A REVISION OF THE GENUS *LEPTOPTERIGYNANDRUM* (BRYOPSIDA, LESKEACEAE)

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**Abstract.** *Leptopterigynandrum* C. Müll. is a pleurocarpous moss genus consisting of ten species (*L. austro-alpinum* C. Müll., *L. auticus* Dix. ex Gangulee & Vohra, *L. brevirete* Dix. ex Blatter & Fernandez, *L. decolor* (Mitt.) Fleisch., *L. incurvatum* Broth., *L. piliferum* S. He, *L. stricticaule* Broth., *L. subintegrum* (Mitt.) Broth., *L. tenellum* Broth., and *L. tenuicaule* (Williams) S. He, *comb. nov.*). It is characterized by the densely verrucose leaf cells, multi-rows of quadrate alar cells, double, often forked costae, subjulaceous to julaceous leafy stems, and reduced hypnoid peristome (cross-striolation and cilia absent). The generic placement in the Leskeaceae rather than its traditional placement in the Thuidiaceae is supported.

**Introduction**

*Leptopterigynandrum* C. Müll. is comprised of ten species of pleurocarpous mosses. The center of diversity of the genus, where all species occur except *L. tenuicaule* (Williams) S. He, is in the southwestern China and Indo-Himalayan regions, typically at high altitudes (from 2,000 to 4,700 m). The genus was once considered to be essentially an Indian-Chinese genus (Gangulee 1978). Its restricted distribution in a relatively small area possibly explains the lack of a comprehensive study for *Leptopterigynandrum*. It has been usually treated with a short description from the commonly encountered species, *L. austro-alpinum* C. Müll. Most species were simply mentioned by listing. The genus itself has not been clearly defined, with a vague conception of its characters such as julaceous stems, ovate to cordate-ovate leaves, short and double costae, and a large group of quadrate alar cells. This broad generic delimitation can provide latitude for circumscriptions of numerous species in the Entodontaceae and Leskeaceae. Species circumscriptions of the genus have been ill delineated, often resulting in misidentifications of specimens. There are also divergent views regarding its inter-generic relationship and systematic position. *Leptopterigynandrum* has been placed into four different families: Entodontaceae, Leskeaceae, Pterigynandraceae, and Thuidiaceae (Brotherus 1925; Buck 1980b; Herzog 1916; Weber 2000). The genus, as previously understood, was basically limited to *L. austro-alpinum*. Before *Leptopterigynandrum* can be meaningfully compared to other closely related genera, the genus must first be critically revised. Judging from its distribution pattern, whether the genus has ten species or has fewer species with a wide range of variation, is worthy of study.

**Taxonomic History**

*Leptopterigynandrum* was established by Müller (1897) to accommodate a sterile Argentinean moss, *L. austro-alpinum*. It was compared to *Pseudoleskea* Bruch & Schimp. in

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having imbricately foliated short branches, cordate-ovate leaves, short double costae, and quadrate alar cells. The genus remained monotypic until Fleischer (1923) incidentally made a combination, *L. decolor* (Mitt.) Fleisch., based on *Stereodon decolor* Mitt. Brotherus (1924, 1925, 1929) subsequently described four species from China, namely *L. incurvatum* Broth., *L. stricticaule* Broth., *L. subintegrum* (Mitt.) Broth., and *L. tenellum* Broth. Four additional species were added to the genus later: *L. brevirete* Dix. from Pakistan (Blatter & Fernandez 1931), *L. autoicum* Dix. ex Ganglee & Vohra from China (Ganglee 1978), *L. clavatum* Buck & Crum from Bolivia (Buck 1980b), and *L. filiforme* (M.-X. Zhang) Stark & Buck from China (Stark & Buck 1986). Three synonyms, *Erythrodontium tenuicaule* Williams, *Garysmithia bifurcata* Steere, and *Leskeopsis peruviana* Broth. were synonymized with *L. austro-alpinum* by Buck (1980b) and Menzel & Schultze-Motel (1987), respectively. *Leptopterigynandrum* has a relatively simple history. When the study began, the genus was comprised of ten specific names worldwide.

