Taxonomic revision of Lejeuneaceae
subfamily Ptychanthoideae (Marchantiophyta) in China
Jian Wang, Rui-Liang Zhu & S. Robbert Gradstein

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With 50 plates (partly coloured) and 2 tables
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Summary

Lejeuneaceae are the largest family of liverworts with two subfamilies: Ptychanthoideae and Lejeuneoideae. Taxonomic revisions of Ptychanthoideae have been made for several parts of the world, but no taxonomic revision of Chinese Ptychanthoideae is hitherto available. Our revision of Ptychanthoideae in China reveals the occurrence of 38 species in 11 genera: *Acrolejeunea* (8 spp.), *Caudalejeunea* (1), *Frullanoloides* (1), *Gradsteinianthus* (1), *Lopholejeunea* (8), *Mastigolejeunea* (4), *Ptychanthus* (1), *Schiffleriejeunea* (3), *Spruceanthus* (6), *Thysananthus* (4) and *Tuzibeanthus* (1). Keys, descriptions and illustrations are provided for genera and species together with data on distribution in China and world range. *Gradsteinianthus* R.L. Zhu & Jian Wang bis gen. nov. is newly described based on molecular and morphological evidence. *Frullanoloides tristis*, *Schiffleriejeunea polycarpa*, *S. pulopenangensis* and *Thysananthus convolutus* are newly recorded for China. The occurrence of *Lopholejeunea aplanata* in China is confirmed. About one third of the species of Chinese Ptychanthoideae (*Acrolejeunea infuscatA*, *A. pusilla*, *A. recurvata*, *A. sandvicensis*, *A. sikkimensis*, *Gradsteinianthus tridentatus*, *Lopholejeunea soae*, *Spruceanthus falcatus*, *S. kiushianus*, *S. mamillilobulus*, *Tuzibeanthus chinensis*), are restricted to continental eastern Asia and do not occur in Malesia. One species, *Acrolejeunea sinensis*, is hitherto only known from China.

Introduction

Lejeuneaceae are the largest family of leafy liverworts with more than a thousand species in 69 genera and in two subfamilies, Lejeuneoideae C.Massal. and Ptychanthoideae Mizut. (e.g., Gradstein 1979, 2013, Mizutani 1961, Schuster 1963). Ptychanthoideae, containing about 180 species in 20 genera, are a main lineage of Lejeuneaceae (Gradstein 2013, Shi et al. 2015, Söderström et al. 2015). Characteristics of this subfamily include the relatively robust size of the plants, the undivided or slightly retuse underleaves, the isodiometrical spores arranged in tetrads, distinctly spiralled elaters attached to capsule valve surface and margin, and a well-developed fenestrate thickening layer on the inner valve surface. Regional revisions of Ptychanthoideae have been done for Australia (Thiers & Gradstein 1989), Japan (Mizutani 1961), New Guinea (Gradstein et al. 2002), Thailand (Kornochalert et al. 2012), Java (Haerida et al. 2010), tropical America (Gradstein 1994) and West Africa (Wigginton 2004). The present paper is the first treatment of the subfamily for China.

The first record of Ptychanthoideae from China was by Stephani (1894) who reported *Acrolejeunea cordistipula* Steph. [= *A. infuscata* (Mitt.) Jian Wang bis & Gradst.] from Yunnan province. In the *Species Hepaticarum* (Stephani 1898–1924) four species of Ptychanthoideae were listed from China, viz. *Brachiolejeunea polygona* (Mitt.) Steph. [= *Acrolejeunea sandvicensis* (Gottsche) Steph.], *Mastigolejeunea formosensis* Steph. [= *Acrolejeunea sandvicensis* (Gottsche) Steph.], *M. mariana* Steph. [= *Ptychanthus striatus* (Lehm. & Lindenb.) Nees] and *Ptychanthus chinensis* Steph. [= *Tuzibeanthus chinensis* (Steph.) Mizut.]. Based on the collections made by Handel-Mazzetti, Herzog (1930) reported seven species of Ptychanthoideae from China, including three new species, *Ptychanthus caudatus* Herzog [= *P. striatus* (Lehm. & Lindenb.)

The most interesting taxon of Ptychanthoidae of China is undoubtedly *Caudalejeunea tridentata* R.L.Zhu et al. This species was first described by Zhu et al. (2011) based on male material from Guangxi province, China. It was tentatively placed in *Caudalejeunea* (Steph.) Schiffn. because of the presence of gemmae, which are unique to *Caudalejeunea* within Ptychanthoidae (Gradstein 1994). However, the species differed from all hitherto known species of *Caudalejeunea* in having isodiometric leaf cells with bulging trigones and segmented oil bodies (Zhu et al. 2011), all of which are important generic features in Ptychanthoidae (Gradstein 1994). Since female plants were lacking, the systematic position of this interesting plant remained an open question.

