contiguous, sometimes slightly caducous, diverging from stem at an angle of 30–50°. Leaf lobes ovate, ovate-lanceolate or irregularly triangular-ovate, usually somewhat or not falcate, highly variable in size, (0.15–)0.20–0.60 mm long, (0.09–)0.12–0.20(–0.30) mm wide, apex acute, short-acuminate, rounded, obtuse, rounded-obtuse, or obtuse-acute, flat, rarely incurved (when short-acuminate), margin entire or slightly crenulate, dorsal margin ± arched. Leaf lobules subquadrate to ovate-oblong, slightly to strongly inflated, 2/5–3/4 as long as the leaf lobes (sometimes strongly reduced), lateral free margin incurved, bordered by 4 subquadrate to short rectangular cells, apex obliquely truncate, usually not constricted, with a unicellular apical tooth towards stem apex, keel arched, smooth, hyaline papilla oblong, 10–13 × 8–10 μm, situated at proximal side of apical tooth. Leaf cells thin-walled, trigones small or indistinct, intermediate thickenings usually infrequent. Marginal cells of leaf lobe quadrate to rectangular, 12–25 × 10–23 μm, median cells ± isodiametric, 14–32 × 10–25 μm, basal cells isodiametric to rectangular, 16–35 × 11–25 μm, dorsal cuticle smooth, occasionally slightly finely punctate. Vitta and ocelli absent. Oil bodies not seen. Underleaves remote, dimorphic; bilobed underleaves longer than wide, rarely as wide as long, nearly as wide as stem, bilobed to ca. 1/2–2/3 underleaf length, sinus U- or V-shaped, lobes triangular to narrowly triangular, acute at apex, 3–4 cells long, 2–3 cells wide at base, margin nearly entire, insertion transverse, base never cordate; unlobed underleaves lanceolate to subulate-ovate, 4–5 cells long, 2–3 cells wide at middle, insertion transverse. Androecia usually on very short lateral branches, terminal, bracts 2–3 pairs, hypostatic, bract lobule almost as large as bract lobe, keel strongly arched, lacking a wing, antheridia 2 per bract, bracteole 1, borne at base of androecium. Gynoecia usually on lateral branches, with one athecal lejeuneoid innovation, innovation short or usually elongate, sterile, bracts oblong-ovate, 0.30–0.46 mm long, 0.12–0.18 mm wide, margin entire, apex subacute, acute or short-acuminate, bract lobule oblong or lingulate, 1/2–4/5 as long as bract lobe, keels 2/3–4/5 as long as bract lobules, apex obtuse or acute, bracteole oblong-ovate, 1/3–1/2 as long as perianth, 0.33–0.40 mm long, 0.13–0.17 mm wide, bilobed to 1/5–1/4 its length at apex, entire at margin, lobes triangular, apex acute, sinus acute. Perianths strongly emergent, cylindrical, 0.72–0.92 mm long, 0.34–0.45 mm wide at middle, slightly compressed dorsiventrally, with 2 indistinct lateral keels, beak 2–3 cells long. Capsules spherical, 0.25–0.30 mm in diameter, dehiscing from

