



A review of Lejeuneaceae (Marchantiophyta) in the Russian Far East

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ABSTRACT

The Russian Far East is on the northern edge of the Lejeuneaceae distribution in Pacific Asia and the majority of taxa known here are restricted to the southernmost flank of the region. Eleven species are confirmed for the Russian Far East: 1 – *Acrolejeunea*, 1 – *Cheilolejeunea*, 4 – *Lejeunea*, 4 – *Cololejeunea* and 1 – *Microlejeunea*. All of them are reviewed in the present account, with data on distribution within the Russian Far East, morphological descriptions and figures based on materials collected in the Far East. In addition, identification keys to genera and species are provided.

Keywords: Lejeuneaceae, *Acrolejeunea*, *Cheilolejeunea*, *Cololejeunea*, *Lejeunea*, *Microlejeunea*, the Russian Far East, East Asia, North-East Asia, taxonomy, distribution

РЕЗЮМЕ

Бакалин В.А. Обзор семейства Лежеунеасеае на российском Дальнем Востоке. Представители Лежеунеасеае обычны только в южной части российского Дальнего Востока, севернее встречается единственный вид – *Lejeunea alaskana*. Всего на Дальнем Востоке выявлено 11 видов: 1 – *Acrolejeunea*, 1 – *Cheilolejeunea*, 4 – *Lejeunea*, 4 – *Cololejeunea* и 1 – *Microlejeunea*. Все они обсуждаются в рамках настоящей статьи, описывающей их распространение, экологию и морфологию по образцам с российского Дальнего Востока. Приводятся иллюстрации всех известных в регионе таксонов и ключи для определения родов и видов семейства.

Ключевые слова: Lejeuneaceae, *Acrolejeunea*, *Cheilolejeunea*, *Cololejeunea*, *Lejeunea*, *Microlejeunea*, российский Дальний Восток, Восточная Азия, таксономия, распространение

Lejeuneaceae are the largest family among the hepatics accounting 74 accepted genera (Zhu et al. 2019) and ca 1300 recognized species. Lejeuneaceae are characterized by terminal-lateral branching (*Lejeunea* type, rarer *Frullania* type, innovations usually of the *Radula* type, the presence of a single archegonium in each gynoeceum (Frey & Stech 2009, Gradstein 2013). The leaves consist of three parts: a large dorsal, incubously oriented and inserted lobe, a ventral smaller lobe, called lobule, that is connected to the lobe, and a stylus that is commonly vestigial or absent. As commented by Frey & Stech (2009: 96), “more than 75% of the liverworts of tropical lowland forests and almost all epiphylls belong to Lejeuneaceae”. The extraordinary speciation in this group is probably connected with the Cretaceous and post-Cretaceous explosion of Angiosperms that provides new ecological niches in tropical forests (Wilson et al. 2007). The highest diversity (still poorly understood) occurs in humid tropical forests, with modern centers of speciation in Southeastern Asia and Northern South America (Frey & Stech 2009).

Although the amphi-Pacific Asian region houses a high number of Lejeuneaceae taxa (more than 500 species), the Russian Far East has a very limited number of recorded species, and all of them are restricted to the southern flank of the area (with one exception for *Lejeunea alaskana*). Due to their peculiar appearance among other Russian Far East liverworts, confusion with other families seems to be hardly

possible, with the exception of *Nipponolejeunea* (Jubulaceae) which, however, has ciliate leaf margins – a feature very rare in Lejeuneaceae worldwide. Lejeuneaceae did not attract special attention of hepaticologists in the Russian Far East. The early record of *Acrolejeunea sandvicensis* (under *Brachiolejeunea*) was comprehensively discussed by Zerov (1965), some others were only listed (e.g. Horikawa 1940). Well known in Russia, Schljakov’s manual (1982) for the hepatics of the northern USSR only included *Lejeunea cavifolia* (Ehrh.) Lindb. (a taxon absent in the Russian Far East as well as in the whole of the western amphi-Pacific). Within the last decades several new records of this family were published. Gambaryan (1992) listed four taxa of the family, with *L. cavifolia* incorrectly identified (specimens belong to *L. japonica*). Potemkin (2003) recorded *Cololejeunea japonica* for the first time in Russia. Bakalin (2007a, 2009) reviewed *Cololejeunea* in Russian Asia (later one more taxon was found in the Russian Far East) and *Cheilolejeunea* in the Russian Far East. Bakalin & Borovichev (2014) and Bakalin et al. (2012) recorded *Lejeunea neelgherriana* and *L. alaskana* as new for Russia. Some taxa were earlier reported without descriptions for the Russian Far East (e.g. *Microlejeunea punctiformis*, under *Lejeunea ulicina* (Taylor) Gottsche, Lindenb. & Nees in Bakalin 2007b). Moreover, many new distributional data were collected within last several years. The latter circumstance, as well as the difficulties in identification of ‘lejeuneaceous’ materials from

the Russian Far East in the absence of keys have initiated the present work. It is worth mentioning that the prominent paper describing Japanese Lejeuneaceae by Mizutani (1961) can be used to identify almost all Lejeuneaceae in the Russian Far East although it is difficult to use due to enormously high diversity of the family in Japan that makes the identification keys relatively difficult. The main goals of the present account were to provide: 1) new data on distribution and ecology of Lejeuneaceae in the Russian Far East, 2) identification keys to all taxa known in the Russian Far East and 3) morphological descriptions and figures based on available material from the Russian Far East. The present work continues the liverwort revisions for the Russian Far East (Bakalin 2016, 2018, 2019; Bakalin & Klimova 2019, Borovichev & Bakalin 2016, Borovichev et al. 2014, 2015, Mamontov et al. 2015, etc.) toward to the preparation of Liverwort flora of the Russian Far East that we plan to publish in the next couple of years.

MATERIAL AND METHODS

The background for the present work was the liverwort specimens collected in the Russian Far East by the author within the past 15 years. The results on taxonomic diversity were preliminary (as it was possible at that time) summarized in distribution dot maps by Bakalin (2010).

In total over 300 specimens of Lejeuneaceae were collected. Aside aforementioned material the herbarium specimens collected by S.K. Gambaryan and previously housed in VLA (now transferred to VBG I) were taken into account. All distribution data were re-checked in the course of the preparation of the present account and the distribution provided for each species is based on studied materials with rare exception, where cited. The valuable vouchers (commonly one per locality studied) are cited at the end of the paper and are housed in VBG I. The general distribution of taxa were obtained from Bakalin (2007a, b, 2008, 2009), Choi (2013), Mizutani (1961, 1982, 1998), Schljakov (1982), So & Zhu (1996), Theirs (2018), Yamada & Iwatsuki (2006) and some other papers cited in the text.

TAXONOMIC TREATMENT

Important features used in identification (and taxonomy) of Lejeuneaceae known in the Russian Far East are the branching type (*Frullania* type [branch replacing the lobule] and *Lejeunea* type [branch just below leaf insertion]) and lobule teeth features, such as the recognition of the first and the second teeth, with their numeration starting at the junction of the lobule with the ventral margin of the lobe. Oil body characteristics are not so valuable for identification of taxa in comparison with, e.g. Solenostomataceae or Lophoziaaceae taxa known in the area treated. However, in some cases cited in the text and key oil bodies can offer additional insights to identify some taxa: the best feature to identify *Lejeunea japonica* are numerous and homogenous oil bodies, *Cheilolejeunea* is very easily identified by a few large oil bodies filling the cell lumen in the leaf lobe. Currently 5 genera with 11 species of Lejeuneaceae are known in the Russian Far East. The genera may be keyed as follow (used features are applied to the taxa known in the Russian Far East):

1. Plants brownish to rusty-brown, robust, with 15–20 longitudinal cell rows in the outer layer of the stem cross section,

branching predominantly of *Frullania* type (branches of *Lejeunea* type are rare), leaf lobule 3–5-toothed, underleaves undivided ***Acrolejeunea***

1. Plants pale green to bright green and whitish, rarely yellowish, never brownish or rusty-brown, with less than 6–8 longitudinal outer cell rows in the stem cross section, branching of *Lejeunea* type, leaf lobule 2-toothed, underleaves bilobed or absent **2**

2. Plants minute, underleaves absent, stylus (sometimes vestigial) regularly present although sometimes easily caducous ***Cololejeunea***

2. Plants minute to moderate in size, regular underleaves present, stylus absent or early and easily caducous **3**

3. Oil bodies (1–)2–4 per cell, brownish, nearly filling cell lumen, the second tooth of the leaf lobule far larger than the first one, leaves imbricate ***Cheilolejeunea***

3. Oil bodies numerous or 5–10 per cell (if fewer – never filling cell-lumen and leaves distant), the second tooth of the leaf lobule smaller than the first one or absent, leaves imbricate to distant **4**

4. Plants very small, less than 0.5 mm in width, leaves distant, lobule only slightly smaller than lobe ***Microlejeunea***

4. Plants larger, wider than 0.7 mm, leaves mostly imbricate, or at least contiguous, lobule far smaller than lobe (less 1/4 of the lobe size) ***Lejeunea***

Acrolejeunea (Spruce) Schiffn., Hepat. (Engl.-Prantl): 128, 1893 (= *Trocholejeunea* Schiffn. Ann. Bryol. 5: 160. 1932; *Brachiolejeunea* (Spruce) Schiffn. Hepat. (Engl.-Prantl): 128, 1893)

The genus includes 21 species and is distributed mostly pantropically, although spreading both southward and northward of the tropical zone. The only taxon known in the Russian Far East is *Acrolejeunea sandvicensis* and its localities are the northernmost for the genus worldwide. Before it was known in Russia as *Trocholejeunea sandvicensis* until Wang et al. (2014) transferred it to *Acrolejeunea* basing on results of molecular-genetic research. Wang et al. (2014: 36) circumscribed *Acrolejeunea* (including *Trocholejeunea*) as “possessing stems with a hyalodermis, entire-margined leaves, underleaves, bracts and bracteoles, leaf cells with cordate trigones and homogeneous oil bodies, androecia with epistatic bracts containing one antheridium, and pluriplicate perianths”. As discussed by Wang et al. (2016), the main features separating *Acrolejeunea sandvicensis* from most other species of the genus are the presence of gynoeical innovations of the *Frullania* type and a more massive seta built of 4–16 inner and 16–32 outer rows of cells. In addition, vegetative branches of the *Frullania* type are more common in *A. sandvicensis* than in most other members of the genus *Acrolejeunea*.

Acrolejeunea sandvicensis (Gottsche) Steph., Bot. Jahrb. Syst. 23 (1/2, 3): 312, 1896 (≡ *Phragmicoma sandvicensis* Gottsche, Ann. Sci. Nat. Bot. (sér. 4) 8: 344, 1857; ≡ *Trocholejeunea sandvicensis* (Gottsche) Mizut. Misc. Bryol. Lichenol. 2(12): 169, 1961)

Description¹. Plants merely rigid, brownish to rusty brown, rarely green in shady places, sometimes with discolored leaf margins in well-exposed sites, in loose pure patches or in the mixture with other hepatics (most frequently with *Frullania*) and mosses, 1.4–1.8 mm wide and 10–20(–40) mm long. Rhizoids sparse to numerous, in erect
¹ Here and below the descriptions, if otherwise not mentioned, are based on specimens from the Russian Far East and/or features observed in studied specimens.

to obliquely spreading fascicles, densely attaching plants to the substratum, including other bryophytes. Stem yellowish brownish, freely irregularly branched (branching of *Frullania* type, rarely with a few *Lejeunea* type branches); cross section of well-developed stems ca 300 µm in diameter, outer layer ca 18–20 cell rows, cells varying in size, smaller in dorsal side, where with thickened walls, 25–38 µm in diameter, ventrally larger, to 70 µm in diameter and with thinner walls, trigones small and concave, inner layer 7–8 cells high, cell walls become thicker dorsally, 17–38 µm in diameter. Leaves imbricate; lobe obliquely to subtransversely inserted, with dorsal margin sometimes recurved when dry, when flattened in the slide broadly ovate to rounded, with rounded apex, well developed leaves 1.0–1.2 × 0.9–1.0 mm; lobule concave (if to view from ventral side), semicircular to subquadrate, with outer side rounded, with 3–5 1–2-celled teeth along margin. Cells in lobe middle thin-walled, subisodiametric to oblong, 25–50 × 20–40 µm, trigones large with all sides convex or concave-convex-convex (cordate), intermediate thickenings common (in apical part of the leaf present in nearly all cells, downward ca. 20–30 % of cells have such kind of thickenings); oil bodies 15–30 and more per cell, small, ellipsoidal to fusiform, homogenous. Underleaves ca 300 × 500 µm, transversely elliptic, mostly appressed to the stem, with recurved margins (sometimes very loosely so). Autoicous. Androecia intercalary in the main axis, with 2–4 pairs of bracts. Perianth obovate, pluriplicate (with 8–12 plicae), well developed exerted for 1/3–1/2 of its length, 0.8–1.0 × 0.8–0.9 mm, with one *Frullania* type subfloral innovation. Figures 1; 2A; 3D. [Capsule wall 2 cells thick; elaters brown, 300–400 × 25 µm, with 1–2-spirals; spores green, irregularly elliptic, 65–85 × 50–70 µm, minutely papillose (Mizutani 1961)].

Comment. The plants are very characteristic in appearance and confusion seems to be hardly possible among regional taxa. The entire leaf lobes with rounded apices, small 3–5-toothed lobule and entire and wide underleaves are distinctive.

Ecology. Neutrophilous meso-xerophyte. The habitats of the species include open to partly shaded rocks, tree trunks, branches in evergreen to deciduous forests. Besides, Zhu & So (2001) reported its epiphyllous occurrence in southern China (Fujian, Guangdong, Yunnan, Xizang and Zhejiang). Within the Russian Far East this is obligate epilithic taxon growing over rocky (of basic to neutral reaction of aqueous extract) outcrops in full sun or open (rarely partly shaded) sites in low altitudes. Commonly occurs in pure mats or mixed with *Frullania taradakensis* Steph., *Porella vernicosa* Lindb.; in the northern extremities of the area associated with *Barbilophozia barbata* (Schmidel ex Schreb.) Loeske, *B. hatcheri* (A. Evans) Loeske and *Frullania appendiculata* Steph. Among our Lejeuneaceae this is the most xerophytic taxon.

Distribution. East Asia and Hawaii (Sun et al. 2018). In Japan from the North to the South, although absent in Hokkaido (Yamada & Iwatsuki 2006). Common in Korean Peninsula (Choi 2013). Already Herzog (1926) noted its wide spreading northward in East Asia to 38°N; the recent research ‘stretched’ its distribution as far as to 54°N in

boreal zone, where its occurrence possesses a relictal nature. Elevation reported for China ranges from 25 to 1920 m a.s.l. that probably depends on latitude (Zhu & So 2001). In the southern flank of the Russian Far East the species is distributed much more evenly across administrative sub-units than do other species of Lejeuneaceae due to its higher drought-tolerance of the taxon. Altitudinal diapason varies from ca 340 m a.s.l. in Amurskaya Province, the same for both localities at 49 and 54°N, with the latter locality being for the taxon the northernmost worldwide), the only locality in Khabarovsk Territory is in the Badzhal Mts. (600 m a.s.l.), that is from rocky outcrops of the large river valley. In Primorsky Territory it is known from low elevations to 600 m a.s.l. in southern part of the territory (not known in northern extremes). The species is not known in Sakhalin and Kurils.

Cheilolejeunea (Spruce) Steph., Bot. Gaz. 15 (11): 284, 1890

Cheilolejeunea is the genus of predominantly Pantropical distribution, although widely spreading northward to the subtropics in the Atlantic region (Azores), Tasmania and New Zealand, and to the temperate zone of East Asia and North America. The genus includes over one hundred extant species, is subdivided into eight sections based on molecular analysis (Ye et al. 2015), and includes strikingly different phenotypical groups such as *Cheilolejeunea* s. str. with relatively narrow and bilobed underleaves and the former genus *Leucolejeunea* A. Evans (= sect. *Leucolejeunea*) with larger, entire underleaves. The congeneric nature of these two entities was first shown by Ye & Zhu (2010) and resulted in difficulties to describe the main uniting features of the genus in morphological terms. A few oil bodies that are somewhat brownish in color and filling cell lumen are one basic character of the genus; another character, separating *Cheilolejeunea* from *Lejeunea* (with which confusion in our area seems to be readily possible), is the well-developed second tooth and the reduced first one (versus well-developed first tooth and usually reduced second tooth in *Lejeunea*). The reduction (= absence) of the first tooth is evident from the position of the hyaline papilla, which is distal to the well-developed tooth (= second tooth) in *Cheilolejeunea*, while being proximal to the well-developed tooth (= first tooth) in *Lejeunea*. Only *Cheilolejeunea obtusifolia* – the smallest taxon among East Asian representatives of the genus – is known in our area. *Cheilolejeunea khasiana* (Mitt.) N. Kitag. mentioned (but not treated) in Gambaryan (1992) is surely a mistake of unclear origin (cf. Bakalin 2009).