Another intriguing Chinese taxon is *Tuzibeanthus chinensis*. This species is the only member of the genus *Tuzibeanthus* S.Hatt. and is restricted to East Asia. The genus shares many characters with *Psychanthus* Nees, e.g. growth habit, branching type, oil bodies and perianths (Awasthi & Srivastava 1987, Mizutani 1961), and the two groups are quite similar in terpenoid chemistry (Asakawa 1982). Parihar (1961–1962) treated *Tuzibeanthus* therefore as a synonym of *Psychanthus*, and Mizutani (1961) and Inoue (1974) suggested it to be a subgenus of the latter. According to Mizutani (1961), *Tuzibeanthus* differs from *Psychanthus* by the rounded to obtuse leaf apex and entire underleaves, female bracts and bracteoles. These characters, however, are usually species-level differences in Ptychanthoidae, not generic differences (e.g., Gradstein 1994, Sukkharak et al. 2011). A more important character of *Tuzibeanthus* is the leaf areolation, which is similar as in *Spruceanthus* (cells isodiometric-rounded to subelliptate, trigones simple-triangulate to swollen to radiate, not cordate) and is a major generic character in Ptychanthoidae (Gradstein 1975, 1994). No molecular studies have been undertaken as yet to clarify the relationship between the two genera.

The aims of the present study were to (1) clarify the taxonomic status of *Caudalejeunea tridentata* and the relationships of *Psychanthus* and *Tuzibeanthus* by using evidence from three molecular markers (*rbcl*, *trnL-F*, *nrITS*) and morphology, and (2) improve our understanding of the diversity of Chinese Ptychanthoidae. Our study incorporates the most recent results of ongoing revisionary work on the genera of Ptychanthoidae based on morphology and molecular analysis (e.g., Gradstein 2015, Shi et al. 2015, Sukkharak 2015, Sukkharak & Gradstein 2014, Wang et al. 2014c).
Acrolejeunea recurvata Gradst.

Plates 7, 48: 4

Plants yellowish-brown when dry, up to 20 mm long, 1.7–2.3 mm wide, branches usually of the Lejeunea-type, rarely of the Frullania-type, flagellae present. Stems fragile, 160–200 μm in diameter, ventral merophyte 4–10 cells wide; stem in transverse section ca. 19 thin-walled epidermal cells and 48 thick-walled medullary cells, epidermal cells slightly larger than medullary cells. Leaves densely imbricate, clasping the stem when dry, widely spreading to squarrose when moist. Lobe asymmetrically ovate-orbicular, 1.0–1.2 mm long, 0.9–1.1 mm wide, apex rounded, plane, margin entire, ventral margin upcurved, keel straight or slightly arched. Lobe cell walls thin to slightly thickened, trigones cordate, intermediate thickenings scarce, marginal cells subquadrate, 10–20 × 6–14 μm, median cells hexagonal, 26–48 × 16–28 μm, basal cells elongate, 32–54 × 16–32 μm. Oil bodies 15–29 per median cell, of the homogeneous type, fusiform or oblong, 3.8–6.7 × 1.5–2.7 μm. Lobule ovate, 2/5–1/2 as long as the lobe, inflated, free lateral margin more or less recurved in the lower half, apex oblique, with 3–4 erect or inflexed teeth, teeth 1–2 cells long and 1 cell wide, hyaline papilla as in the genus. Underleaves imbricate, transversely oblong, 0.34–0.42 mm long, 0.54–0.62 mm wide, 3–4 times as wide as the stem, apex rounded to truncate, recurved, margin entire, rounded or weakly auriculate at bases, insertion line slightly arched. Androecia, gynoecia and perianth not seen. Asexual reproduction by means of small caducous leaves produced on upright flagelliform shoots.

Taxonomic notes: Acrolejeunea recurvata can be separated from other Chinese species of the genus by the presence of upright flagellae producing caducous leaves, the lobule with 3–4 teeth, and the recurved underleaf apex.

Habitat and distribution in China: On tree bark. The species has been reported from Hunan and Yunnan (Jia & He 2013, Zhu & So 1999) and is newly recorded here from Xizang.


Acrolejeunea sandvicensis (Gottsche) Steph.