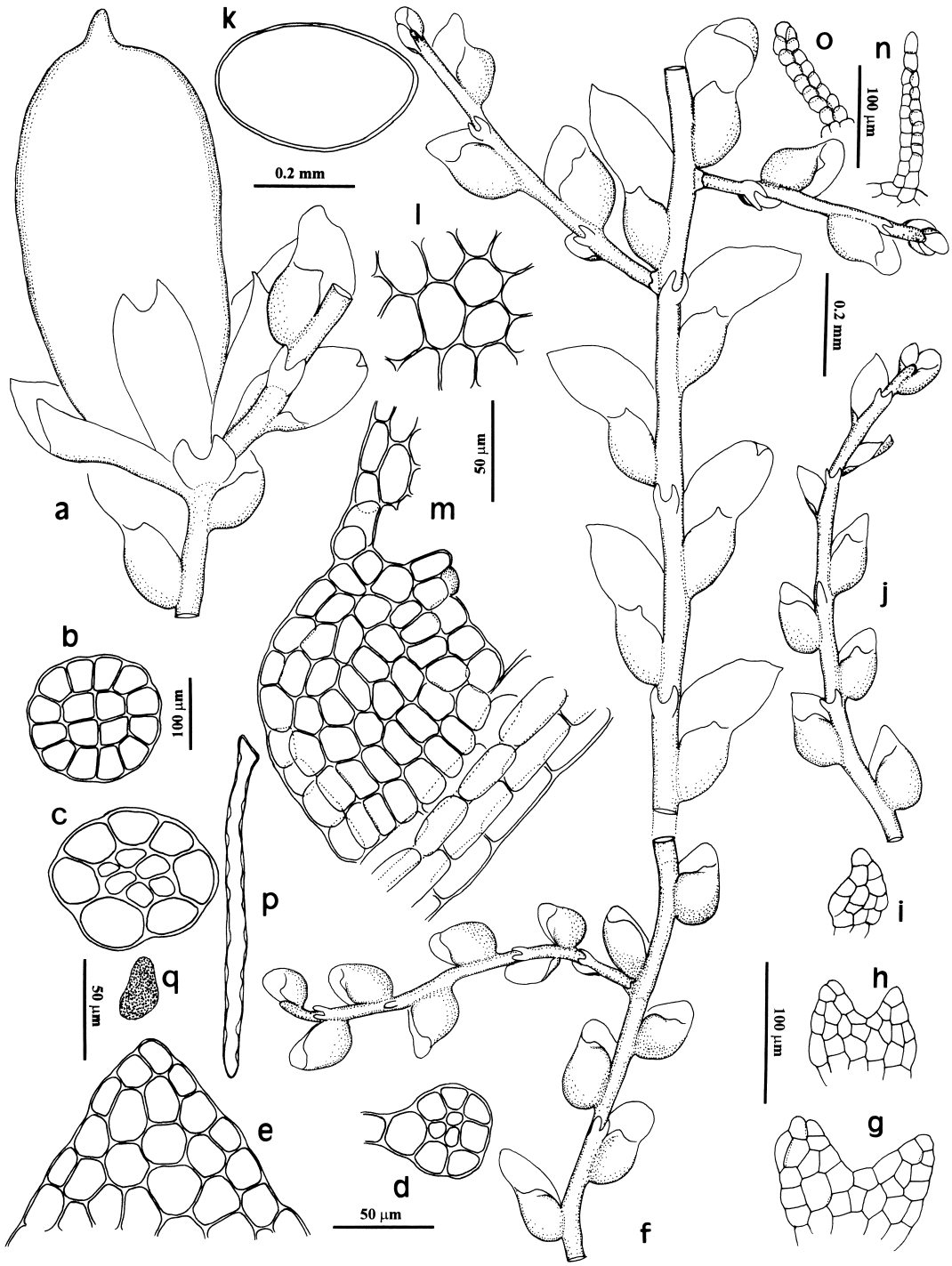

Fig. 1. *Lejeunea exilis* (**d** and **m** from *Streimann 5383*; **f** and **j** from *Zanten 741476*; **n** and **o** from *Verdoorn 2031*; the others from *Schuster 67-6556*). — **a**: Gynoecium, ventral view. — **b**: Transverse section of seta. — **c** and **d**: Transverse section of stem. — **e**: Apex of leaf lobe. — **f**: Portion of shoot showing dimorphic leaves on the same stem, ventral view. — **g–i**: Underleaves. — **j**: Portion of shoot showing dimorphic underleaves on the same stem. — **k**: Transverse section of perianth at middle. — **l**: Median cells of leaf lobe. — **m**: Leaf lobule and its insertion to stem, ventral view. — **n** and **o**: Marginal regenerant. — **p**: Elater. — **q**: Spore.