*Leptopterigynandrum* was considered by Müller (1897) to be gametophytically similar to *Pseudoleskea* of the Leskeaceae; but Herzog (1916) indicated that it also shared similarities to *Erythrodontium* Hampe and *Trachyphyllum* Gepp of the Entodontaceae. The type species, *L. austro-alpinum*, was placed under *Heterocladium* Bruch & Schimp. of the Thuidiaceae by Brotherus (1907), but he (Brotherus 1925) later changed his view by recognizing the genus *Leptopterigynandrum*. The latter view was supported by Dixon (Blatter & Fernandez 1931) who stated that *Leptopterigynandrum* could be separated from *Heterocladium* on the basis of its well differentiated alar cells and erect, symmetric capsules. Fleischer (1923), without mentioning *L. austro-alpinum*, put *Leptopterigynandrum* in the Thuidiaceae as represented by *L. decolor*. Buck (1979) considered *Leptopterigynandrum* neither close to *Erythrodontium* in the Entodontaceae nor to *Trachyphyllum* in the Thuidiaceae, but rather considered its belonging to the Leskeaceae. Weber (2000) argued that there was little justification for including *Leptopterigynandrum* in the Leskeaceae and suggested its placement in a more naturally related family, the Pterigynandraceae according to his view. The most recent study by Buck & Goffinet (2000) concluded that *Leptopterigynandrum* was closely related to *Pseudoleskea* in the Leskeaceae.

The genus *Leptopterigynandrum* is characterized by the densely verrucose (minutely roughened) laminal cells, a large group of quadrate alar cells, extending about 1/4 the way up the leaf at margins, double or often forked costae, and the imperfect hypnoid peristome or leskeoid peristome. The verrucose leaf cells were first noticed by Steere (1977) in *Garysmithia bifurcata* (= *L. austro-alpinum*) as finely papillose cells. The SEM photos of verrucose leaf cells provided by Tan (1979) show this clearly and Buck (1980b) confirmed this type of papillosity. Other characteristic features of the genus include julaceous or subjulaceous stems that are sparsely to irregularly or sometimes pinnately branched, similar stem and branch leaves, a diminutive or weakly developed central strand, usually erect and symmetric capsules, papillose exostome teeth that are not bordered and inserted well below the mouth, linear endostome segments that are shorter, about 1/2–2/3 the exostome teeth, a relatively high membrane, and the absence of cilia. The distinctions between *Leptopterigynandrum* and its related genera, *Erythrodontium*, *Trachyphyllum*, *Pseudoleskea* Kindb., and *Pterigynandra* Hedw. are shown in Table 1.
<table>
<thead>
<tr>
<th>Characters</th>
<th>Leptopterigynandrum</th>
<th>Erythrosontium</th>
<th>Trachyphyllum</th>
<th>Pseudoleskea</th>
<th>Pterigynandrum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leafy stems</td>
<td>julaceous or subjulaceous</td>
<td>julaceous</td>
<td>julaceous</td>
<td>julaceous or not julaceous</td>
<td>terete or julaceous</td>
</tr>
<tr>
<td>Central strand</td>
<td>diminutive or very weak</td>
<td>relatively well developed</td>
<td>absent</td>
<td>diminutive or absent</td>
<td>absent</td>
</tr>
<tr>
<td>Pseudoparaphyllia</td>
<td>foliose, mixed with filamentous</td>
<td>foliose</td>
<td>small, foliose</td>
<td>foliose</td>
<td>filamentous</td>
</tr>
<tr>
<td>Leaves</td>
<td>stem and branch leaves similar</td>
<td>stem and branch leaves slightly differentiated</td>
<td>stem and branch leaves quite differentiated</td>
<td>stem and branch leaves slightly differentiated</td>
<td>stem and branch leaves similar</td>
</tr>
<tr>
<td>Costae</td>
<td>double or forked</td>
<td>short, double, or absent</td>
<td>short, double</td>
<td>single or double or mixed</td>
<td>unevenly double or single</td>
</tr>
<tr>
<td>Margins</td>
<td>not decurrent at base</td>
<td>decurrent at base</td>
<td>not decurrent at base</td>
<td>not decurrent at base</td>
<td>decurrent at base</td>
</tr>
<tr>
<td>Leaf cells</td>
<td>densely verrucose (minutely roughened)</td>
<td>smooth</td>
<td>prorate at both ends</td>
<td>smooth or papillose at back</td>
<td>prorate at upper ends</td>
</tr>
<tr>
<td>Alar cells</td>
<td>quadrate, 1/4 the way up the leaf at margins</td>
<td>subquadrate, 1/4–1/2 the way up the leaf at margins</td>
<td>subquadrate in several rows at the basal margins</td>
<td>subquadrate, few in extreme basal angles</td>
<td></td>
</tr>
<tr>
<td>Sexual condition</td>
<td>autoicous or dioicous</td>
<td>autoicous</td>
<td>dioicous</td>
<td>dioicous</td>
<td>dioicous</td>
</tr>
<tr>
<td>Capsules</td>
<td>erect, symmetric</td>
<td>erect, symmetric</td>
<td>inclined, asymmetric</td>
<td>inclined, curved, asymmetric</td>
<td>erect, symmetric</td>
</tr>
<tr>
<td>Exostome teeth</td>
<td>inserted well below the mouth, not bordered, papillose</td>
<td>inserted well below the mouth, bordered, usually striate</td>
<td>inserted at the mouth, strongly bordered, cross-striolate below</td>
<td>inserted at the mouth, bordered, obliquely striolate below</td>
<td>inserted below the mouth, short, scarcely bordered, variously striolate below</td>
</tr>
<tr>
<td>Endostome</td>
<td>segments linear, 1/2–2/3 the exostome length; basal membrane relatively high; cilia absent</td>
<td>segments rudimentary or linear; basal membrane absent; cilia absent</td>
<td>segments lanceolate, nearly as long as exostome; basal membrane high; cilia well developed, 1–3</td>
<td>segments lanceolate, slightly keeled; basal membrane high; cilia mostly well developed, 2</td>
<td>segments linear, short or nearly as long as the teeth; basal membrane very low; cilia absent</td>
</tr>
</tbody>
</table>
Erythrodontium is characterized by the julaceous habit, relatively broad leaves with numerous differentiated alar cells, which are mostly wider than long, smooth upper leaf cells, and an erect capsule with cross-striolate exostome teeth and rudimentary endostome segments. Leptopterigynandrum is similar to Erythrodontium in several aspects of these features, but it is different from the latter in having densely verrucose leaf cells, non-striate exostome teeth, well developed endostome segments, and a relatively high basal membrane.