Cheilolejeunea obtusifolia (Steph.) S.Hatt., J. Hattori Bot. Lab. 18: 116, 1957 (≡ *Harpalejeunea obtusifolia* Steph., Sp. Hepat. 5: 265, 1913)

Description. Plants green to deep green, yellowish green and greenish yellowish, commonly brownish yellow in the herbarium, 400–600 µm wide and 5–15 mm long. Rhizoids virtually absent. Stem with *Lejeunea*-type branches and 1–2 *Radula*-type subfloral innovations that commonly soon become fertilized again; stem cross section ca 70 µm in diameter, with 6–7 rows of outer cells, 20–25 µm in diameter, inner cells in 6 rows, 7–12 µm in diameter, cell walls slightly thickened throughout. Leaves contiguous to imbric-

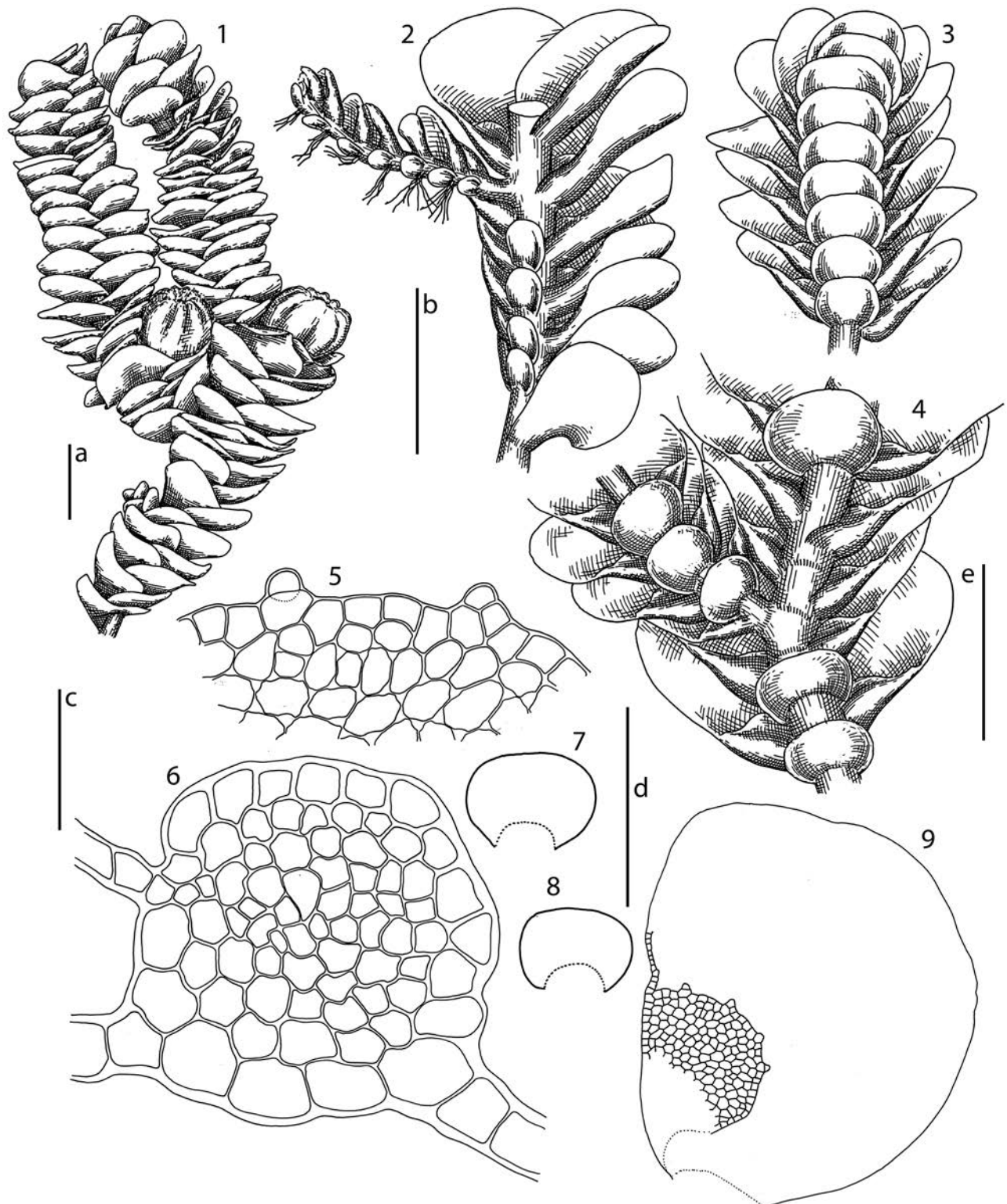


Figure 1 *Acrolejeunea sandvicensis* (Gottsche) Steph.: 1 – plant habit, dorsal view; 2 – shoot fragment, ventral view, with *Lejeunea* type branching; 3 – shoot fragment, ventral view; 4 – shoot fragment, ventral view, with *Frullania* type branching; 5 – leaf lobule apical part; 6 – stem cross section; 7, 8 – underleaves; 9 – leaf (all from P-68-21-11, VBGI). Scales: a – 1 mm, for 1; b – 1 mm, for 2–4; c – 100 μ m, for 5, 6; d – 1 mm, for 7, 8; e – 500 μ m, for 9

cate, lobes convex, obliquely oriented, with apex commonly curved to ventral side, when flattened in the slide 250–320 \times 200–250 μ m, obliquely ovate, with rounded apex, margin entire; lobule convex (if to view from ventral side), involute inward, nearly ovate, ca. 170 \times 150 μ m in well developed plants, the first tooth reduced to 1 cell, the second tooth prominent, 1(–2) cells wide and 1(–2) cells long, with end

cell long and curved to the keel, keel rounded. Cells in leaf lobe middle 12–20 \times 12–17 μ m, thin-walled, trigones moderate in size, slightly convex, intermediate thickenings rarely occurs in longer side of the cell; oil bodies 2–3 per cell, irregularly oblong, finely papillose, filling cell lumen. Underleaves regular, rounded, 120–150 μ m in diameter, 1.7–2.2 of stem width, sinus narrow, to 2/5 of underleaf length.



Figure 2 Plant habits: A – *Acrolejeunea sandvicensis* (Gottsche) Steph. (Kh-31-11-16, VBGJ); B – *Cheilolejeunea obtusifolia* (Prim-16-6-16, VBGJ); C – *Lejeunea alaskana* (R.M. Schust. et Steere) Inoue et Steere (Kh-17-38-16, VBGJ); D – *Lejeunea japonica* Mitt. (P-37-16-14, VBGJ); E – *Lejeunea neelgheriana* Gottsche (V-4-57-17, VBGJ); F – *Microlejeunea punctiformis* (Taylor) Steph. (V-2-18-16, VBGJ)

Autoicous. Androecia terminal or intercalary on leading axis or on short branches. Perianth rarely produced, distinctly 5-keeled (2 – ventral, 2 – lateral, 1 – dorsal), with keels shallowly crisate, exerted for $1/2-3/5$ of its length, not or shortly beaked at the mouth, ca. $500 \times 400 \mu\text{m}$, bracteole as large as bract, incised by U-shaped sinus descending to $1/5-1/4$ of the length, bracts with both lobes of similar size. Figures 2B; 3E; 4.

Comment. This species is the only representative of this genus in Russia. It resembles small *Lejeunea* from which it is distinguishable by well-developed second tooth in leaf lobule (as indicated by the hyaline papilla at the lobule apex being distal in position to the well-developed tooth) and a few in number oil bodies in leaf cells (observable in fresh material only).

Ecology. Acido- and basi-tolerant neutrophilous meso-xerophyte. Commonly it occupies open or semi-shaded rocky substrates of neutral reaction and (rarely) tree trunks; in Japan also reported from limestone and decaying wood (Mizutani 1982). Within the Russian Far East it commonly occurs in semi-shaded cliffs in coniferous (oro-hemiboreal) forest belt, as exclusion penetrates to stony fields (where in the crevices) in the mountains (1660 m a.s.l. in southernmost Primorsky Territory). Commonly forms pure patches. It worth noting, in the northern extreme of the area (Badzhal Mts. at 50°N), the species was found only over rock outcrops with scattered *Duschekia*, *Picea*, *Pinus pu-*

mila (Pallas) Regel and *Weigela suavis* (Kom.) L.H. Bailey intermingled with alpine tundra plots in steep slopes at the diapason between 1570 to 1640 m a.s.l., where once collected with pronouncedly arctomontane *Frullania subarctica* Vilnet, Borovich. et Bakalin. The species forming pure patches in the majority of other areas, although is commonly growing in Iturup Island as admixture to other hepatics like *Diplophyllum taxifolium* (Wahlenb.) Dumort., *Eremonotus myriocarpus* (Carrington) Lindb. et Kaal. ex Pearson, *Metzgeria lindbergii* Schiffn., *Plectocolea infusca* Mitt. s.str. Nearby, in Shikotan Island, this species forms pure patches, although once was collected in moist cliffs together with *Marsupella tubulosa* Steph. and more than once with *Preissia quadrata* (Scop.) Nees and *Plectocolea ovalifolia* (Amakawa) Bakalin et Vilnet.

Distribution. This species generally is characterized by a Japanese-Korean oro-temperate to oro-hemiboreal distribution, where known across both countries then becoming much rarer in southward extremes. The southernmost outpost of the species area (ca. 28°N) based on specimens from Zhejiang, China, was reported by So and Zhu (1996) that is. The cited authors (l.c.) also suggested occurrences of the species in other provinces of China lying northward of Zhejiang. This point of view looks highly probable, taking into account the distribution of the taxon in the Russian Far East mainland southern extreme, where the species is sparsely distributed although sometimes is locally abundant. The elevations across Japan (where from Hokkaido

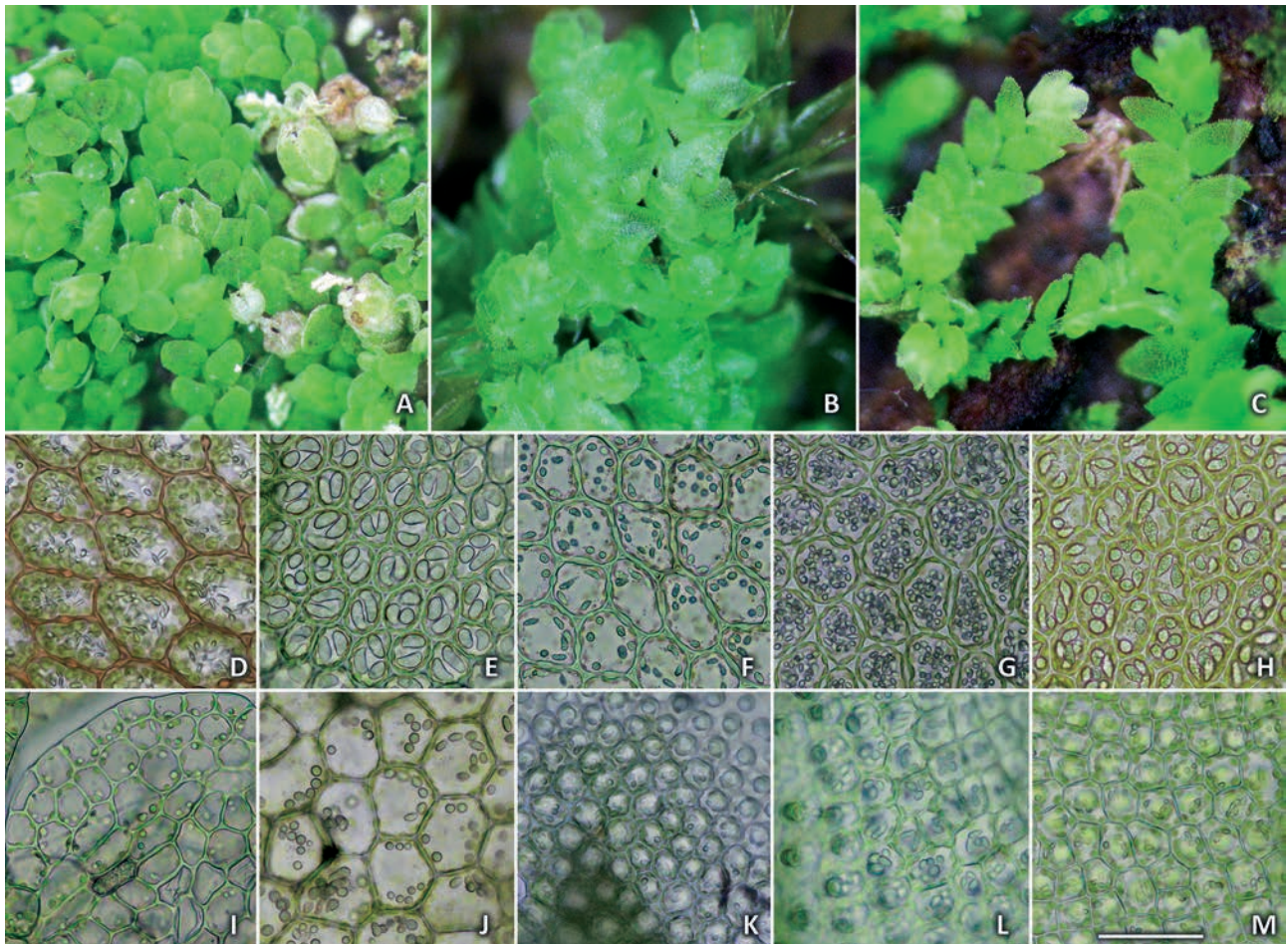


Figure 3 Plant habits: A – *Cololejeunea macounii* (Spruce) A. Evans (Prim-16-36-16, VBG1); B – *Cololejeunea ornata* A. Evans (P-38-5-16, VBG1); C – *Cololejeunea subkodamae* Mizut. (Prim-16-26-16, VBG1). Oil bodies: D – *Acrolejeunea sandvicensis* (Gottsche) Steph. (Kh-31-11-16, VBG1); E – *Cheilolejeunea obtusifolia* (Steph.) S.Hatt. (S-48-8-16, VBG1); F – *Lejeunea alaskana* (R.M. Schust. et Steere) Inoue et Steere (S-18-18-17, VBG1); G – *Lejeunea japonica* Mitt. (P-37-16-14, VBG1); H – *Lejeunea neelgherriana* Gottsche (EB-5-9-15, VBG1); I – *Microlejeunea punctiformis* (Taylor) Steph. (V-10-49-17, VBG1); J – *Lejeunea japonica* Mitt. (P-37-16-14, VBG1); K – *Cololejeunea japonica* (Schiffn.) Mizut. (J-1-19-13, VBG1); L – *Cololejeunea macounii* (Spruce) A. Evans (Prim-16-36-16, VBG1); M – *Cololejeunea ornata* A. Evans (P-38-5-16, VBG1); N – *Cololejeunea subkodamae* Mizut. (Kh-14-35-16, VBG1). Scale: 50 μ m, for F–M

to Kyushu) varies from 400 m a.s.l. in Hokkaido to over 1000 m a.s.l. in Shikoku and Kyushu, with the highest observed locality in Saitama Prefecture (Honshu) at 1700 m a.s.l. Within the Russian Far East *Cheilolejeunea obtusifolia* is known in Khabarovsk Territory, where in relatively high elevations (1570–1640 m a.s.l.), only in Badzhal Mts. Within Primorsky Territory it is distributed in its southern third, where elevation varies from 350 to 1660 m a.s.l. that corresponds to vegetation gradient from mixed Manchurian hemiboreal forest to stony fields above the subalpine belt. In Sakhalin Province known both from South Kurils (Shikotan, Iturup) and southern part of Sakhalin, throughout in lower altitudes (15–320 m a.s.l.), not passing the hemiboreal forest belt.