Autoicous or paroicous. Plants green when fresh, yellowish-brown when dry, up to 3 cm long, 1.2–2.4 mm wide, branches of the Frullania-type, rarely of the Lejeunea-type. Stems 70–145 μm in diameter, ventral merophytes 4–6 cells wide; transverse section of stem with ca. 20 epidermal cells and 31 medullary cells, cells thin-walled or slightly thick-walled, epidermal cells slightly larger than medullary cells. Leaves densely imbricate, convolute the stem when dry, widely spreading and strongly squarrose when moist. Lobe ovate, 0.9–1.3 mm long, 0.7–1.1 mm wide, apex rounded, plane, margin entire, ventral margin plane or upcurved, keel slightly arched. Lobe cell walls thin to slightly thickened, trigones cordate, intermediate thickenings present, marginal cells subquadrate, 14–31 × 11–24 μm, median cells hexagonal, 30–48 × 22–36 μm, basal cells elongate, 36–54 × 23–38 μm. Oil bodies 15–50 per median cell, of the homogeneous type, fusiform or oblong, 3.0–5.7 × 1.6–2.4 μm. Lobule ovate or semi-orbicular, ca. 2/5 as long as the lobe, inflated, free lateral margin plane, apex oblique, with 3–5 erect or partially inflexed teeth, teeth 1–2 cells long and 1–2 cells wide at base, hyaline papilla as in the genus. Underleaves densely imbricate, reniform, 0.2–0.6 mm long, 0.4–0.9 mm wide, 3–5 times as wide as the stem, apex rounded, plane or weakly recurved, margin entire, rounded at bases, insertion line slightly arched. Androecia terminal or intercalary on stem or on subfloral innovation of gynoeica, innovations sterile or fertile bracts in 1–3 pairs, similar to leaves. Gynoeica with 1–2 Frullania-type innovations or innovation absent, bracts and bracteoles in 2–3 series, bract lobes broadly ovate, 0.9–1.5 mm long, 0.8–1.1 mm wide, apex rounded, margin entire, bract lobule absent or present, if present oblong, ca. 1/2 as long as bract lobe, bracteoles broadly oblong or suborbicular, 0.7–0.9 mm long, 0.7–1.0 mm wide, apex rounded, plane, margin entire. Perianth obovate or oblong, 1.0–1.3 mm long, 0.6–0.8 mm wide, with 6–10 keels, keels straight, somewhat flexuose, beak 2 cells long. Asexual reproductive organs absent.

Taxonomic notes: Acrolejeunea sandvicensis is the most common species of Ptychanthoidae in China. It resembles A. fertilis (Reinw. et al.) Schiffn. in the densely imbricate leaves which are strongly squarrose when moist and the semi-orbicular leaf lobules with several small teeth along the free lateral margin. The latter species differs mainly by the larger leaf lobe with more numerous (5–9) teeth, the absence of innovations, and male bracts with more strongly inflated lobules. Interestingly, one plant of A. sandvicensis (1974 Expedition Team 2597) from China without innovation was observed (Plate 9). The occasional lack of innovations further supports the placement of this species, and of Trocholejeunea, in Acrolejeunea.
**Habitat and distribution in China:** On tree bark, rock, rotten logs, leaves, sandstone and soil. The species has been reported from Anhui, Chongqing, Fujian, Guangdong, Guangxi, Guizhou, Hainan, Hebei, Heilongjiang, Henan, Hong Kong, Hubei, Hunan, Jilin, Jiangsu, Jiangxi, Liaoning, Nei Mongol, Ningxia, Shaanxi, Shandong, Shanghai, Shanxi, Sichuan, Taiwan, Xizang, Yunnan and Zhejiang (Jia & He and Zhu 2000 as *Trocholejeunea sandwicensis*), and is newly recorded here from Macau.

Thysananthus Lindenb.