The genus Trachyphyllum is characterized by having differentiated stem and branch leaves, prorate upper leaf cells at both ends resulting from projections, and inclined capsules with perfect hypnoid peristome. The remarkable papillosity of leaf cells at both ends is a distinctive character in defining the genus Trachyphyllum, which is best placed in the Thuidiaceae near Heterocladium (Buck 1979, 1980a). Trachyphyllum seems closest to the genus Heterocladium, but differs in having a large number of quadrate to subquadrate alar cells and the leaf cells that are prorate at both ends rather than only at the apical ends as those in Heterocladium. Gepp (1901) considered Trachyphyllum close to Erythrodontium and placed it in the Entodontaceae. Fleischer (1923) shared a similar view: “The genus Trachyphyllum is connected to Erythrodontium through E. fluminense (= Haplocladium microphyllum) and likewise to Leptopterigynandrum, which already belongs in the group of Heterocladium.” Buck (1980b) did not think that Leptopterigynandrum has anything to do with this relationship. The present study agrees with this view.

Leptopterigynandrum has a remote connection to the genus Pterigynandrum (Pterigynandraceae) even though the generic names somewhat suggest this relationship. Buck (1980a) provided a detailed description characterizing Pterigynandrum. The following features of that genus contrast to those of Leptopterigynandrum: filamentous pseudoparaphyllia, lack of a central strand in stem cross section, decurrent leaf bases, single or often distinctly unevenly double costae, conspicuously prorate leaf cells at back from prominent, usually almost bulbous prorulae at cell ends, fewer alar cells in extreme basal angles, deciduous annuli consisting of 2–3 rows of enlarged thick-walled cells, relatively short exostome teeth that are variously striolate below, very short endostome segments, and a very low basal membrane. The systematic position of Pterigynandrum was one of the most problematic subjects in Buck’s study (1980a).