Lejeunea Lib., Ann. Gen. Sci. Phys. 6: 373, 1820

Description. Plants 0.7–1.3 mm wide, pale to bright green and yellowish, sometimes glossy, in loose mats, loosely attached to the substratum. Rhizoids a few, in short obliquely to erect spreading fascicles from underleaf bases. Stems freely regularly to irregularly pinnately branched, branching of *Lejeunea*-type, cross section with 6–10 outer and 12–35 inner cell rows, outer cells larger, ventral merophyte 2 cells

wide. Leaves contiguous to imbricate, lobe convex, slightly to strongly curved to ventral side, lobule nearly plane to involute inward, with two teeth, the first tooth larger than the second, slime papilla near proximal base of the first tooth (thus between the first and the second teeth). Cells in lobe middle with thin to somewhat thickened walls, intermediate thickenings regularly present (although sometimes a few), cuticle smooth (our taxa), oil bodies small and more than 5 per cell. Underleaves regular, bilobed (our taxa), lobes acute to obtuse, equal or nearly so. Autoicous (our taxa). Androecia intercalary to virtually terminal in leading axes or in lateral branches. Perianth on branches, with 1 *Radula*-type innovation, distinctly (4–)5-keeled, somewhat beaked.

One of the largest genera in Lejeuneaceae, counting for over 170 taxa and being most diverse in Central America, East Africa (including adjacent islands), East and Southeast Asia. In many areas the real diversity remains poorly understood (also due to occurrence of many undescribed taxa). Within our flora the genus may be distinguished by plants moderate in size (0.7–1.3 mm wide), ventral merophyte two cells wide, thin-walled leaf cells, regular and bilobed underleaves, the first tooth better developed than the second one

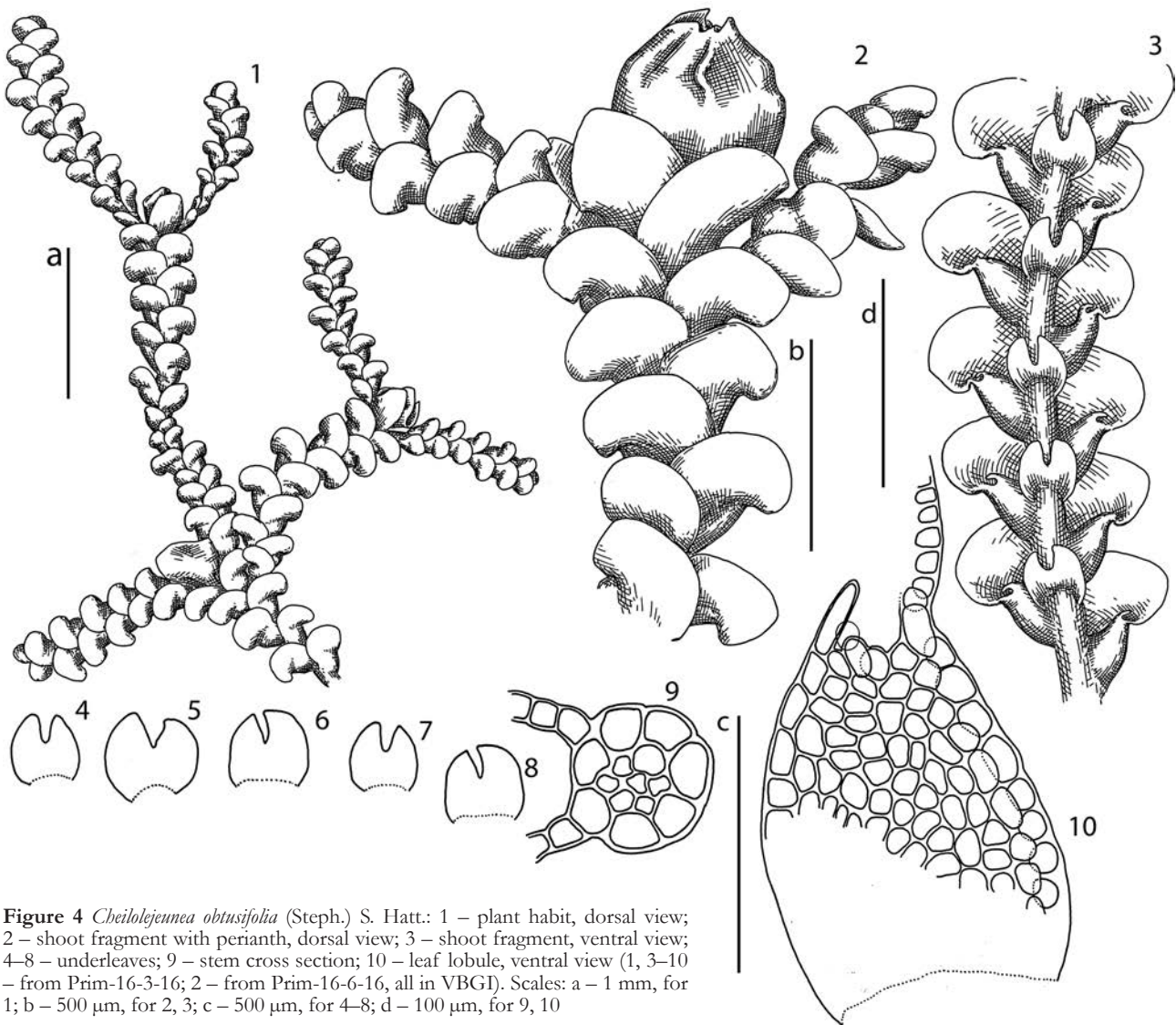


Figure 4 *Cheilolejeunea obtusifolia* (Steph.) S. Hatt.: 1 – plant habit, dorsal view; 2 – shoot fragment with perianth, dorsal view; 3 – shoot fragment, ventral view; 4–8 – underleaves; 9 – stem cross section; 10 – leaf lobule, ventral view (1, 3–10 – from Prim-16-3-16; 2 – from Prim-16-6-16, all in VBGI). Scales: a – 1 mm, for 1; b – 500 μm, for 2, 3; c – 500 μm, for 4–8; d – 100 μm, for 9, 10

(hence hyaline papilla at lobule apex proximal in position to the best-developed tooth), and oil bodies small and more than 5 per cell. Four taxa are known in the Russian Far East that may be keyed as follow:

- 1. Leaf lobes with apices acute to apiculate, plants calciphilous *Lejeunea neelgherriana*
- 1. Leaf lobes with rounded to obtuse apex, plants neutrophilous **2**
- 2. Leaf lobes strongly curved to ventral side, underleaves ca 0.5–0.7 of lobe in size, arctic-alpine *Lejeunea alaskana*
- 2. Leaf lobes convex to nearly plane, not or loosely curved to ventral side, underleaves less than 1/3 of lobe in size, temperate **3**
- 3. First tooth of lobule prominent, 2–4 cells long, 2–3 cells wide, oil bodies 10–12 per cell in lobe middle, granular
..... *Lejeunea otiana*
- 3. First tooth of lobule smaller, 1(–2) cell long and 1 cell wide, oil bodies more numerous (15–25 and more per cell in lobe middle), homogeneous *Lejeunea japonica*

Lejeunea alaskana (R.M. Schust. et Steere) Inoue et Steere, J. Hattori Bot. Lab. 44: 330, 1978 (≡ *Hygrolejeunea alaskana* R.M. Schust. et Steere, Bull. Torrey Bot. Club 85 (3): 190, 1958)

Description. Plants prostrate to ascending, yellowish green to pale yellowish green, 0.7–0.7 mm wide and 7–12 mm long. Rhizoids virtually absent or in short fascicles originating from underleaf bases, nearly colorless. Stems usually sparsely pinnately branched, cross section slightly transversely elliptic, ca. 110–120 × 100–110 μm; outer cells in 7 rows, 32.5–50.0 × 20–25 μm, slightly thick-walled, yellowish green, inner cells smaller than cortical, 20–25 × 10–20 μm, in (12–)14–16 rows, thin-walled, trigones concave to rarely triangular. Leaves imbricate, obliquely spreading and obliquely to subhorizontally oriented, lobes obliquely ovate to oblong, strongly convex, 650–800 × 450–550 μm, margin entire, apex broadly rounded, curved to ventral side; lobules strongly inflated, somewhat involute inward, ovate-oblong, 150–180 × 200–250 μm, apex constricted, first tooth subacute, indistinct, second tooth almost disappearing, hyaline papilla on the proximal side of first tooth, keel strongly arched. Cells in the lobe middle 30–38 × 20–25 μm, with slightly thickened walls, trigones concave, intermediate thickenings distinct to virtually absent; oil bodies granulate, irregularly oblong to fusiform, 4–13 per cell. Underleaves contiguous to imbricate, broadly

ovate to orbicular, cordate at base, 4–5 times as wide as stem, 400–450 × 450–500 µm, divided by narrow sinus descending 1/3–2/5 of underleaf length into two triangular lobes. Figures 2C; 3F; 5:1–13.

Comment. A very easily distinguishable species, with an unusual distribution. Whereas the present species shows a distinctly arctic-alpine range, other taxa of the genus in the Russian Far East are limited to temperate communities, rarely occurring in hemiboreal forests. The peculiar morphological traits include large underleaves ca. 0.5–0.7 of lobe in size and leaf lobes strongly curved (to almost involute in some phases) to ventral side. The distinction from the Japanese-Korean, south-temperate *Lejeunea compacta* (Steph.) Steph. remains unclear (aside from geographical distribution).

Ecology. Basiphilous to neutrophilous meso-hygrophyte. Occurs in mountain mossy tundras (including edge of solifluction spots) in open sites, as well as in open to partly shaded moist cliff crevices (including pure limestone in Sakhalin!) in alpine and (rarely) subalpine belts. In pure mats or, in the cliffs, with admixture of hepatics, e.g. in Khabarovsk Territory together with *Anastrophyllum assimile* (Mitt.) Steph., *Frullania davurica* Hampe ex Gottsche, Lindenb. et Nees, *F. subarctica*, *Herbertus dicranus* (Gottsche, Lindenb. et Nees) Trevis., *H. arcticus* (Inoue et Steere) Schljakov, *Sphenobolopsis pearsonii* (Spruce) R.M. Schust., and *Trilophozia quinqueidentata* (Huds.) Bakalin. In subalpine belt (*Pinus pumila* thickets with many limestone outcrops in Sakhalin Island) together with *Frullania subarctica*, *Metzgeria pubescens* (Schrank) Raddi, *Plagiobhila porelloides* (Torr. ex Nees) Lindenb., *Schljakovianthus quadrilobus* (Lindb.) Konstant. et Vilnet, *Trilophozia quinqueidentata*. Northward, to Kolyma Upland over moist hummocks in mossy tundra together with *Aneura pinguis* (L.) Dumort., *Frullania subarctica*, *Plagiobhila arctica* Bryhn et Kaal.; in basic cliff crevices with *Frullania subarctica*, *Mesoptychia heterocolpos* (Thed. ex Hartm.) L. Söderstr. et Vána, *Radula prolifera* Arnell, *Scapania simmonsii* Bryhn et Kaal., and *Trilophozia quinqueidentata*.

Distribution. An Arctic-alpine mega-Beringian taxon. The distribution is poorly understood: the species was described from Arctic Alaska, where it may be locally abundant, then recorded in Magadan Province (Bakalin et al. 2012), and later was found in several localities including Kodar Range in Eastern Siberia, South-East Taimyr (the westernmost known locality, Fedosov et al., 2015), Tardoki-Yani Mts. in Khabarovsk Territory (southernmost locality worldwide, known in the area with many other arctic alpine relicts, Bakalin 2015), after recorded in East-Sakhalin Mountains (also in relict environments, unpublished record). The report of *Lejeunea cavifolia* for lower course of Lena River (Konstantinova & Filin 1997) belong to *L. alaskana* too (author was able to see micrographs from the specimen on which the cited report is based, kindly provided by Dr. V. Fedosov, MW). The species is probably distributed wider than it is now known. Throughout its distribution across the Russian Far East (Magadan Province, Khabarovsk Territory, Sakhalin Island) it does not descend below 850 m a.s.l. (in East Sakhalin Mts., where in subalpine belt). It is known in inner areas of Kolyma Upland (Olskoye Plateau and Kilganskiye Mts., from 1000 to 1400 m a.s.l.), then in two localities in

Khabarovsk Territory (Badzhal Mts. and Tardoki-Yani Mts., from 1570 to 1884 m a.s.l.). Sakhalin Island, despite its more southern position than Badzhal, provides elevations from 850 to 1385 m a.s.l. in one locality (East Sakhalin Mts.) only. The species meets *L. japonica* in the same local flora in southern part of mountainous Khabarovsk Territory in Tardoki-Yani Range, where distribution of *L. japonica* stops below 750 m a.s.l., whereas the only locality observed for *L. alaskana* lying at 1884 m a.s.l.

Lejeunea japonica Mitt., Trans. Linn. Soc. London, Bot. 3 (3): 203, 1891

Description. Plants deep green to yellowish green and greenish, rarely yellowish, distinctly glossy when dry, 0.8–1.3 mm wide and 10–20(–30) mm long, in loose patches, commonly among or over bryophytes. Rhizoids virtually absent, if present a few, colorless, separated or in unclear fascicles, erect spreading from underleaf bases. Stems yellowish greenish, freely pinnately branched; cross section slightly transversely elliptic (ca. 100 × 110 µm), with 6–8 rows of outer cells, that are larger than inner, 25–32 µm in diameter, inner cells in 18–24 rows, 9–13 µm in diameter, trigones vestigial throughout. Leaves contiguous to imbricate, obliquely to very obliquely oriented; lobe 370–600 × 270–480 µm, obliquely ovate, with somewhat obtuse to rounded apex; lobule varying in size, from very small in depauperate plant to 125 × 110 µm, with the first tooth 1-celled, obtuse, the second tooth as ‘crenation’ near the first tooth, reduced. Cells in lobe middle subisodiametric to oblong, 25–38 × 25–30 µm, thin-walled, with small, concave to triangular trigones, intermediate thickenings common in longer cell wall, oil bodies small, spherical to fusiform, homogenous, (15–)25–40 per cell. Underleaves distinctly wider than long, 2.5–3.5 times wider than stem, somewhat cordate near base, appressed to the stem or obliquely to almost erect spreading, underleaf lobes obtuse to acute. Autoicous. Androecia intercalary to terminal, on short or long branches, with male bracteoles throughout the androecia. Perianth 0.7–0.8 × 0.4–0.5 mm, exerted for 1/2 of its length, terminal on short branch, commonly with 1 subfloral innovation that become to intercalary or terminal androecia, perianth distinctly 5-keeled (1 dorsal, 2 lateral, 2 ventral keels), keels smooth or loosely crenate. Figures 2D; 3G; 6.

Comment. There are many historic reports of *Lejeunea cavifolia* for the Russian Far East – the species closely related to *L. japonica*, but absent in East Asia. It seems the easternmost outposts of *L. cavifolia* are in the Ural and Caucasus. Eastward of the latter (like Yakutia and South Siberia, cf. Konstantinova et al. 2009) may belong either to *L. alaskana* or *L. japonica*. All specimens seen from the Russian Far East named as *L. cavifolia* really belong to *L. japonica*. Indeed, these two taxa are very similar in morphology and differ in the shape of underleaves where they are wider than long in *L. japonica* and longer than wide in *L. cavifolia*. Besides, the underleaves of *L. japonica* are cordate near the base – the feature not observed in *L. cavifolia*. Moreover, the two taxa are strongly different in distribution with the gap stretching from Ural Mountains to East Asia. The record of *Lejeunea cavifolia* for Arctic Yakutia, cited by Konstantinova et al. (2009), belongs to *L. alaskana*.