Autoicous or dioicous. Plants dull green when fresh and yellowish brown when dry. Transverse section of stem with 25–30 epidermal cells, epidermal cells not larger than medullary cells, all cells with thickened walls; ventral merophyte 6–18 cells wide. Shoots fragile or rigid, irregularly pinnate, branching of the Lejeunea-type. Leaves imbricate, rarely contiguous, suberect and convolute when dry (wide spreading and plane in T. retusus), weakly concave with apical part plane and not recurved to strongly concave with apical part turned to ventral side and recurved (in T. convolutus). Lobe symmetrically ovate, oblong-ovate or asymmetrically oblong-ovate, apex rounded to acute, acuminate, dorsal margin entire or irregularly dentate, ventral margin usually upcurved (plane in T. retusus), becoming plane near the apex, entire or dentate. Lobe cell walls thin, trigones usually large, cordate, intermediate thickenings frequent. Vitta cells absent or present in median of lobe, extending to base, ocelli absent. Oil bodies segmented. Lobule oblong-rectangular, inflated, occasionally with a tiny appendage on the surface at the base, keel sometimes with an appendage, apex oblique, with 1–2 teeth, hyaline papilla on the inner surface of the lobule at the proximal base of the first tooth. Underleaves broadly obovate or suborbicular, insertion line slightly arched, apex rounded or emarginate, entire or irregularly dentate, base cuneate or auriculate, underleaf bases free or adnate with leaves on one side. Androecia terminal or intercalary on branches, bracts imbricate, hypostatic, apex acute to apiculate, margins entire or dentate, lobules strongly inflated, bracteoles similar to underleaves in size and shape. Gymnecia terminal on long branches, with 1–2 arillod, arillodium sequence lejeuneoid, bract lobe acute to apiculate at apex, margin entire or dentate, appendages sometimes present on one or both sides of keel, lobules broadly ovate, apex apiculate or bifid, bracteole spathulate, apex bifid or emarginate, margin dentate, plane or recurved. Perianth obovate, with 3 sharp keels, keels in upper 1/3 with numerous laciniate teeth, beak 3–5 cells long. Asexual reproductive organs absent.

Thysananthus is a pantropical genus with 15 species (Sukkharak 2015). The centre of diversity is Southeast Asia with eight species occurring in the area. Four species are known from China. The genus is closely related to Mastigolejeunea, but can be separated from the latter by the keels of perianths, being toothed in Thysananthus and entire in Mastigolejeunea (Sukkharak 2015).

Key to Chinese species of Thysananthus

1. Leaves widely spreading when dry; leaf lobe with vitta; leaf cells subsodiametric (except for vitta) .................................................. T. retusus
2. Apex of leaf lobe convolute when dry; leaf lobe without vitta; leaf cells elongate ................................. 2
2. Apex of leaf lobe positioned towards the ventral side of the leaf .................................................. T. convolutus
3. Leaf lobes asymmetric; apex of leaf lobe truncate, not or shortly continuing into the ventral lobe margin; underleaves obovate to suborbicular; channelled / hollow .................................................. T. aculeatus
3. Leaf lobes symmetric; apex of leaf lobule oblique, longly continuing in the
ventral lobe margin; underleaves spathulate, not channelled / hollow

Thysananthus aculeatus Herzog

Plates 40, 41


Plants yellowish brown when dry. Stem 135–165 μm in diameter, transverse
section with ca. 40–42 epidermal cells and 86–105 medullary cells, epidermal
cells not larger than medullary cells, all cells with thickened walls; ventral
merophyte 9–10 cells wide. Shoots rigid, 2.0–4.5 cm long, 1.3–2.0 mm wide,
branching of the Lejeunea-type. Leaves imbricate, lobe asymmetrically oblong
or broadly ovate, concave, 0.7–1.2 mm long, 0.4–0.8 mm wide, apex acute,
dentate, dorsal margin entire or dentate toward the apex, ventral margin upcurved,
dentate. Lobe cell walls thickened, trigones large, cordate, intermediate
thickenings frequent, marginal cells subquadrate, 6–14 × 6–10 μm, median cells
hexagonal, 20–30 × 8–12 μm, basal cells elongate, 44–70 × 12–26 μm. Vitta
and ocelli cells absent. Oil bodies not seen. Lobule oblong-ovate, ca. 1/3 as long
as the lobe, free lateral margin plane or incurved, apex truncate, not or shortly
continuing into the ventral lobe margin, with 1–2 teeth, first tooth 2–6 cells long,
1–3 cells wide at base, second tooth one cell, usually obsolete, tooth usually
up to 7 cells long when with only one tooth, hyaline papilla as in the genus,
keel straight, without appendage. Underleaves imbricate, channeled or hollow, slightly squarrose when wet, obovate or suborbicular, 0.36–0.50 mm long, 0.40–
0.64 mm wide, 3–4 times as wide as the stem, apex truncate, dentate, lateral
margin usually recurved, insertion line slightly arched, base cuneate, underleaf
bases adnate with leaves on one side, on left-hand side for right branches and
right-hand side for left branches. Androecia and gynoeceia not seen.

Taxonomic notes: Thysananthus aculeatus is characterized by the asymmetrically
ovate leaf lobes, truncate lobules and hollow, obovate underleaves. The species
resembles T. spathulistipus; their differences are given under the latter species.
Plants from Taiwan have a rectangular leaf lobule with only one large lobular
tooth, ca. 6 cells long and 3 cells wide at base (Plate 41).