Compared to Leptopterigynandrum, the leaves of Pseudeskeella can have a single costa and smooth leaf cells, while those of Leptopterigynandrum lack a single costa and always have densely verrucose leaf cells. In addition, Pseudeskeella has curved, asymmetric capsules, while Leptopterigynandrum has erect, more or less symmetric capsules. The well-defined differences between the two genera are in their peristome structures. In Pseudeskeella, the exostome teeth are bordered, obliquely striolate below, and inserted at the mouth, and the endostome segments are lanceolate, keeled, and with 2 cilia; while in Leptopterigynandrum, the exostome teeth are not bordered, only papillose below, and inserted well below the mouth, and the endostome segments are linear, not keeled, and without cilia. In reply to Dr. Steere on the taxonomic position of Garvsmithia (Steere 1977), Ando wrote “…As to the family position I cannot give a decisive conclusion. It is connected with the Leucodontaceae through Pterogonium; on the other hand, with the Leskeaceae
through Pseudoleskeella tectorum. At any rate I don’t think that it belongs in the Hypnaceae.” Steere (1977) ultimately placed Garysmithia in the Leskeaceae, citing that minutely papillose leaf cells played a key role in this placement. It appears that the view of placing the genus Leptopterigynandrum in the Leskeaceae has been gradually achieved and it has been accepted by most recent studies (Buck 1980b; Sharp et al. 1994; Buck & Goffinet 2000; Gradstein et al. 2001).

MORPHOLOGY

Plants of Leptopterigynandrum often occur in loosely interwoven or somewhat compact mats. They are not glossy, usually yellowish green to dull yellowish or pale brown, sometimes glaucous-green or dull green when moist in the field, as indicated by Weber (2000). The leafy stems are often julaceous or subjulaceous with short branches, and are usually irregularly branched, occasionally pinnately branched as in L. piliferum, which lacks distinct julaceous branches because its piliferous leaves are not strongly imbricate.

No species of Leptopterigynandrum has paraphyllia on stems and branches, but they all have pseudoparaphyllia. The pseudoparaphyllia occur around and encircling branch primordia. They are usually foliose, but sometimes with filamentous ones intermixed with foliose ones. All species have similar internal stem structure. In cross sections the stems consist of 3–4 layers of small, thick-walled epidermal cells, a cortex of large, thin-walled cells, and a weakly developed central strand of slightly smaller, thin-walled cells (Fig. 14). The axillary hairs in the genus are few. Each hair is 4–6 cells long with 1–2, small, quadrate, reddish brown basal cells and 2–4 narrow, elongate, hyaline cells.

Leaves of Leptopterigynandrum are usually broadly ovate or cordate at bases and often acuminate and secund at apices. The leaf tips are often broken off easily in most species. The leaves are slightly concave and essentially are not decurrent at base. The leaf margins are mostly entire to subentire, rarely serrulate or serrate near leaf apices. The costae are always double, often forked at or above the bases. They reach 1/4–1/2 or slightly more of the leaf length. The costae are thin, without much internal cell differentiation. In cross section it consists of a non-stereid dorsal layer of smaller cells and a ventral layer of undifferentiated laminal cells.