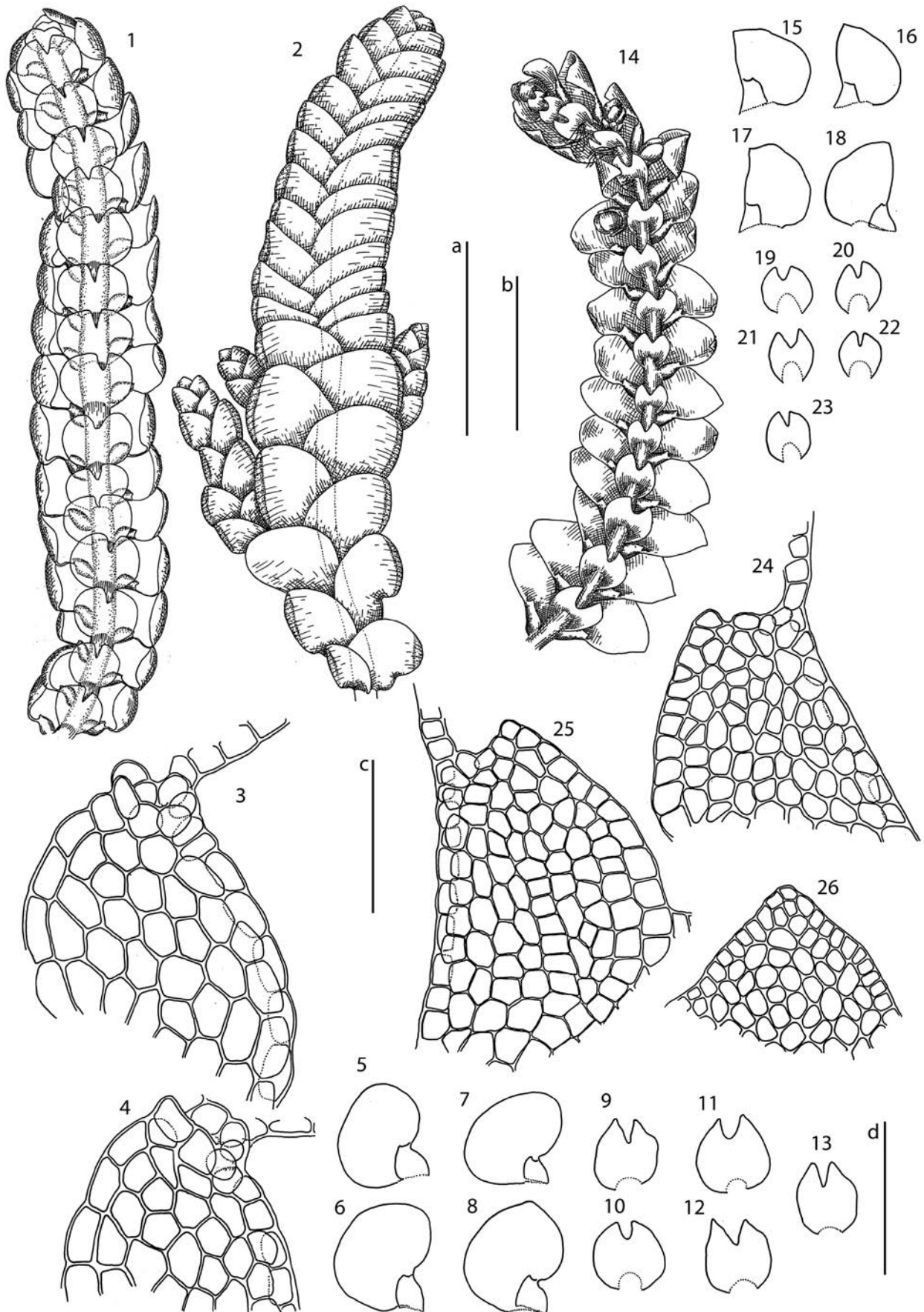


Figure 5 *Lejeunea alaskana* (R.M. Schust. et Steere) Inoue et Steere: 1 – plant habit, ventral view; 2 – plant habit, dorsal view; 3, 4 – leaf lobules, ventral view; 5–8 – leaves, ventral view; 9–13 – underleaves (1, 2 – from Mag-28-25-12; 3–13 – from Kh-19-1-16, all in VBGI). *Lejeunea neelberriana* Gottsche: 14 – plant habit, ventral view; 15–18 – leaves, ventral view; 19–23 – underleaves; 24, 25 – leaf lobules, ventral view; 26 – leaf lobe apex (all from EB-5-9-15, VBGI). Scales: a – 1 mm, for 1, 2; b – 1 mm, for 14; c – 100 μ m, for 3, 4, 24–26; d – 1 mm, for 5–13, 15–23

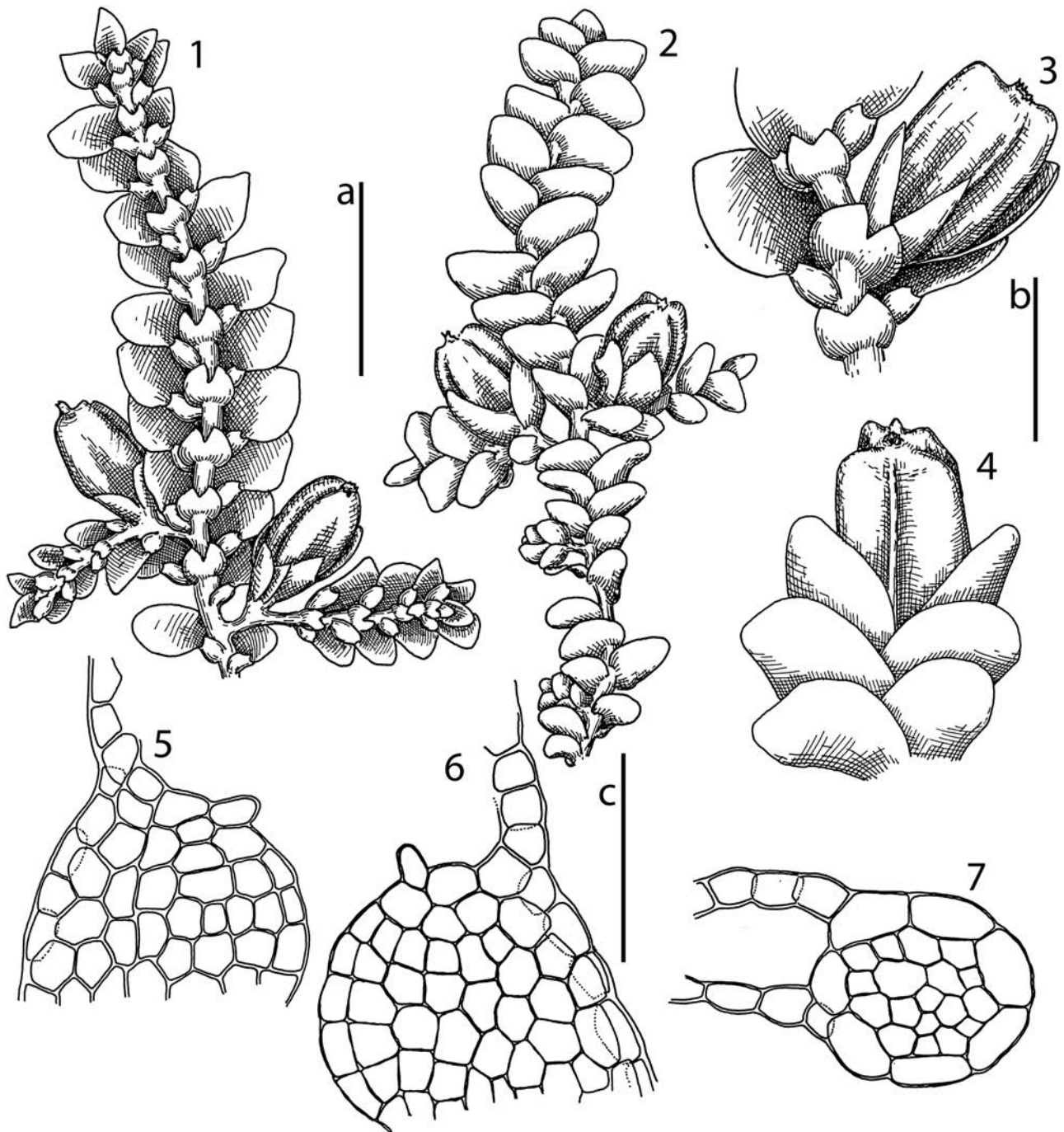


Figure 6 *Lejeunea japonica* Mitt.: 1 – plant habit, ventral view; 2 – plant habit, dorsal view; 3 – perianthous shoot fragment, ventral view; 4 – perianthous shoot fragment, dorsal view; 5, 6 – leaf lobule, ventral view; 7 – stem cross section (1–4 – from P-61-25-08; 5–7 – from Prim-19–8–16, all in VBGI). Scales: a – 1 mm, for 1, 2; b – 500 μ m, for 3, 4; c – 100 μ m, for 5–7

Ecology. Neutro- to acidophilous mesophyte. The basic habitats for the species are rocks and tree trunks; although in southern China it was reported also as epiphyllous (Zhu & So 2001). Within the Russian Far East the species is malleable in ecology and possesses itself as meso-hygrophytic acidophyte. It occupies bases of tree trunks, stones and rocks in partly shaded places, including those along streams, but aside of direct impact of running water, sometimes growing over dense pleurocarpous moss mats in the base of boulders, rarely on moist fine soils in steep slopes and along streams in forested areas. It occurs in broadleaved cool-temperate (multi- and monodominant), mixed (of Manchurian type) and rarely oro-

hemiboreal coniferous forests. As exclusions once collected on the base of *Betula lanata* (Regel) V.N. Vassil. trunk in sub-alpine belt and even in the crevice in stony field near the top of Olkhovaya Mt. (1600 m a.s.l.), where found together with *Frullania appendiculata* Steph. and *Herbertus dicranus*. The species forms pure patches or growing together with *Frullania appendiculata*, *Lophocolea heterophylla* (Schrad.) Dumort., *Metzgeria pubescens*, *Plagiobhila ovalifolia* Mitt., *Porella grandiloba* Lindb., *P. vernicosa* Lindb., *Radula obtusiloba* Steph., *Preissia quadrata* over acid to neutral reaction stones and cliff crevices; with *Cololejeunea ornata* over limestone cliffs; with *Lophocolea minor* Nees over bark of broadleaved trees; with *Metzgeria pubescens*

and, as exotic variants, with *Radula japonica* Gottsche, *Nipponolejeunea subalpina* (Horik.) S. Hatt. over conifer trunks; with *Radula complanata* (L.) Dumort., *Metzgeria lindbergii* Schiffn. over partly shaded *Juniperus sargentii* (A. Henry) Takeda ex Nakai branches in South Kurils (Shikotan Island); in moist cliffs once observed together with *Chiloscyphus polyanthos* (L.) Corda. Once the species was collected on a wet boulder along stream, that had unusual associates, including *Lophozia lantratoriae* Bakalin, *Plagiochila ovalifolia*, *Scapania crassiretis* Bryhn and *Tritomaria exsecta* (Schmidel) Schiffn. ex Loeske.

Distribution. Temperate East Asian, the most common species of the genus in Japan, Korean Peninsula and the southern Russian Far East. In China it is reported from Guangdong, Guizhou, Sichuan, Taiwan and Zhejiang (Zhu & So 2001). The altitudinal range covers elevations from sea level to middle elevations of mountains. The highest observed elevation is in Sichuan (2400 m a.s.l., where it grows on tree trunk, cf. Zhu & So 2001). Within the Russian Far East is known from two localities in southern part of Khabarovsk Territory (765 m a.s.l., Tardoki-Yani Range and 202 m a.s.l., Anuj River Basin), the northernmost at 49°N. Within Primorsky Territory all localities lie between 43 and 44°N and vary in elevation from low level (35 m a.s.l.) to 1250 (Chuguevsky District) and 1600 m a.s.l. (Partizansky District). Within Sakhalin Province known only from several localities in Shikotan Island. There are reports for Sikhotealin Reserve (Gambaryan 2001) and for Kunashir Island (Bakalin et al. 2009), where the species likely should be expected, but vouchers were not observed.

Lejeunea neelgherriana Gottsche, Syn. Hepat. 3: 354, 1845

Description. Plants prostrate to loosely ascending at shoot apices, bright green to yellowish green, slightly glistening, 1.0–1.2 mm wide, 5–10 mm long, forming loose patches over moss mats. Stems sparsely branched, 80–100 µm in diameter, with 6–8 outer and 12–18 inner cell rows, the outer cells thin-walled, inner cells with thickened walls and with large convex trigones. Rhizoids short, ca. 150–200 µm long, colorless to grayish, in dense, erect, spreading fascicles originating in underleaf bases. Leaves contiguous to imbricate, lobe slightly convex to nearly plane when wet and incurved to dorsal side of shoot when dry, when flattened in the slide obliquely ovate, with acute to loosely apiculate apices, 550–650 × 400–500 µm; lobule 200–250 × 140–160 µm, inflated, slightly involute inward, with slightly convex keel, the first tooth 1-celled, composed of triangular to widely triangular cell, the second tooth reduced. Cells in the middle of the lobe 20–26 × 15–18 µm, thin-walled, with small to moderately in size, concave trigones, intermediate thickenings absent, oil bodies coarsely granulate, sausage-shaped to irregularly fusiform, 6–13 × 4–5 µm, 3–6 per cell. Underleaves nearly rounded to slightly transversely elliptic, 350–400 × 350–450 µm, with entire to slightly crispate margins, divided by a U- to V-shaped sinus into two lobes with obtuse apices. Figures 2E; 3H; 5:14–26.

Comment. This species is easily distinguished among regional taxa by the prominently acute-apiculate lobe apices that separate it from all other known taxa of the genus in our area.

Ecology. Probably a neutrophilous mesophyte, although also able to grow on acidic and basic substrates. In our area and in the adjacent Korean Peninsula, it behaves as a calciphilous mesophyte. Known in the Russian Far East from the only collection obtained from a limestone cliff cave (where together with *Cololejeunea ornata*) surrounded by cool-temperate broadleaved deciduous forest in steep NE-facing slope, in area of northernmost outpost for series of temperate and subtropical bryophyte species (Bakalin & Borovichev 2014). However, within China it commonly growing over tree trunks, branches and rocks, rarely occurring over living leaves (Zhu & So 2001).

Distribution. Oro-subtropical South Asian (India, Nepal, Bhutan, Sri Lanka) to East Asian taxon spreading to the warm temperate zone. The occurrences in our area and central part of the Korean Peninsula possess an interesting relictal character and are associated with several bryophytes showing similar disjunct occurrences among the dominant temperate vascular vegetation. The nearest locations to the both the Korean and Russian occurrences are in southern Japan (Kyushu and adjacent islands, Yamada & Iwatsuki 2006). Moreover, the distribution of this taxon in northern extremes (both in Russian Far East and Korean Peninsula) seems to be restricted by limestone, whereas in area core of this species it is associated with trunks, branches, rotten logs, rarely occurring in rocky substrata and living on leaves (Zhu & So 2000). Within the Russian Far East it is known from the only locality in southern flank of Primorsky Territory (Sestra Mt. near Nakhodka City). The altitude varies from near sea level in the North to 2520 m a.s.l. in Xizang (Tibet), where it occurs over tree trunks. The anomaly in distribution and morphology of the taxon was discussed in a broader context by Bakalin & Borovichev (2014).

Lejeunea otiana S. Hatt., Bot. Mag. (Tokyo) 65 (763/764): 15, 1952

Description. Plants prostrate, yellowish greenish (whitish yellowish in the herbarium), forming loose patches with other liverworts, 0.8–1.1 mm wide, 8–15 mm long. Rhizoids virtually absent or solitary, colorless, erect spreading. Stems freely pinnately branched (also commonly as subfloral innovation); cross section of well-developed stems ca 110 µm in diameter, outer cells large, in 8 rows, 25–40 µm in diameter, inner cells in 12–15 rows, thin-walled, 12–20 µm in diameter. Leaves contiguous, lobes 600–700 × 450–550 µm, ovate, with obtuse apex, slightly convex, with apex not or loosely turned to ventral side, very obliquely to subhorizontally oriented; lobule 200–220 × 130–150 µm, ovate, with the first tooth prominent, acute, 2–4 cells high and 2–3 cells wide, the second tooth reduced, 1-celled, obtuse. Cells in lobe middle subsodiametric to oblong, 25–40 × 20–25 µm, thin-walled, trigones small, concave, intermediate thickenings common. Underleaves suborbicular, mostly appressed to the stem, 300–400 µm in diameter, divided by V- to U-shaped sinus descending to 1/3–2/5 of the length, lobes triangular, merely acute. Autoicous. Perianth terminal, on leading axis, obovate to subclavate, loosely folded in upper 1/3–1/4 of the length or inflate with folds indistinct, ca. 0.7–1.0 × 0.5 mm, mouth distinctly beaked. Androecia terminal on branches, with or without bracteoles. Figure 7.