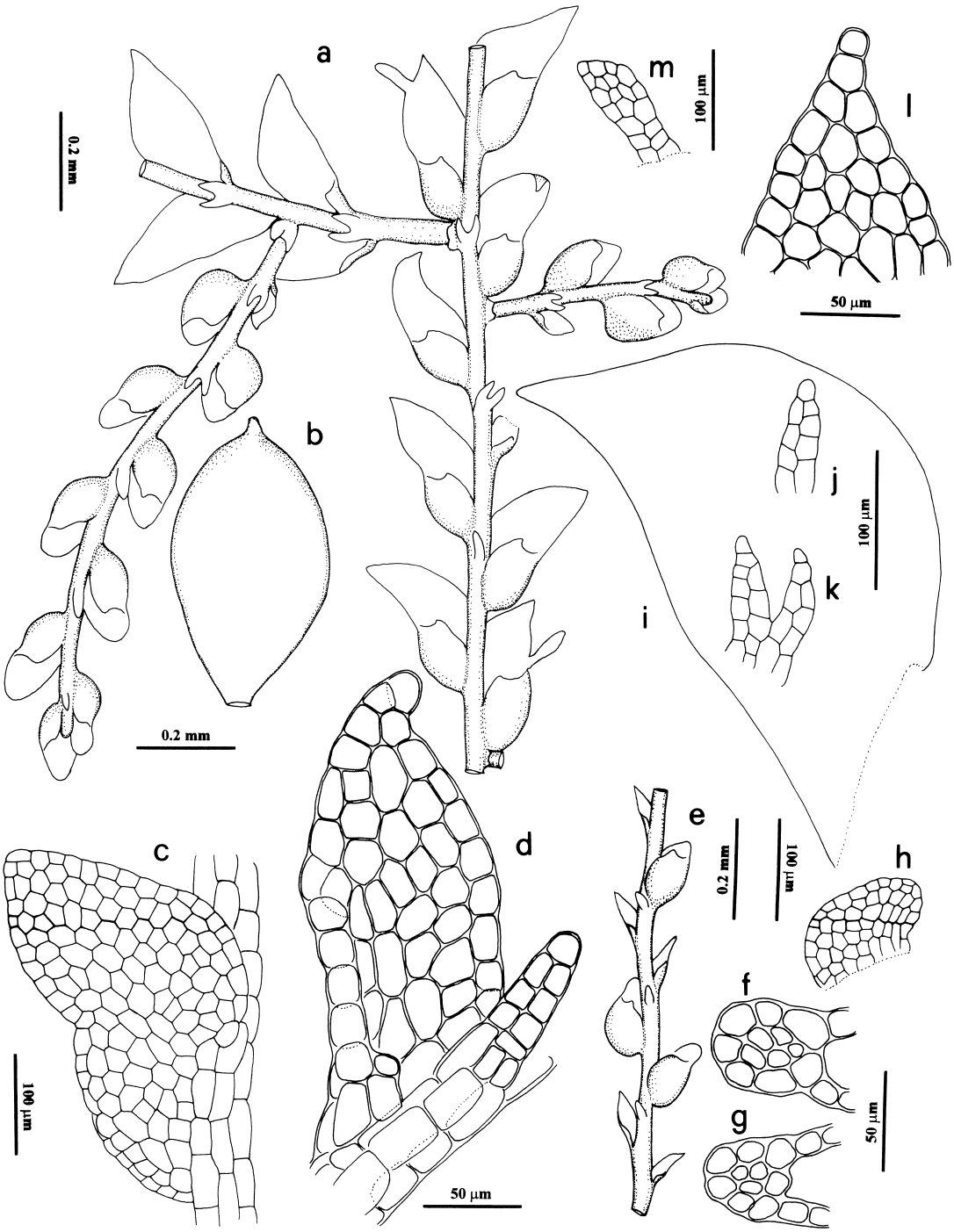

Fig. 2. *Lejeunea exilis* (**c** from *Schuster 67-6556*; **e** and **h** from *Li 04768a*; the others from *Horikawa 15216 p.p. (a)*). — **a**: Portion of shoot, showing two leaves with marginal, ribbon-like regenerants, ventral view. — **b**: Perianth, ventral view. — **c**: Leaf and portion of stem, dorsal view. — **d**: leaf, underleaf, and portion of stem, ventral view. — **e**: Portion of shoot, ventral view. — **f** and **g**: Transverse section of stem. — **h** and **i**: Leaves, dorsal view. — **j** and **k**: Underleaves. — **l**: Leaf apex. — **m**: Marginal regenerant.

apex down into 4 valves when mature, valves non-recurving, capsule wall smooth on surface, consisting of 2 layers of cells, seta articulate, 12 outer cells surrounding 4 inner cells in transverse section. Elaters linear, marginal, 180–250 μm long, 6–10 μm wide, wall ± sinuately thickened. Spores brown in dry condition, irregularly oblong in shape, 25–50 × 13–20 μm, minutely papillose on surface, without rosettes. Asexual reproduction by means of regenerants at the margin of leaf lobe, regenerants ribbon-like, unistratose, mostly 2 cells wide at middle.

ILLUSTRATIONS: Herzog (1941, 1948) as *Byssolejeunea abnormis*; Bischler *et al*. (1962) as *Microlejeunea exilis*; Furuki (1998); Pócs *et al*. (1995).

Lejeunea exilis exhibits pronounced variation in several features. Underleaves are dimorphic, viz. bifid and unlobed. In some collections, subulate-ovate, unlobed underleaves are sometimes developed, especially on weak shoots. Leaves are rather variable in shape and size even on the same plant (Fig. 1f). In most material from New Guinea, leaves are usually ovate with an obtuse to obtuse-acute apex (Fig. 1e and f). Well-developed leaves, however, are long triangular-ovate, usually larger, and their apices are usually short-acuminate (Fig. 2i) in the collections from Japan. The underleaf shape and size are also variable. Bilobed underleaves are usually as wide as long in several collections from New Guinea (Fig. 1g and h), but in most material, they are longer than wide (Fig. 2k). Leaf lobules on weak shoots are strongly inflated, but sometimes strongly reduced (Figs. 1j and 2e). Ribbon-like regenerants ("gemmae") are sometimes developed at leaf margins, but their size varies greatly (Figs. 1n, 1o and 2m).