The leaf cells of Leptopterigynandrum are more variable than previously described. They were often characterized as being rhombic to oblong-rhombic, largely based on L. austro-alpinum. The leaf cells in the genus can be elliptical, rounded-rhombic to oblong-rhombic or rhomboidal to linear-rhomboidal. All species have minutely roughened, wart-like elevations on cell walls, namely verrucose (hardly discernible at high-dry magnifications-about ×400, more distinctive at a higher magnification, e.g., ×600). The peculiar papillosity of leaf cells in Leptopterigynandrum appears to be smooth as often observed under low-power light microscope. Thus, the leaf cells were often described as smooth by several authors (Gangulee 1978; Vohra 1983; Zeng 1985; Wu 2000). The upper leaf cell ends are generally not prorate except that L. autoicum has strongly prorate upper cell ends and L. stricticaule has less prominent projection. The alar cells are typically quadrate or subquadrate occupying a large triangular group in about 1/4 the way up the leaf length at margins and 5–10 rows of cells toward to costae.
Asexual propagula are not known for the genus. The sexual condition of *Leptopterigynandrum* is either autoicous or dioicous. Six species are known to bear fertile plants and two species are autoicous (*L. autoicum* and *L. tenuicaule*). *Leptopterigynandrum tenuicaule* (basionym *Erythrodontium tenuicaule* Williams) was described as dioicous by Williams (1928), but both archegonia and antheridia were found from the same stem in the type specimen. All species that are fertile have elongate setae. The setae are either twisted at the upper part or straight throughout. The capsules are generally erect, smooth, and oblong-ovoid to cylindrical. The stomata are few at the base of capsules and are either superficial or immersed. The opercula are shortly rostrate. The annuli are only slightly developed, consisting of several rows of small, thick-walled cells. The calyptrae have not been seen, thus their morphologies are unknown. The peristome morphology within *Leptopterigynandrum* is consistent without much variation among species. The peristome is double and belongs to “leskeoid” type. The exostome consists of 16 lanceolate and papillose teeth that are inserted well below the mouth. They do not show any striolation. The endostome consists of linear segments arising from a high basal membrane, but cilia are absent. The peristome of *Leptopterigynandrum* is fundamentally a reduced “hypnoid” type, and possibly a reduction form of the peristome of *Pseudoleskeella* through the disappearance of striolation and cilia.

**Taxonomic Treatment**


Plants small to medium-sized, sometimes elongate, loosely interwoven or in somewhat compact mats, dull yellowish to pale brown, not glossy, sometimes glaucous-green when moist in the field, sparsely and irregularly branched, occasionally pinnately branched. Leafy stems up to 8 cm long, 0.20–0.70 mm wide, often julaceous or subjulaceous when dry, tips of branches straight or curved; paraphyllia absent; pseudoparaphyllia mostly foliose, sometimes filamentous; central strand poorly developed. Leaves imbricate-appressed when dry, erect-tumid when moist, plane or concave, lanceolate to narrowly ovate-lanceolate or ovate, oblong-ovate, or cordinate at base, somewhat homomallous to subsecund, often abruptly acuminate or slenderly acuminate, occasionally piliferous, leaf tips often easily broken off, not at all decurrent at bases; costa thin, double, usually short, but sometimes reaching beyond the midleaf, nearly parallel to divergent, or sometimes forked at base or above the base; leaf margins plane, entire, subentire or serrulate, serration usually from the outward prorate cell ends, especially in the upper margins and near the apex; leaf apex short- to long-acuminate, sometimes up to 10-cell long filiform acumina; leaf cells thin- to thick-walled, elliptical, rhombic to rounded-rhombic, short- to elongate-rhomboidal, shorter at margins, more elongate in the upper part and at the center, minutely roughened ( verrucose), often seemingly smooth at low magnifications, sometimes strongly prorate at upper ends; alar cells quadrate or somewhat oblrate, extending up to 1/4 the leaf length, forming a distinct triangular region. Axillary hairs inconspicuous, few, 6–8 cells long, including 2
shorter, brownish basal cells. Setae elongate, smooth, sometimes twisted above; capsules erect, rarely suberect; peristome double; exostome teeth lanceolate, inserted well below the mouth, papilllose, with distinct zig-zag median line; endostome segments linear, somewhat reduced, shorter than the teeth; basal membrane relatively high; cilia absent; opercula conical, shortly rostrate; annuli weakly differentiated, but not inflated, consisting of 3–5 rows of smaller, quadrate to subquadrate or oblate, thick-walled cells. Spores spherical, finely to distinctly papillose. Calyptrae not seen.

Etymology. The name *Leptopterigynandrum*, combing *Lepto-* (from Greek, meaning thin, slender) and the generic name, *Pterigynandrum*, refers to the plants which are similar to, but slender and thinner than, *Pterigynandrum*.

**DISTRIBUTION**

Nine of the ten species recognized in *Leptopterigynandrum* occur in Asia, primarily in southwestern China and Indo-Himalayan regions, including India, Pakistan, and Sikkim. The genus is also known from Mongolia and Russia. There is no species of *Leptopterigynandrum* occurring in Europe, Australia, and New Zealand. It is sporadically recorded from South Africa and little known from North America (Colorado and Alaska) except being more widely known in Mexico. *Leptopterigynandrum* has a wider distribution in South America ranging from Peru, Bolivia, Argentina to Chile.