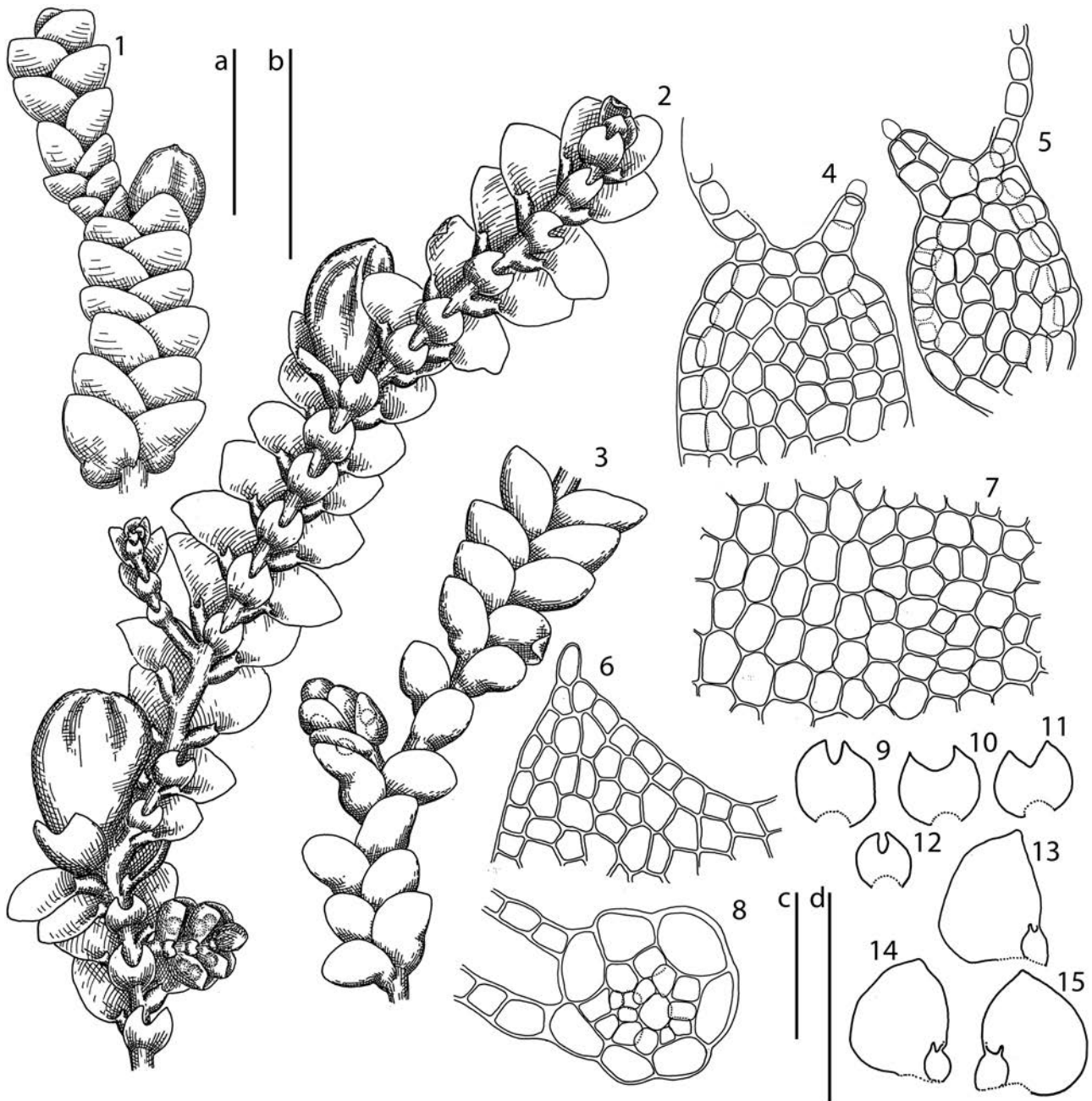


Figure 7 *Lejeunea otiana* S. Hatt.: 1, 3 – plant habit, dorsal view; 2 – plant habit – ventral view; 4, 5 – leaf lobule, ventral view; 6 – underleaf lobe apex; 7 – cells in leaf lobe middle; 8 – stem cross section; 9–12 – underleaves; 13–15 – leaves, ventral view (all from K-41-16-07, VBGI). Scales: a – 1 mm, for 1; b – 1 mm, for 2, 3; c – 100 µm, for 4–8; d – 1 mm, for 9–15

Comment. A rare and relatively small-sized species of *Lejeunea*. Careful examination of the lobule teeth is needed for correct identification. Unlike the widely distributed *L. japonica*, this species possesses a large first tooth of 2–4 cells high. In other respects it resembles a small *L. japonica*, although commonly being paler and never glossy. Some difference may be in oil bodies that are still unknown in the present taxon.

Ecology. Acidophilous mesophyte. In Japan, from where it was described, it is observed over wet rocks including those covered with a thin layer of humus enriched soil (Mizutani 1961). The habitat in Shikotan Island of the southern Kurils, where the species was only recorded, is quite distinctive. *Lejeunea otiana* was gathered from thin

semi-shaded branches in dense thickets of *Juniperus sargentii* that form large clumps on the island. The juniper formation is somewhat of a relict nature in Shikotan where it forms a peculiar ‘juniper belt’ (Barkalov 2009) instead of *Pinus pumila* that is widely distributed over other Kuril Islands, and is the probable result of an insular effect. If so, *Lejeunea otiana* may also be regarded as the relict of the temperate flora dominance in the island.

Distribution. Regarded as a rare Japanese endemic by Mizutani (1961), it occurs throughout Honshu, Shikoku and Kyushu (Yamada & Iwatsuki, 2006). Later it was found in the southern part of South Korea (Choi 2013). The only record from the Russian Far East is from 200 m a.s.l. in the southernmost Kurils (Shikotan Island).

Microlejeunea (Spruce) Steph., Hedwigia 27 (2): 61, 1888

This is a relatively small genus of Lejeuneaceae counting ca 25 extant taxa with the largest diversity in Tropical America and East Africa (including adjacent islands), and, to a lesser extent, Southeast Asia. The genus is characterized by distant leaves with leaf lobe commonly housed basal ocelli, relatively large leaf lobule and regular underleaves. Among regional taxa the confusion seems to be hardly possible due to distanced leaves and small size. Following the current point of view (Söderström et al. 2016), *Microlejeunea* is treated at the generic level here.

Microlejeunea punctiformis (Taylor) Steph., Hedwigia 29 (2): 90, 1890 (\equiv *Lejeunea punctiformis* Taylor, London J. Bot. 5: 398, 1846)

Description. Plants tiny, very soft, pallid, pale green to yellowish greenish, in loose mats over tree bark or together with other epiphytes, 200–300 μ m wide and 2–6 mm long. Rhizoids colorless, in short obliquely spreading fascicles, ‘pseudopodially’ branched at terminal ends, originated in underleaf bases. Stem 37–50 μ m in diameter, freely pinnately to bipinnately branched (branching of *Lejeunea*-type), cross section suborbicular, with 6–7 outer and 3 inner cell rows. Leaves distant, lobes convex, well developed 130–180 \times 100–140 μ m, nearly ovate, with slightly attenuate or obtuse apex; lobule convex (if to view from ventral side), well developed ca 150–175 \times 100 μ m, ovate, apex with 2 teeth, the first tooth larger, 1-celled, ca 25–30 μ m long, the second tooth smaller, obtuse, 1-celled. Cells in leaf lobe middle 12–20 \times 10–13 μ m, thin-walled, intermediate thickenings unclear, trigones small and concave; ocelli 1–2, if 2 then in short row or separated by ordinary cells; oil bodies granulate, small, spherical to fusiform. Underleaves narrowly obtrapezoidal, 90–110 \times 75–100 μ m, divided by V-shaped sinus descending to 1/2 of underleaf length. Dioicous. Perianth obovate (obconical), 4-keeled, ca. 0.4 \times 0.3 mm. Figures 2F; 3I; 8. [Elaters 120–160 \times 12 μ m, colorless, indistinctly unispiral (Mizutani 1961).]

Comment. This species is easily identified due to its small size (even smaller than our *Cololejeunea*), distanced leaves with large lobules, regular underleaves and presence of ocelli in the leaf lobe base. The species was firstly recorded (Bakalin 2007b) under *Lejeunea ulicina* (Taylor) Steph., following the concept in Yamada and Iwatsuki (2006). However, already Zhu and So (2001) were inclined to treat the Asian specimens as different, although closely related to *L. ulicina*, *Microlejeunea punctiformis* (*Lejeunea punctiformis* in Zhu and So, 2001). The latter point of view seems more reasonable from a geographical perspective. *M. ulicina* (T. Taylor) Steph. is restricted to eastern North America and Europe, while *M. punctiformis* is an Asian taxon. This point of view was also accepted in Söderström et al. (2016).

Ecology. Acidophilous mesophyte. The species is commonly growing on tree trunks, decaying wood, sometimes on vascular plant leaves and rarely on rocks. Within the Russian Far East it is restricted to epiphytic habitats and may be called as acidophilic mesophyte. It grows in coniferous and mixed (coniferous-broadleaved) forests in the southernmost Kurils, thus under a condition of high air humidity. Over tree bark it forms pure patches or growing together with *Nipponolejeunea subalpina* (Horik.) S. Hatt. and *Neobattoria herzogii* (S.Hatt.) Kamim.

Distribution. This is mainly an East Asian taxon stretching from India, Nepal and Bhutan, then widely distributed via China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hong Kong, Jiangxi, Taiwan, Yunnan, Xizang, Zhejiang) and reaching Korean Peninsula and Japan in the north and South-East Asia (Thailand, Vietnam) in the south (Zhu & So 2001). Within Japan it is distributed from Honshu to Ryukyu and Bonin, but not known in Hokkaido (Yamada & Iwatsuki 2006). Within the Korean Peninsula it is relatively common in southern flanks, but becomes rare to the middle part of the peninsula (Choi 2013). Within the Russian Far East known from the southernmost islands of Kurils: Kunashir and Shikotan, where collected in low elevations (110–150 m a.s.l.).

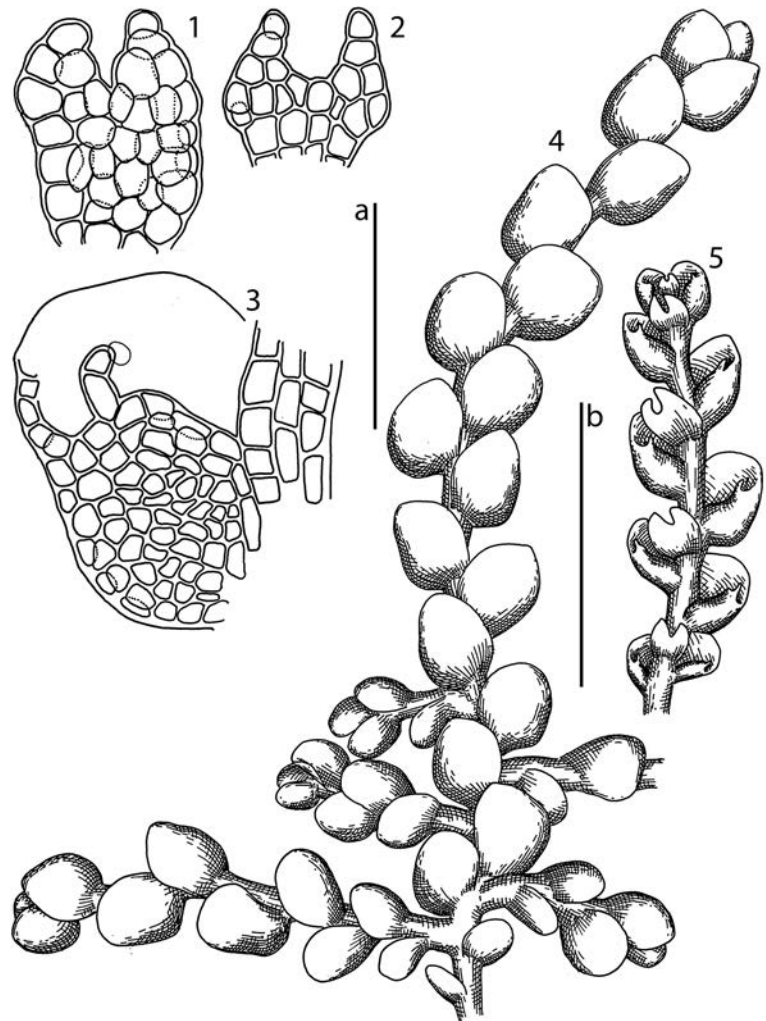


Figure 8 *Microlejeunea punctiformis* (Taylor) Steph.: 1, 2 – underleaves; 3 – leaf lobule, ventral view; 4 – plant habit, dorsal view; 5 – shoot fragments, ventral view (all from K-47-26-06, VBGI). Scales: a – 100 μ m, for 1–3; b – 500 μ m, for 4, 5

Cololejeunea (Spruce) Steph., Hedwigia 30 (5): 208, 1891

Description. Plants pale colored, greenish, yellowish greenish to whitish, in loose mats, mostly creeping over surface, less 1000 µm wide and 10 mm long. Rhizoids well-developed, in short fascicles between lobule adnations (two fascicles per leaf pair). Stem branching of *Lejeunea*-type, cross section with 5 outer and one inner cell rows. Leaves contiguous to imbricate, mostly strongly dorsiventrally conduplicate, lobe nearly ovate, with rounded, acute to apiculate apex, margin entire to crenulate due to papillose-mamillose protrudences, dorsal surface smooth or roughly papillose-mamillose; lobule ca 1/3 of lobe in size, mostly involute inward, with two distinct teeth of similar size, or teeth obsolete. Styli developed, small and easily caducous in older parts to robust and persistent. Cells in lobe middle thin-walled, intermediate thickenings absent. Underleaves absent. Autoicous (our taxa). Androecia on main axis or on lateral branches, terminal to intercalary. Perianth terminal on branches, 5-plicate, mostly beaked.