Although *Lejeunea exilis* is very variable, it can be recognized by (1) small, slender plants, (2) the common presence of subulate-ovate underleaves, especially on weak shoots, (3) small, remote underleaves, (4) eplicate perianths always strongly emergent, (5) acute to apiculate leaf apices of the leaf in well developed plants, and (6) asexual reproduction usually by means of ribbon-like, marginal regenerants. It is closely related to *Lejeunea cocoes* Mitt., because they share several features: small size of plants, few rows of cortical cells of stem, dioicous sexuality, and occurrence of ribbon-like regenerants at leaf margins. The latter species, however, is distinguished by absence of dimorphic underleaves, perianths with five keels, and rounded to rotund-obtuse apices of leaves. Weak shoots of *Lejeunea exilis* are easily confused with *Lejeunea* subg. *Microlejeunea* such as *L. punctiformis*, which differ in presence of basal ocelli in leaf lobes, a distinct wing at female bract keel, smaller leaf cells, a small and keeled perianth, and absence of ribbon-like regenerants at leaf margins.

The type material of *Microlejeunea subacuta* represents weak shoots of *Lejeunea exilis*. The leaves of *Microlejeunea lancistipula* in the type specimen are rather variable in shape and size. Unlobed, subulate underleaves are sometimes present on weak shoots. However, there are no taxonomically meaningful differences among *Microlejeunea lancistipula*, *M. subacuta*, and *Lejeunea exilis*. *Microlejeunea lancistipula* and *M. subacuta* are here proposed as taxonomic synonyms of *Lejeunea exilis*.

The systematic position of *Lejeunea exilis* is controversial. Pócs *et al*. (1995) hesitatingly treated it under *Lejeunea* owing to the presence of "linear gemmae" at leaf margins. They stated "It may be that after examination of more material, *L. exilis* will also prove to be a member of *Stenolejeunea*". As observed by Pócs, ribbon-like marginal regenerants (linear gemmae) at leaf margins are sometimes developed in some material of *L. exilis* from Japan and Papua New Guinea as in *Stenolejeunea* (Figs. 1n, 1o, 2a and 2m). Such regenerants, however, are also developed in some species of typical *Lejeunea*, including *L. cocoes*, *L. infestans* (Steph.) Mizut., *L. subigiensis* (Steph.) Steph., and *Lejeunea boryana* Mont. (type of *Crossotolejeunea* (Spruce) Schiffn.) (Reiner-Drehwald & Goda 2000, Zhu & So 2001), and other genera of Lejeuneaceae such as *Pictolejeunea*. Therefore, the presence or absence of ribbon-like marginal regenerants is not a crucial difference between *Lejeunea* and *Stenolejeunea*, and *Lejeunea exilis* is a true member of *Lejeunea*.

REPRESENTATIVE SPECIMENS EXAMINED. **Australia**. Norfolk Island, Norfolk Island National Park, 160 m, on tree

fern (*Cyathea*) stem, 160 m, 1994 *H. Streimann 53837* (JE, HSNU). Queensland, Start of Bartle Frere walking track, Bellenden Ker Range, 17 km W of Malanda, 730 m, on fallen twigs, *J. A. Curnow 4061* (EGR). **China**. Hainan, Diaoluoshan, Xinanlinchang, 930 m, on tree trunks, 1977 *D.-K. Li 04768-a* (HSNU). **Indonesia**. Java, 1420–1650 m, 1930 *F. Verdoorn 2031* (U); Sumatra Occid.: Ad decliv. occid. montis ignivomi Merapi, in regione infra silvam primaevam, ad arbores, 1400–1520 m, 1894 *V. Schiffner 3909 p.p.* (U, in a packet of *Lejeunea subacuta*). **Papua New Guinea**. Central District, around Woitape, 1500 m, epiphytic, *H. Inoue 30346* (EGR); ibid., Mt. Wilhelm, 11 600 ft., 1967 *R. M. Schuster 67-6556* (JE); Morobe District, epiphyllous in montane rainforest on Mt. Kaindi near Wau, 2000–2300 m, *B. O. & H. van Zanten 741476* (EGR), on rotten wood, 2200–2350 m, 1981 *S. R. Gradstein 3906* (U). **Japan**. Iwo Islands, Minami-Iwo Island, the summit area, epiphyllous, 1936 *Y. Horikawa 15216 p.p. (a)*; *15194 p.p. (b)* (HIRO).

HABITAT: On various substrates at 400 (Seram, Mizutani 1986) — 4050 m (New Guinea, cf. Grolle & Piippo 1984).

DISTRIBUTION: As 2: Japan, China (Hainan (new), Taiwan); As 4: Philippines, Malaysia, Indonesia, Papua New Guinea; Oc: Caroline Is; Austr 1: Queensland; Austr 2 (new): Norfolk Island. Presence in As 3 is expected. The record of *Drepanolejeunea subacuta* from Anhui of China (Piippo 1990, Liu *et al*. 1993, He 1997) was based on erroneous determination.

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