**KEY TO SPECIES**

1. Stems pinnately branched; branches more or less subjulaceous; leaf apices ending in long, piliferous points, 5–10 cells long .................................................................6. *L. piliferum*
2. Median leaf cells elliptical or rounded-rhombic, 15–20 μm long ..................................................3
3. Plants small; leafy stems mostly less than 1.0(–2.0) cm long, 0.20–0.25 mm wide; leaves narrowly ovate-lanceolate, apices not or only slightly reflexed; pseudoparaphyllia filamentous to slenderly lanceolate; perichaetial leaves ecostate ..............................................................3. *L. brevirete*
4. Branches not tapering at apex; leaves ovate at base, 0.4–0.5 mm wide, shortly acuminate and serrulate at apex; leaf cells distinctly prorate ........................................2. *L. autoicum*
5. Leafy stems slender, 0.20–0.25 mm wide; leaves narrowly lanceolate or narrowly ovate-lanceolate, 0.8–1.0×0.2–0.4 (–0.5) mm .................................................................7.
6. Branches subjulaceous; leaves narrowly lanceolate, apices ending in a point 4 cells long; median leaf cells 6–7 μm wide; pseudoparaphyllia slenderly foliose ........................................9. *L. tenellum*
7. Leaves 0.3–0.4 (–0.6) mm wide; leaves cordate, ovate, oblong-ovate or nearly rounded at base, abruptly slenderly acuminate at apex, 1.0–1.5×0.5–0.8 mm ........................................7.
8. Branches julaceous; leaves narrowly ovate-lanceolate, apices ending in a point 2 cells long; median leaf cells 8–9 μm wide; pseudoparaphyllia foliose ........................................8. *L. subintegrum*
7. Branches strongly curved or circinate; leaves oblong-ovate at base, distinctly asymmetric; costae forked well above the bases; capsules suberect ..................................................... 5. L. incurvatum
7. Branches straight or only slightly curved; leaves cordate or ovate at base, more or less symmetric; costae often divided at bases; capsules erect ..................................................... 8
8. Leaves cordate at base, only slightly reflexed near the apex; median leaf cells 8–10 μm wide; perichaetal leaves ecostate; capsules oblong-ovoid ................................. 4. L. decolor
8. Leaves ovate at base, strongly reflexed near the apex; median leaf cells 6–8 μm wide; perichaetal leaves sinicostate; capsules cylindrical ..................................................... 9
9. Leaf apices shortly acuminate, ending in a point 1–2 cells long, often clearly serrulate or serrate; costae ca. 1/3 to less than 1/2 the leaf length; median leaf cells 28–32×7–8 μm; alar cells in 6–9 rows toward costa; stomata immersed; dioicus ........................................ 1. L. austro-alpinum
9. Leaf apices slenderly acuminate, ending in a point 3–4 cells long, subentire or nearly so, costae clearly reaching beyond 1/2 the leaf length; median leaf cells 40–50(–55)×6–7 μm; alar cells in 5–6 rows toward costa; stomata superficial; autoicus ..................................................... 10. L. tenuicaule


Pterigynandrum austro-alpinum C. Müll. in Fleisch., Hedwigia 59: 218. 1912, nom. nud. in synon.

Type: ARGENTINA. Tucuman, April 1872, Lorentz s.n. (holotype B!, probably destroyed; lectotype FH!, designated here; islectotype H!).