Cololejeunea is the largest genus of Lejeuneaceae that counts for over 300 extant species (some names may represent synonyms and many taxa are still undescribed). The greatest diversity occurs in the tropics (mostly Paleotropics than Neotropics). In Japan, where Lejeuneaceae was an object of careful revision by Mizutani (1961, etc.) it accounts for high diversity of ca. 50 species. Within Japan the majority of taxa is distributed in its southern half (or even fringes). Within the Russian Far East *Cololejeunea* occurs sparsely southward of 48°N, being relatively common only in Manchurian temperate (multidominant broadleaved or mixed) forests in the southern flanks of Primorsky Territory. Besides aforementioned, *Cololejeunea* are known in the southern Kurils, where, however, they are rarities. The taxa of *Cololejeunea* are easily differ from other members of Lejeuneaceae known in the Russian Far East by the minute size, absence of underleaves and presence of styli. Four species are known in the Russian Far East with one (*C. japonica*) belonging to subg. *Pedinolejeunea* Benedix ex Mizut. and three others to subg. *Cololejeunea*. Among taxa recognized in Russia, three further species are known, with two belonging to the latter subgenus (*C. calcarea* (Lib.) Schiffn. and *C. rossettiana* (C. Massal.) Schiffn.) and one more (*Cololejeunea nakajimae* S. Hatt.) to subg. *Taeniolejeunea* (Zwicker) Benedix. The systematics at the subgeneric level is morphologically based on features of lobe margin, leaf cuticle, position of hyaline papilla in leaf lobule and distribution of ocelli (absent in our taxa). Molecular-phylogenetic analysis of the whole genus, however, showed that the subgenera of *Cololejeunea* as currently circumscribed are not well founded. The taxa known in the Russian Far East may be distinguished by the following key:

1. Papillose-mamillose protrudences are absent over dorsal surface of leaf lobe [subg. *Pedinolejeunea*] *Cololejeunea japonica*
1. Papillose-mamillose protrudences are well developed over dorsal surface of leaf lobe [subg. *Cololejeunea*] 2
2. Terminal cell of the first tooth of the lobule ob-trapezoidal and tooth somewhat hammer-shaped, apices of papillose-mamillose protrudences semispherical *Cololejeunea macounii*

2. Terminal cell of the first tooth of the lobule conical, tooth never hammer-shaped, apices of papillose-mamillose protrudences conical 3

3. Stylus well-developed 5–12 cell long, outer surface of lobule with papillose-mamillose protrudences throughout (with exception of a few rows adjacent to ventral lobule margin) *Cololejeunea ornata*

3. Stylus reduced, 1–2(-3) cell long, outer surface of lobule with papillose-mamillose protrudences in several rows adjacent to the keel *Cololejeunea subkodamae*

Cololejeunea japonica (Schiffn.) Mizut., J. Hattori Bot. Lab. 24: 241, 1961 (≡ *Leptocolea japonica* Schiffn., Ann. Bryol. 2: 92, 1929)

Description. Plants pale greenish to whitish greenish, creeping, over rocks or bark or over other bryophytes, 700–900 µm wide and 5–10 mm long, strongly dorsiventrally flattened. Rhizoids sparse, in fascicles or ‘rosettes’ from initial area between lobule adnations, distinctly ‘pseudopodiate’ at the ends. Stem 40–70 µm in diameter, sparsely pinnately branched, cross section with 5 outer and 1 inner cell rows. Leaf lobes subimbricate, when flattened in the slide obliquely ovate, with rounded apex, ca. 40–500 × 300–400 µm, outer surface smooth, margin entire; lobule very varying in shape, from highly reduces and narrowly triangular with apiculate apex (2-celled uniseriate end) to narrowly lingulate and truncate in the apex, slime papilla in inner side near apex, the first and the second teeth hardly developed, well developed lobes 100–170 × 60–90 µm. Cells in leaf lobe middle 20–32 × 20–25 µm, thin-walled, intermediate thickenings obscure, trigones small and concave; oil bodies smooth to finely granulate, colorless to greenish, 5–7(-13) per cell, spherical to elliptic in projection, 3.0–3.5 × 3.5–5.0 µm. Leaves freely gemmiparous, gemmae distributed over inner surface of the lobe, discoid, 20–60 µm in diameter. Figures 3K; 9: 1–4. [Autoicous. Male inflorescences in the main axis or on the branch with 2–3(-7) pairs of bracts. Perianth inflated, 5-keeled, 0.6–0.7 × 0.35–0.5 mm. Capsule wall hyaline, pale brown; elaters 130–220 × 15 µm with walls sinuately thickened; spores irregular in shape 40–53 × 20–30 µm, minutely papillose (Mizutani 1961)]

Comment. Among regional taxa this species is very easily identified due to smooth leaf lobe surface with entire lobe margin and common production of discoid gemmae over inner surface of leaf lobe. It may be confused with poorly developed *Lejeunea japonica* rather than with our other *Cololejeunea*, from which, however, it easily differs in the absence of underleaves and completely another shape of leaf lobule.

Ecology. Neutrophilous mesophyte. Southward of the Russian Far East the common habitats of the species are tree bark and leaves (Zhu & So 2001). However, in the studied area the species is known from two collections in the Russian Far East; the first one is that by A.D. Potemkin & V.M. Kotkova (Potemkin 2003) where the species was collected over semi-shaded stones [of neutral reaction?] in *Taxus cuspidata* Siebold & Zucc. forest. Potemkin (2003) also noted that this species may be epilithic in Japan. The second Russian collection is also from cliffs in part shade in W-facing slope covered by broadleaved forest.

Distribution. Generally a Korean-Japanese oro-temperate taxon, rarely occurring in lowlands. Southward it is re-

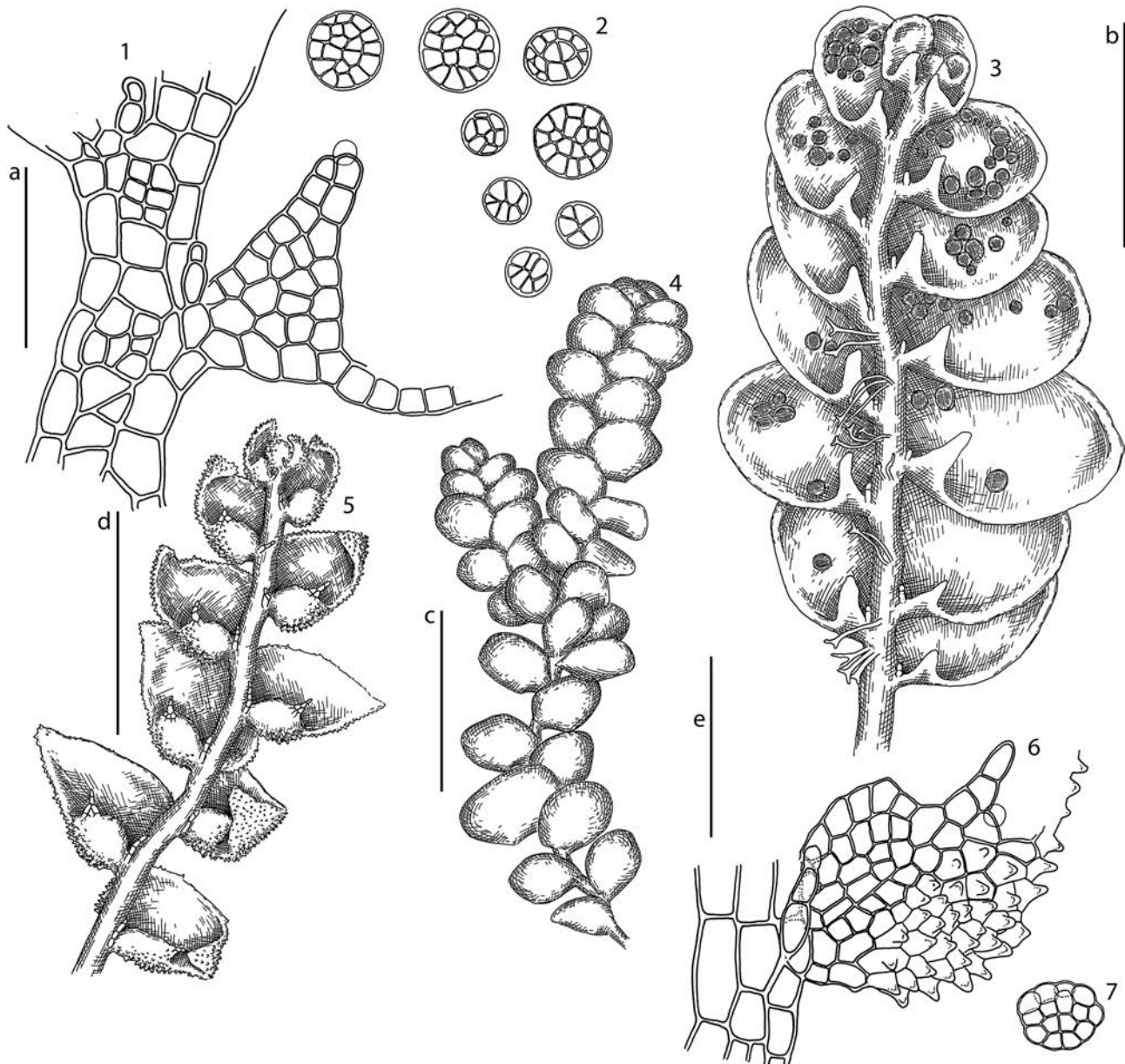


Figure 9 *Cololejeunea japonica* (Schiffn.) Mizut.: 1 – lobule and stylus, ventral view; 2 – gemmae; 3 – shoot fragments, ventral view (with gemmae production); 4 – plant habit, dorsal view. *Cololejeunea subkodamae* Mizut.: 5 – shoot fragment, ventral view; 6 – lobule and stylus, ventral view; 7 – gemma. 1–4 – from Kor-10-3-11; 5–7 – from Kh-14-35-16 (all in VBGJ). Scales: a – 100 µm, for 1, 2; b – 500 µm, for 3; c – 1 mm, for 4; d – 500 µm, for 5; e – 100 µm, for 6, 7

ported in two provinces of China (Fujian, Shanghai, cf. Zhu & Lu 1995, Zhu & So 2001), both are in middle elevation of mountains in oro-subtropic belt. In Japan known from Honshu, Shikoku, Kyushu, Bonin (Yamada & Iwatsuki, 2006), and in the Korean Peninsula sparsely occurs in its southern part. Within the Russian Far East (and in Russia as a whole) known from the southern portion of Primorsky Territory, in Petrova Island (altitude unknown, although should be low) near to western coast of the Sea of Japan and in Mikhajklovsky Range (280 m a.s.l.). Both localities are near 43°N.

Cololejeunea macounii (Spruce) A. Evans, Mem. Torrey Bot. Club 8 (2): 171, 1902 (≡ *Lejeunea macounii* Spruce, Bull. Torrey Bot. Club 17 (10): 259, 1890)

Description. Plants prostrate, whitish greenish to yellowish greenish, always pale, in loose mats over rocks, bark

and larger bryophytes, commonly densely attached by rhizoids to the substratum, 700–1000 µm wide and 3–8 mm long. Rhizoids colorless or nearly so, in obliquely spreading fascicles, originating in areas between of lobule adnations. Stems freely pinnately branched (branches commonly with smaller leaves), 70–90 µm in diameter. Leaf lobes imbricate, when flattened in the slide obliquely ovate, with apex loosely or strongly curved to ventral side, dorsal surface with papillose-mamillose protrudences, semispherical in apices; lobule nearly obovate, large ca 300 × 200 µm, with the first tooth 2-celled, somewhat hammer-shaped, terminal cell obovate to obtrapezoidal, the second tooth triangular, 2–3 cells wide and 2–3 cells long, outer surface nearly smooth (roughly papillose-mamillose only near the keel, in apical part of lobule 2–4 cell rows are papillose too). Cells in lobe middle 12–17 µm, thin-walled, trigones small, concave,

intermediate thickenings absent; oil bodies spherical to oblong, 3–6 per cell, very finely papillose. Stylus very small, easily caducous, 1(–3)-celled. Autoicous, freely fertilized. Androecia on leading axis or on branches, virtually terminal. Perianth terminal on branches, with 1 subfloral innovation, obovate, distinctly 5-keeled (2 – lateral, 2 – ventral, 1 – dorsal), roughly papillose-mamillose throughout. Capsule shortly exerted, spherical, 200–300 μm in diameter, with colorless walls. Figures 3A, L; 10:1–3.

Comment. Among regional taxa this is easily identified species due to hemispherical apices of papillose-mamillose protrudences and obovate to hammer-shaped first tooth of leaf lobule. This species is the largest among regional taxa and more than other inclined to occupy basiphilous rocky substrata.

Ecology. Neutrophilous to acidotolerant mesophyte. In southern and eastern China it is known from tree trunks, branches, stumps, decaying wood and leaves of vascular plants and ferns (Zhu & So 2001). In Japan and the Korean Peninsula (the southern part of the latter) it is common over bark of trees and shrubs, with rare occurrences over rocky substrates. Within the Russian Far East this is mostly an epilithic taxon preferring rocks of neutral reactions including those near water courses (aside of direct impact of running water), and may be characterized as a neutrophilic to acido-tolerant mesophyte. Rarely this taxon occurs over bark near trunk base of coniferous trees (mostly *Abies*). *Cololejeunea macounii* is almost restricted in our area to oroboreal belt in the mountains, although once observed in stony field (above 1300 m a.s.l.) in Livadijsky Range of Primorsky Territory. In the Russian Far East it forms pure patches or once found with *C. subkodamae*.

Distribution. Temperate, mostly an East Asian species, with several occurrences in Canadian British Columbia, where it is the only species of *Cololejeunea* (mainland of British Columbia and Moresby Island of the Queen Charlotte Islands, cf. Theirs, 2018). In East Asia the area of *C. macounii* covers Japan, the Korean Peninsula (although quite sparse there), Taiwan, China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hunan, Jiangxi, Sichuan, Yunnan, Zhejiang) and Vietnam. In China it is known from altitudes below 1900 m a.s.l. (Zhu & So 2001). Within Japan the species is known from Hokkaido to Kyushu, Yakushima and Ryukyu, in altitudes throughout Japan lying mostly below 500 m a.s.l., exceeding this elevation in Shikoku and Honshu (it is worth noting, even in these islands most of the localities of this taxon are below 500 m a.s.l.). However, in Taiwan this species was collected in 3630 m a.s.l. (Mizutani 1998). Within the Russian Far East it occurs in oro-hemiboreal belt of mountains in the southern flank of the area. The northernmost locality is in the southern extreme of Khabarovsk Territory (Tardoki-Yani), where it was found between 540 and 765 m a.s.l.; southward distributed through Primorsky Territory (350–1300 m a.s.l.), and also southernmost Kurils (Kunashir Island, 150 m a.s.l.).

Cololejeunea ornata A. Evans, Bryologist 41 (4): 73, 1938

Description. Plants pale greenish to bright and almost yellow-green, 300–450 μm wide and 2–5 mm long, freely

branched, in loose mats over rocky substrates, bark and other bryophytes. Rhizoids sparse, colorless to brownish, in obliquely spreading fascicles, closely attaching plants to the substratum. Stem 40–50 μm in diameter, freely pinnately branched, cross section with 5 outer and one inner cell rows. Leaf lobe obliquely inserted and oriented, slightly convex to canaliculate, with apex distinctly curved to ventral side, obliquely ovate with acute-apiculate apex, with conical mamilllose-papillose protrudences over surface, also including the keel, keel with spines 12–15 μm long (5–6 μm thickness of terminal papilla); lobule convex, merely involute, with conical mamilllose-papillose protrudences over surface, the first tooth 2 cells long, 1 cell wide, conical, with acute apex, the second tooth reduced, obtuse, 1 cell high. Cells in lobe middle 10–15 \times 10–13 μm , thin-walled, with small, concave trigones, intermediate thickenings absent; oil bodies oblong, very finely papillose, 2–6 per cell. Stylus robust, 2 cells wide and 8–12 cells long, uniseriate end 3–5 cells long, with mamilllose-papillose protrudences over the margin. Autoicous, freely fertilized. Androecia 1(–2)-androus (the second antheridium, if present, much smaller than the first one). Perianth loosely 4–5-keeled (1–2 – ventral, 2 – lateral, 1 – dorsal), obovate, ca 400 \times 280 μm , densely spinose over surface, exerted for 1/2–2/3 of the length, bract lobule almost the same length with lobe. Figures 3B, M; 10:4, 5)

Comment. This easily identified taxon is due to its spinose surface of the outer side of the dorsal lobe and obliquely oriented (not dorsiventrally appressed) lobe that is sometimes somewhat canaliculate. Confusion is only possible with *Cololejeunea subkodamae* as discussed under the latter.

Ecology. Neutro- to basiphilous mesophyte. In North America (south-eastern coast) known from calcareous rocks. In China reported only from epiphyllous habitat (Zhu & So 2001). Contrary, in Japan it is growing as “creeping over mosses and ferns on calcareous rocks” (Mizutani 1961: 266). Within the Russian Far East the species prefers open to semi-shaded bases of tree trunks (both of deciduous and coniferous taxa) and neutral and basic (including pure limestone) rocks, including those near streams, but aside of direct impact of running water, and may be characterized as neutrophilic mesophyte. It forms pure patches or growing together with other Lejeuneaceae (*Lejeunea neelgherriana*, *Lejeunea japonica*), *Frullania davurica*, *Metzgeria pubescens*, *Porella caespitans* (Steph.) S.Hatt., *P. vernicosa* Lindb., *Radula obtusiloba*, *R. complanata* (L.) Dumort.