Habitat and distribution in China: On tree bark. The species has been reported from
Hainan and Taiwan (Pippo 1990).

Representative specimens examined: Hainan. Ledong Co., Jianfengling
National Nature Reserve, Nanya Forest Farm, on tree bark, 570 m, 11 Feb.
1962, P.-C. Chen et al. 753C (HSNU); Lingshui Co., Diaoluoshan National
Nature Reserve, on tree bark, 1020 m, 24 Nov. 1977, 1977 Expedition Team
2906 (HSNU, IBSC). Taiwan. Taiou, Shinsuei-Shuchokyokai, on tree bark, 3
Jan. 1933, Y. Horikawa 10642 (HIRO).

Range: China, Japan, Malaysia, Philippines (Sukkharak 2015).
Thysananthus convolutus Lindenb.

Plate 42

Autoicous. Plants yellowish brown when dry. Stem 185–240 μm in diameter, transverse section with ca. 36 epidermal cells and 90 medullary cells, epidermal cells not larger than medullary cells, all cells with thickened walls; ventral merophyte 7–10 cells wide. Shoots rigid, 1.7–2.7 cm long, 1.6–2.6 mm wide, branching of the Lejeunea-type. Leaves strongly imbricate, lobe asymmetrically ovate, when dry strongly convolute, when moist strongly concave or clasping the stem, apical parts turn to ventral side, recurved, 1.1–1.5 mm long, 0.9–1.1 mm wide, apex acute or apiculate, dorsal margin entire or dentate near the apex, dorsal base auricate, ventral margin upcurved or inrolled, entire or dentate near the apex. Lobe cell walls thickened, trigones large, cordate; intermediate thickening frequent, marginal cells subquadrate, 8–18 × 4–10 μm, median cells hexagonal, 16–28 × 8–12 μm, basal cells elongate, 36–50 × 10–20 μm. Vitta and ocelli cells absent. Oil bodies not seen. Lobule rectangular, ca. 1/3 as long as the lobe, free lateral margin plane or incurved, apex oblique, with 2 teeth, first tooth 1–4 cells long, 1–3 cells wide at base, second tooth 1–2 cells long, 1 cell wide, hyaline papilla as in the genus, keel straight, without appendage. Underleaves imbricate, slightly squarrose, broadly spatulate, 0.9–1.2 mm long, 0.8–1.0 mm wide, 4–5 times as wide as the stem, apex truncate to slightly emarginate, dentate, lateral basal margin recurved, insertion line slightly arched, base cuneate, underleaf bases adnate with leaves on one side, on left-hand side for right branches and right-hand side for left branches. Androecia on long branches, bracts in 6–7 pairs. Gynoecia on stems or long branches, with 1 innovation, innovation leaf sequence lejeuneoid, bract lobe oblong or widely ovate, 1.6–1.8 mm long, 0.9–1.1 mm wide, apex acute or apiculate, margin near the apex dentate, lobules broadly ovate, 1/4–1/3 as long as the lobes, apex apiculate, margin dentate; bracteole spatulate, 1.7–1.9 mm long, 0.8–1.0 mm wide, apex emarginate, lateral margin recurved. Perianth oblong, 2.3–2.5 mm long, 0.5–0.8 mm wide, with 3 keels, keels in upper 1/3 with triangular teeth, teeth consisting of 7–8 cells, 2–3 cells wide at base and ending in a row of 1–2 cells, base 3–4 cells long or obsolete.

Taxonomic notes: Thysananthus convolutus is characterized by asymmetrically ovate leaf lobes, leaves clasping the stem when moist, and underleaf bases adnate with leaves on one side and without auricles. The species is closely related to T. gottschei but the latter species differs by the entire margin of leaf lobes and the laciniate perianth teeth, being 2–4 cells long. Thysananthus convolutus has been described as being dioicous (e.g., Sukkharak 2015) but the Chinese plants are autoicous with gynoecia and androecia on separate branches.

Habitat and distribution in China: On tree bark. The species is newly recorded from Hainan.

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Wang, Zhu & Gradstein
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The present study confirms the taxonomic status of Caudalejeunea tridentata and the relationships of Ptychanthus and Tuzibeanthus by using evidence from three molecular markers (rbcL, trnL-F, rnlTS) and morphological traits, improving the understanding of the diversity of Chinese Ptychanthoideae. It incorporates the most recent results of the ongoing revision of the genera of Ptychanthoideae based on morphology and molecular analysis.

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