Distribution. Among our taxa of the genus it is one of the most widely distributed species. Aside the Russian Far East, where relatively common in the southern flank of the area, it is quite rare in Japan and Korea (Mizutani 1961, Choi 2013). Besides known in North America from the southern part of Atlantic U.S.A. (low elevations in South Carolina, Tennessee, Florida, cf. Theirs 2018). Only two locations are known in China (Anhui, Zhejiang, cf. Zhu & So 2001). Also known from Pakistan (Furuki et al. 1993). Within the Russian Far East it is characterized by a more southern distribution than *C. macounii*, although in large scale the areas are overlapping. However, the northernmost locality among *Cololejeunea* is that of *C. ornata* (49°22'N

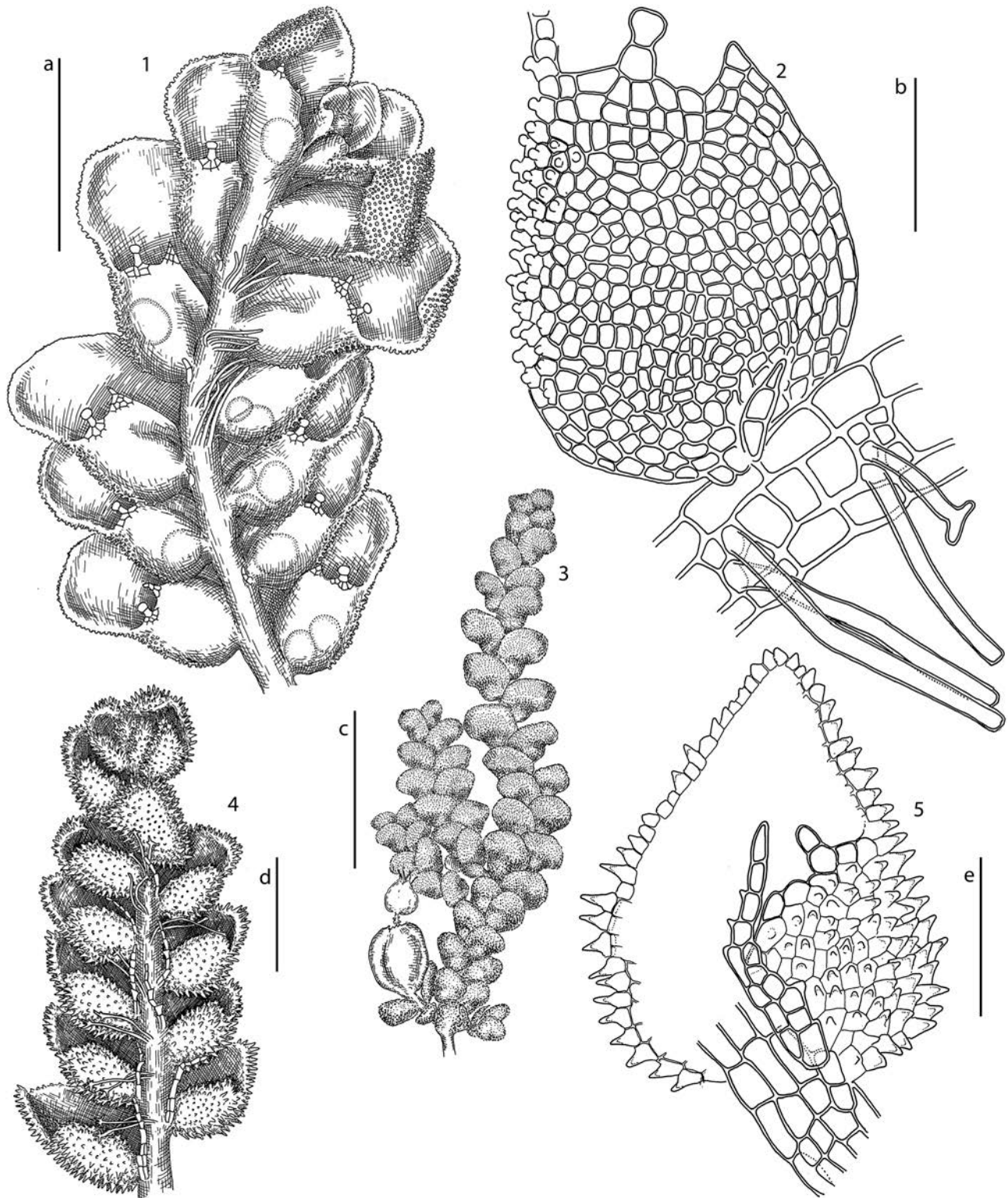


Figure 10 *Cololejeunea macounii* (Spruce) A. Evans: 1 – shoot fragment, androecial branch; 2 – lobule and stylus, ventral view; 3 – plant habit, dorsal view. *Cololejeunea ornata* A. Evans: 4 – plant habit, ventral view; 5 – lobe, lobule and stylus, ventral view. 1, 2 – from P-17-3-12; 3 – from Prim-16-26-16; 4, 5 – from Prim-17-10-16 (all in VBGI). Scales: a – 500 μ m, for 1; b – 100 μ m, for 2; c – 1 mm, for 3; d – 400 μ m, for 4; e – 100 μ m, for 5

in Anuj River). The latter occurrence may have the relict nature because it is from low elevation (202 m a.s.l.) larch forest, not from hemiboreal Ussuri taiga like the northernmost occurrence of *C. macounii*. Southward of Khabarovsk Territory through southern half of Primorsky Territory (likely should be found in its northern part), where below 400 m a.s.l., with one locality in 520 m a.s.l. in the middle

part of the territory. Before it was reported for Khingansky Reserve in Amurskaya Province (Gambaryan & Cherdantseva 1998), Komsomol'sky Reserve in Khabarovsk Territory (Cherdantseva & Gambaryan 1989) and Sikhote-Alin Reserve in Primorsky Territory (Gambaryan 2001). In all these localities it may be expected, however, vouchers were not found in VLA.

Cololejeunea subkodamae Mizut., J. Hattori Bot. Lab. 60: 448, 1986

Description. Plants greenish to deep green, prostrate to loosely ascending, well-developed 600–700 µm wide and 3–10 mm long, in loose patches over other bryophytes, tree bark and rocks. Rhizoids virtually absent or solitary, colorless, obliquely spreading in the area between lobule adnations (two zones of rhizoids origin per leaf pair). Stems freely to sparsely branched, with 5 outer and one inner cell rows. Leaf lobes imbricate, when flattened in the slide obliquely ovate-triangular, well-developed 350–400 × 200–250 µm, erect spreading, slightly convex, not or obscurely turned to dorsal side, densely papillose-mamillose throughout outer surface, papillae conical or nearly so, margin distinctly crenulate; ventral lobe obovate, convex (if to look from ventral side), curved to almost involute inward, keel area and adjacent cell rows with conical papillae that disappear to the lobule outer surface middle, the first tooth narrowly triangular, 1–2 cells wide, 2–3 cells long (uniseriate end 1–2 cells long), terminal cell conical, not thickened apically, slime papilla on inner surface of subapical cell, the second tooth as only unclear crenation or nearly smoothed curvature or 1-celled, with rounded apex. Cells in lobe middle 12–17 µm in diameter, trigones very small, concave, intermediate thickenings absent or obscure; oil bodies 2–6 per cell, ellipsoidal to shortly fusiform, finely granulate. Stylus small, 1–2(–3)-celled, easily caducous in older part of shoots. Gemmae discoid, 30–40 µm in diameter. Figures 3C, N; 9:5–7.

Comment. This tiny species may be easily confused with *Cololejeunea ornata*, which shares the conical protrudences over the dorsal surface of the leaf lobe. The main attention should be paid to the stylus characteristics that is vestigial (1–2-celled) and easily caducous in older part of shoot in *C. subkodamae*, versus more persistent and long (2 cells wide and commonly over 10 cells long) in *C. ornata*. Moreover the mamilllose-papillose protrudences are distributed over the outer surface of the leaf lobule in *C. ornata*, whereas their distribution in *C. subkodamae* is restricted by several cell rows adjacent only to the keel. Potemkin and Afonina (2008) recorded *C. nakajimae* for Zabaikalsky Territory of Eastern Siberia. Despite the latter belonging to subg. *Taenirolejeunea* (cf. Soderstrom et al. 2016), it does not show the characteristic traits of that subgenus including 4-keeled perianth and seriate ocelli. Contrary, ocelli are absent in the species and the perianth is 5-keeled. The latter permitted Mizutani (1961) to treat it as member of subg. *Cololejeunea*. *Cololejeunea nakajimae* somewhat resembles *C. subkodamae* from which it differs in completely smooth outer surface of the lobule (versus with papillose-mamillose protrudences in several cell rows near the keel). Other features, including lobe cell size and plant size seem to be largely overlapping. Formally the cell size in our specimens from the Russian Far East is rather like the cell size of *C. nakajimae* than in *C. subkodamae*. *Cololejeunea nakajimae* is a rare species of middle Japan (Honshu) that does not go outside and the distribution in the Russian Far East looks less probable (if to put apart the enigmatic collection from Zabaikalsky Territory mentioned in Potemkin & Afonina 2008).

Ecology. Acidophilous mesophyte. In Japan known from various habitats, including tree trunks, branches, rocky substrates and living leaves of ferns and vascular plants, whereas in China the distribution of the species is limited by epiphyllous habitats in moist (subtropical?) forests only (Zhu & So 2001). Ecology of the species in the Russian Far East is poorly understood due to under-collecting. It occurs over bases of *Abies nephrolepis* (Trautv. ex Maxim.) Maxim., where it forms thin pure patches or growing together with *Cololejeunea macounii*. Rarely may be found over cliffs of neutral reaction in the northernmost extremes of the distribution in the Russian Far East. Based on the information at hand it probably may best be characterized as an acido- to neutrophilic mesophyte.

Distribution. Basically a Japanese-Korean taxon sparsely distributed throughout Japan (from Honshu to the southernmost extremes: Iriomote Island) and South Korea, northward becoming very rare in Primorsky Territory and (probably) South Kurils as well as known from one very distant locality in Central Asia (Republic of Tuva), if the latter report does not actually belong to another, probably previously undescribed species. The epiphyllous habitats in China occur from 400 to 1250 m a.s.l. in the provinces of Fujiang, Guizhou, and Zhejiang (Zhu & So 2001). The distribution of the taxon in the Russian Far East may be called as ‘pseudo-enigmatic’. Indeed the species is known from only two localities: Badzhal Mts. in Khabarovsk Territory (550 m a.s.l. in 50°N) and from Livadijsky Range of Primorsky Territory (695 m a.s.l. near 43°N). This distribution pattern is rather the consequence of under-collecting than the consequence of real disjunctions. There is one obscure report of the species for Shikotan Island (Horikawa 1940) that may be based on a mistake in identification (cf. Bakalin 2007).

PHYTOGEOGRAPHICAL REMARKS

The southern flank of the Russian Far East is the only place that belongs to the northern extreme of the East Asian floristic province – one of worldwide diversity centers of Lejeuneaceae. Therefore, only remnants of the enormous East Asian diversity occur in our area. In total, the occurrence of 11 taxa of Lejeuneaceae was confirmed for the Russian Far East: 1 – *Acrolejeunea*, 1 – *Cheilolejeunea*, 1 – *Microlejeunea*, 4 – *Lejeunea* and 4 – *Cololejeunea*. Only one species, the arctic-alpine, mega-Beringian *Lejeunea alaskana* does not occur in the East Asian Province, all other taxa occur southward at least in Japan and, almost all, in China and the Korean Peninsula.

On the other hand, the diversity of Lejeuneaceae in the Russian Far East is high in comparison with other Russian macro-regions. Two of eleven taxa recognized in the area treated are known in Russia outside of Russian Far East, among them *Lejeunea alaskana* westwardly reaches Taimyr, *Cololejeunea subkodamae* – known from one locality in South Siberia (Tuva Republic). Only a few taxa recorded from other Russian regions do not occur in the Far East, including *Lejeunea cavifolia* (European part and Caucasus), *Lejeunea patens* Lindb. (Caucasus), *Cololejeunea calcarea* (Lib.) Steph. and *Cololejeunea rossettiana* (C. Massal.) Schiffn. (Caucasus) and *Cololejeunea nakajimae* S. Hatt. (South Siberia).

The majority of Lejeuneaceae (except of the aforementioned *Lejeunea alaskana*) are restricted to the southern flank of the Russian Far East. Most of them are usual component of the flora in the southern half of Primorsky Territory and, to a lesser extent in the southernmost Kurils. The populations between 48 and 54°N (where Lejeuneaceae are conspicuous rarity), at least some of them, should be regarded as having a relict nature due to obvious dissonance of those taxa with surrounding vegetation environments. Moreover, a few taxa common and relatively frequent in temperate forests, including those with many evergreen trees, occur in the northern extremity of the area, and not at the lowest altitude here but even at the highest! The most striking example is *Cheilolejeunea obtusifolia* occurring in northern-boreal larch forests at the highest elevations in the Badzhal Mts., together with e.g. *Lejeunea alaskana* and *Frullania subarctica*. This phenomenon of unexpectedly northern occurrence of temperate taxa is probably somewhat related to ‘Umiat Syndrome’ described and discussed by Steere (1965, 1976).

The Lejeuneaceae occurring in the Russian Far East (as well as most of them in the worldwide flora) are very sensitive to air moisture (a possible exception may be *Acrolejeunea sandvicensis*). The latter circumstance may explain the occurrence of many taxa mostly or only in the middle elevation belt of Primorsky and Khabarovsk Territories (thus continent mainland) – an area moistened by Pacific monsoon (see Bakalin 2008), contrary to lower elevations in southernmost Kurils. The following examples (basing on specimens examined) are illustrative: 1) *Cheilolejeunea obtusifolia* distributed in (350–)500–1660 in the mainland and 15–320 m a.s.l. in Sakhalin Province; moreover the species does not avoid lower elevations much southward in Japan; 2) *Cololejeunea macounii* – (350–)528–1300 m a.s.l. in the mainland versus 150 in Kurils; 3) *Lejeunea japonica* (35–)300–1600 m a.s.l. versus 120–300 in Kurils.

Notable differences are seen between Lejeuneaceae of the insular region and of the continental mainland. For instance, the only insular region houses very sensitive to air humidity *Microlejeunea punctiformis*, a species very sensitive to air humidity, and the Japanese (in broad sense of this term) endemic taxon – *Lejeunea otiana*. In contrast, the only continental mainland houses *Lejeunea neelgherriana* (the area of common fog going from the sea), probably *Cololejeunea subkodamae* (if the report for Shikotan is incorrect), and furthermore *C. ornata*, *C. japonica* and *Acrolejeunea sandvicensis*. The taxa restricted to the continental mainland seems to be more drought tolerant than those limited by insular part. Another reason that I can see is that the environments of continental mainland in the southern Russian Far East might be more stable and more heterogeneous, and thus offer more suitable microhabitats to accommodate the mostly tropical Lejeuneaceae which, in a general sense, are alien elements in the modern vegetation of the Russian Far East.

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Attachment 1

SPECIMENS EXAMINED (only selected specimens are cited; the specimens outside of the Russian Far East are cited only if they were drawn or otherwise mentioned).

Acrolejeunea sandvicensis: **RUSSIA: Amurskaya Province**: Khingansky Reserve (49°12'03"N 130°34'46"E), 343 m a.s.l., leg. Cherdantseva V.Ya., 18.IX.1992 (s.n., VBG1); Zejsky District (54°15'45"N 126°50'53"E), 340 m a.s.l., leg. Dudov S.V., 26.VII.2012 (Br_12_012, VBG1); **Khaborovsk Territory**: Badzhal Mts. (50°15'43"N 134°41'48"E), 600 m a.s.l., leg. Bakalin V.A., 2.VIII.2016 (Kh-16-22-16, VBG1); **Primorsky Territory**: Anuchinsky District (43°51'55"N 132°55'33"E), 280 m a.s.l., leg. Borovichev E.A. & V.A. Bakalin, 9.XI.2014 (BB5/11-14, VBG1); Anuchinsky District (43°51'55"N 132°55'33"E), 280 m a.s.l., leg. Bakalin V.A., 3.VI.2010 (P-3-6-10, VBG1); Kavalerovsky District (44°14'58"N 135°03'19"E), 321 m a.s.l., leg. Bakalin V.A., 17.IX.2011 (P-68-21-11, VBG1); (44°14'58"N 135°03'19"E), 321 m a.s.l., leg. Bakalin V.A., 17.IX.2011 (P-68-20-11, VBG1); Khankajsky District (44°50'00"N 131°41'45"E), 330 m a.s.l., leg. Bakalin V.A., 2.IV.2011 (P-1-11-11, VBG1); (44°50'52"N 131°42'39"E), 607 m a.s.l., leg. Bakalin V.A., 3.IV.2011 (P-2-23-11, VBG1); (42°34'02"N 130°48'12"E), 150 m a.s.l., leg. Bakalin V.A., 29.IV.2016 (P-7-9-16, VBG1); Khasansky District (42°37'15"N 131°08'10"E), 180 m a.s.l., leg. Bakalin V.A., 15.X.2004 (s.n., VBG1); (42°37'10"N 131°08'05"E), 180 m a.s.l., leg. Bakalin V.A., 15.X.2004 (140-12-04, VBG1); Lazovsky District (43°23'45"N 134°11'59"E), 356 m a.s.l., leg. Bakalin V.A., 20.IX.2012 (P-43-15-12, VBG1); Olginsky District (43°44'38"N 135°12'24"E), 25 m a.s.l., leg. Bakalin V.A., 22.IX.2007 (P-84-16-07, VBG1); Partizansky District (43°13'53"N 133°24'19"E), 600 m a.s.l., leg. Gambaryan S.K., 25.IX.1978 (s.n., VBG1).

Cheilolejeunea obtusifolia: **JAPAN: Miyazaki Prefecture**: Nichinan (31°44'00"N 131°22'00"E), 300 m a.s.l., leg. Bakalin V.A. & M. Matsumoto, 14.V.2015 (J-40-16-14, VBG1). **RUSSIA: Khaborovsk Territory**: Badzhal Mts. (50°18'29"N 134°39'52"E), 1570 m a.s.l., leg. Bakalin V.A., 4.VIII.2016 (Kh-17-38a-16, VBG1); Badzhal Mts. (50°20'44"N 134°39'42"E), 1640 m a.s.l., leg. Bakalin V.A., 6.VIII.2016 (Kh-19-13-16, VBG1); **Primorsky Territory**: Lazovsky District (43°14'05"N 133°44'07"E), 350 m a.s.l., leg. Bakalin V.A., 23.IX.2011 (P-74-38-11, VBG1); Lazovsky District (43°14'45"N 133°43'02"E), 500 m a.s.l., leg. Bakalin V.A., 6.X.2006 (P-68-12-06, VBG1); Lazovsky District (43°14'45"N 133°43'05"E), 570 m a.s.l., leg. Bakalin V.A., 8.VII.2016 (P-10-4-16, VBG1); Partizansky District (43°26'48"N 133°39'21"E), 1660 m a.s.l., leg. Bakalin V.A., 12.IX.2014 (P-35-10-14, VBG1); Shkotovsky District (43°06'56"N 132°47'26"E), 489 m a.s.l., leg. Klimova K.G. & V.A. Bakalin, 15.X.2016 (Prim-16-6-16, VBG1); (43°07'10"N 132°47'31"E), 550 m a.s.l., leg. Bakalin V.A., 25.VI.2012 (P-15-60-12, VBG1); **Sakhalin Province**: Iturup Island (45°20'02"N 148°37'04"E), 100 m a.s.l., leg. Bakalin V.A., 11.IX.2015 (K-71-44-15, VBG1); Shikotan Island (43°44'29"N 146°41'20"E), 15 m a.s.l., leg. Bakalin V.A., 2.IX.2007 (K-59-2-07, VBG1); (43°47'47"N 146°35'50"E), 110 m a.s.l., leg. Bakalin V.A., 30.VIII.2007 (K-51-18-07, VBG1); (43°46'34"N 146°44'19"E), 320 m a.s.l., leg. Bakalin V.A., 25.VIII.2007 (K-42-49-07, VBG1); Zhdanko Mt. (48°05'28"N 142°31'30"E), 300 m a.s.l., leg. Bakalin V.A., 1.X.2016 (S-48-8-16, VBG1). **REPUBLIC OF KOREA: Jeju-do**: (33°17'56"N 126°35'08"E), 250 m a.s.l., leg. Bakalin V.A., 14.V.2015 (Kor-30-39-15, VBG1).

Cololejeunea japonica: **RUSSIA: Primorsky Territory**: Lazovsky District (42°52'N 133°48'E), below 100 m a.s.l., leg. Potemkin A.D. & V.M. Kotkova, X.2002 (211401, VBG1); Anuchinsky District (43°51'55"N 132°55'33"E), 280 m a.s.l., leg. Bakalin V.A., 3.VI.2010 (P-3-3-10, VBG1). **REPUBLIC OF KOREA: Jeonnam Province**: (34°32'35"N 126°55'48"E), 238 m a.s.l., leg. Bakalin V.A., 19.V.2011 (Kor-16-03-11, VBG1).

Cololejeunea macounii: **RUSSIA: Khaborovsk Territory**: Tardoki-Yani Mts. (48°48'12"N 138°05'31"E), 543 m a.s.l., leg. Bakalin V.A., 28.VIII.2013 (Kh-46-2-13, VBG1); (48°50'05"N 138°04'45"E), 765 m a.s.l., leg. Bakalin V.A., 20.VIII.2013 (Kh-32-16-13, VBG1); **Primorsky Territory**: Lazovsky District (43°14'15"N 133°44'07"E), 350 m a.s.l., leg. Bakalin V.A., 23.IX.2011 (P-74-2-11, VBG1); Partizansky District (43°20'50"N 133°39'22"E), 1000 m a.s.l., leg. Bakalin V.A., 11.IX.2010 (P-45-28-10, VBG1); Shkotovsky District (43°07'10"N 132°47'31"E), 550 m a.s.l., leg. Bakalin V.A., 25.VI.12 (P-15-17-12, VBG1); (43°06'36"N 132°47'19"E), 695 m a.s.l., leg. Klimova K.G. & V.A. Bakalin, 15.X.2016 (Prim-16-26-16, VBG1); (43°06'33"N 132°47'13"E), 800 m a.s.l., leg. Klimova K.G. & V.A. Bakalin, 15.X.2016 (Prim-16-36-16, VBG1); (43°06'18"N 132°47'15"E), 1000 m a.s.l., leg. Bakalin V.A., 26.VI.2012 (P-17-3-12, VBG1); (43°06'18"N 132°47'15"E), 1000 m a.s.l., leg. Bakalin V.A., 26.VI.2012 (P-17-2-12, VBG1); (43°04'15"N 132°41'37"E), 1300 m a.s.l., leg. Bakalin V.A., 6.IX.2010 (P-40-9a-10, VBG1); Ternejsky District (45°53'44"N 137°18'53"E), 528 m a.s.l., leg. Pimenova E.A., 2.VIII.2013 (s.n., VBG1); Sakhalin Province; Kunashir Island (43°50'13"N 145°32'43"E), 150 m a.s.l., leg. Bakalin V.A., 7.IX.2006 (K-47-18a-06, VBG1).

Cololejeunea ornata: **RUSSIA: Khaborovsk Territory**: Anuj River (49°22'36"N 137°43'11"E), 202 m a.s.l., leg. Bakalin

V.A., 21.IX.2009 (Kh-72-9-09, VBG); **Primorsky Territory:** Dalnegorsk Municipality (44°35'07"N 135°33'22"E), 520 m a.s.l., leg. Bakalin V.A., 26.VIII.2016 (P-38-5-16, VBG); Krasnoarmejsky District (45°46'47"N 135°19'13"E), 380 m a.s.l., leg. Gambaryan S.K., 19.VI.1991 (s.n., VBG); Lazovsky District (43°14'05"N 132°44'07"E), 350 m a.s.l., leg. Bakalin V.A., 23.IX.2011 (P-74-23-11, VBG); Nadezhdinsky District (43°38'59"N 131°55'09"E), 35 m a.s.l., leg. Klimova K.G. & V.A. Bakalin, 16.X.2016 (Prim-17-10-16, VBG); Nakhodka Municipality (42°49'39"N 132°59'38"E), 300 m a.s.l., leg. Bakalin V.A., 21.IX.2011 (P-70-13-11, VBG); (42°49'39"N 132°59'39"E), 328 m a.s.l., leg. Bakalin V.A., 17.X.2008 (P-69-9-08, VBG); Partizansky District (43°01'43"N 133°01'24"E), 300 m a.s.l., leg. Bakalin V.A., 7.X.2006 (P-69-11-06, VBG); Shkotovsky District (43°08'03"N 132°47'56"E), 400 m a.s.l., leg. Bakalin V.A., 27.VI.2012 (P-20-18-12, VBG); Ussurijsky District (43°37'04"N 132°14'00"E), 130 m a.s.l., leg. Komarov V.L., 17.VIII.1930 (s.n., VBG).

Cololejeunea subkodamae: RUSSIA: **Khabarovsk Territory:** Badzhal Mts. (50°17'10"N 134°42'49"E), 550 m a.s.l., leg. Bakalin V.A., 31.VI.2016 (Kh-14-35-16, VBG); **Primorsky Territory:** Shkotovsky District (43°06'36"N 132°47'19"E), 695 m a.s.l., leg. Klimova K.G. & V.A. Bakalin, 15.X.2016 (Prim-16-26-16, VBG).

Lejeunea alaskana: RUSSIA: **Khabarovsk Territory:** Badzhal Mts. (50°18'29"N 134°39'52"E), 1570 m a.s.l., leg. Bakalin V.A., 4.VIII.2016 (Kh-17-38-16, VBG); Badzhal Mts. (50°20'44"N 134°39'42"E), 1640 m a.s.l., leg. Bakalin V.A., 6.VIII.2016 (Kh-19-1-16, VBG); (50°20'44"N 134°39'42"E), 1640 m a.s.l., leg. Bakalin V.A., 6.VIII.2016 (Kh-19-6a-16, VBG); Tardoki-Yani Mts. (48°54'08"N 137°59'59"E), 1884 m a.s.l., leg. Bakalin V.A., 25.VIII.2013 (Kh-41-14-13, VBG); **Magadan Province:** Kilganskiya Mts. (61°11'43"N 153°58'53"E), 1400 m a.s.l., leg. Bakalin V.A., 9.VIII.2012 (Mag-28-28-12, VBG); Olskoye Basalt Plateau (60°39'11"N 151°28'12"E), 1056 m a.s.l., leg. Bakalin V.A., 5.VIII.2014 (Mag-39-11-14, VBG); (60°38'58"N 151°21'39"E), 1580 m a.s.l., leg. Bakalin V.A., 8.VIII.2011 (Mag-52-16-11, VBG); **Sakhalin Province:** East-Sakhalin Mts. (50°37'41"N 143°22'38"E), 850 m a.s.l., leg. Bakalin V.A., 8.VII.2017 (S-18-12-17, VBG); (50°38'41"N 143°22'38"E), 1140 m a.s.l., leg. Bakalin V.A., 10.VII.2017 (S-22-21-17, VBG); (50°38'02"N 143°21'56"E), 1385 m a.s.l., leg. Bakalin V.A., 13.VII.2017 (S-25-7-17, VBG).

Lejeunea japonica: RUSSIA: **Khabarovsk Territory:** Tardoki-Yani Mts. (48°50'05"N 138°04'45"E), 765 m a.s.l., leg. Bakalin V.A., 20.VIII.2013 (Kh-32-17-13, VBG); Anuj River (42°22'36"N 137°43'11"E), 202 m a.s.l., leg. Bakalin V.A., 21.IX.2009 (Kh-72-26a-09, VBG); **Primorsky Territory:** Chuguevsky District (43°39'06"N 133°35'03"E), 1250 m a.s.l., leg. Bakalin V.A., 14.IX.2014 (P-37-16-14, VBG); Kavalerovsky District (44°14'58"N 135°03'19"E), 321 m a.s.l., leg. Bakalin V.A., 17.IX.2011 (P-68-12-11, VBG); Khasansky District (43°21'55"N 131°38'30"E), 81 m a.s.l., leg. Klimova K.G. & V.A. Bakalin, 16.X.2016 (Prim-19-8-16, VBG); (43°21'55"N 131°38'30"E), 81 m a.s.l., leg. Klimova K.G. & V.A. Bakalin, 16.X.2016 (Prim-19-8-16, VBG); (42°37'10"N 131°08'05"E), 180 m a.s.l., leg. Bakalin V.A., 15.X.2004 (140-6a-04, VBG); (43°05'34"N 131°31'18"E), 286 m a.s.l., leg. Bakalin V.A., 17.V.2007 (P-2-22-07, VBG); (43°05'19"N 133°32'02"E), 320 m a.s.l., leg. Bakalin V.A., 11.VII.2015 (P-40-2-15, VBG); Lazovsky District (43°04'02"N 133°36'37"E), 227 m a.s.l., leg. Bakalin V.A., 22.IX.2011 (P-73-20-11, VBG); (43°14'45"N 133°43'05"E), 570 m a.s.l., leg. Bakalin V.A., 8.VII.2016 (P-10-1-16, VBG); (43°26'32"N 134°13'20"E), 800 m a.s.l., leg. Bakalin V.A., 21.IX.2012 (P-45-16-12, VBG); Nadezhdinsky District (43°38'59"N 131°55'09"E), 35 m a.s.l., leg. Klimova K.G. & V.A. Bakalin, 16.X.2016 (Prim-17-9-16, VBG); (43°39'01"N 131°55'02"E), 100 m a.s.l., leg. Bakalin V.A., 18.V.2010 (P-1-23a-10, VBG); Nakhodka Municipality (42°49'39"N 132°59'39"E), 328 m a.s.l., leg. Bakalin V.A., 17.X.2008 (P-69-9-08, VBG); Olginsky District (43°37'11"N 134°25'37"E), 407 m a.s.l., leg. Bakalin V.A., 19.IX.2007 (P-80-8-07, VBG); Partizansky District (42°58'08"N 133°02'41"E), 148 m a.s.l., leg. Bakalin V.A., 19.X.2005 (P-76-11-05, VBG); (43°29'36"N 133°34'48"E), 850 m a.s.l., leg. Bakalin V.A., 5.X.2006 (P-67-13b-06, VBG); (43°29'38"N 133°34'45"E), 915 m a.s.l., leg. Bakalin V.A., 22.IX.2011 (P-72-3-11, VBG); (43°20'50"N 133°39'22"E), 1000 m a.s.l., leg. Bakalin V.A., 11.IX.2010 (P-45-32-10, VBG); (43°20'50"N 133°39'22"E), 1600 m a.s.l., leg. Bakalin V.A., 10.IX.2010 (P-44-13-10, VBG); Shkotovsky District (43°08'50"N 132°42'05"E), 142 m a.s.l., leg. Bakalin V.A., 24.X.2004 (142-11-04, VBG); (43°41'06"N 132°28'11"E), 235 m a.s.l., leg. Bakalin V.A., 14.X.2008 (P-61-25-08, VBG); (43°06'42"N 132°47'22"E), 639 m a.s.l., leg. Klimova K.G. & V.A. Bakalin, 15.X.2016 (Prim-16-23-16, VBG); Ussurijsky District (43°36'29"N 132°14'59"E), 126 m a.s.l., leg. Bakalin V.A., 28.V.2008 (P-1-17-08, VBG); Vladivostok Municipality (43°12'36"N 131°59'21"E), 44 m a.s.l., leg. Bakalin V.A., 18.X.2003 (117-9-03, VBG); Sakhalin Province; Shikotan Island (43°48'08"N 146°38'46"E), 120 m a.s.l., leg. Bakalin V.A., 28.VIII.2007 (K-49-40-07, VBG); (43°47'09"N 146°41'10"E), 200 m a.s.l., leg. Bakalin V.A., 25.VIII.2007 (K-41-13-07, VBG); (43°48'08"N 146°38'46"E), 300 m a.s.l., leg. Bakalin V.A., 27.VIII.2007 (K-48-15a-07, VBG).

Lejeunea neelgherriana: RUSSIA: **Primorsky Territory:** Nakhodka Municipality (42°49'40"N 132°59'41"E), 320 m a.s.l., leg. Borovichev E.A. & V.A. Bakalin, 30.X.2013 (BP-5-9-13, VBG).

Lejeunea otiana: RUSSIA: **Sakhalin Province:** Shikotan Island (43°47'09"N 146°41'10"E), 200 m a.s.l., leg. Bakalin V.A., 25.VIII.2007 (K-41-16-07, VBG).

Microlejeunea punctiformis: RUSSIA: **Sakhalin Province:** Shikotan Island (43°47'48"N 146°35'50"E), 110 m a.s.l., leg. Bakalin V.A., 30.VIII.2007 (K-50-38-07, VBG); Kunashir Island (43°50'13"N 145°32'43"E), 150 m a.s.l., leg. Bakalin V.A., 7.IX.2006 (K-47-26-06, VBG).