Plants medium-sized, sometimes smaller and slender, grayish green to yellowish green, dull yellowish to pale brown or yellowish brown, not glossy, in compact or loosely interwoven mats; leafy stems julaceous, mostly ca. 2–4 cm long, (0.30–0.45–0.65(–0.80) mm wide, irregularly branched or subpinnately branched, sometimes bearing many young short, julaceous branchlets, usually curved at tips, sometimes clavate (from wet habitat); branchlets 2.5–3.5 mm long, sometimes filiform branches present; stems in cross section with 2–3 layers of small, thick-walled epidermal cells, a cortex of enlarged, hyaline, thin-walled cells, central strand weakly developed; pseudoparaphyllia foliose. Main stem leaves 1.0–1.3×0.5–0.7 mm, imbricate when dry, erect-tumid when wet, broadly ovate at base, somewhat concave and more or less symmetric, reflexed or secund to subsecund at apex, abruptly short-acuminate, ending in a point 1–2 cells long; margins entire below, often clearly serrate; costae thin, double or often forked above the base, reaching up to 1/3–1/2 the leaf length, in cross section cells not very differentiated, stereids absent; upper leaf cells rhombic to short rhomboidal, 16–19×8–9 μm; median cells rhomboidal, 28–32×7–8 μm, verrucose, moderately thick-walled; basal juxtacostal cells rounder-quadrated to rounder-rhombic, ca. 7–9 μm wide; alar cells quadrate or rounded-square, in 6–9 rows toward costa, forming a distinct alar group; branch leaves similar to stem leaves, but smaller.
Figs. 1–16. *Leptopterigynandrum* *austro-alpinum*. (1, habit; 2, branch; 3–5, 8–9, 11, stem leaves; 6–7, 10, 12, branch leaves; 13, leaf cross section; 14, stem cross section; 15, pseudoparaphyllia; 16, perichaetial leaf). Scales in mm: bar = 4.16 (1); bar = 1.04 (2); bar = 0.50 (3–12, 16); bar = 0.056 (13); bar = 0.083 (14–15). Figures 1–7, 13–15, from *Lorentz* s.n. (FH); 8–10, from *Williams* 2775a (NY); 11–12, from *Smith* 304 (NY); 16, from *Herzog* 5112 (JE).
Dioicus. Perichaetial leaves oblong-lanceolate, singly costate. Setae 0.9–1.1 cm long, smooth; capsules erect, oblong-ovoid to short-cylindrical, 2.2–2.5×1.0–1.2 mm; opercula conic, 0.35–0.45 mm high; exothecial cells short-rectangular or irregularly rounded-pentagonal, thick-walled, not collenchymatous; stomata immersed; annuli in 3–4 rows of small, quadrate, thick-walled cells; peristome double, exostome teeth dark brown, lanceolate, inserted well below the mouth, 0.35–0.45 mm high, papillose throughout, outer surface with zig-zag line, inner surface strongly trabeculate; endostome segments shorter than

Figs. 17–26. *Leptopterigynandrum austro-alpinum*. [17, apical leaf cells; 18–19, median leaf cells; 20, basal leaf cells; 21, capsule; 22, exothecial cells; 23, stoma; 24, peristome teeth (outer surface view); 25, peristome teeth (inner surface view); 26, spores]. Scales in mm: bar=0.056 (17–20, 22–23); bar=1.25 (21); bar=0.125 (24–25); bar=0.084 (26). Figures 17–20, from Lorentz s.n. (FH); 21–26, Herzog 5112 (JE).
the teeth, 0.20–0.25 mm high, basal membrane 70–90 \( \mu \)m high; cilia absent. Spores 16–19 \( \mu \)m in diameter, papillose. Calyptrae not seen.

Illustrations. Figs. 1–26.

Etymology. The name *austro-alpinum*, combining *austro-* (Latin, south or southern) and *alpinum* (Latin, alpine), refers to the distribution in southern alpine zone.

Habitat. On rocks, thin sandy soil over rocks, branches or trunks; alt. 3000–4400 m.

Distribution. China, Mongolia, Russia, USA (Alaska), Bolivia, Peru, Argentina, and Chile; Fig. 27.

Anderson et al. (1990) synonymized *Hypnum vaucheri* subsp. *coelophyllum* (Mol.) Mol. as a synonym of *Leptopterigynandrum austro-alpinum* without any explanation. Molendo (1864) described *Hypnum coelophyllum* based on three specimens from the Alps, Austria. Molendo (1865) changed his view and considered it to be a subspecies of *H. vaucheri*. Since then, several authors had treated them as variety of *Drepanium vaucheri* (Lesq.) Roth (Roth 1904) or *Stereodon vaucheri* (Lesq.) Lindb. (Herzog 1912). Ando (1977) treated it as synonym of *Hypnum revolutum* fo. *pumilum* (Husn.) Ando. After examining the syntypes of *Hypnum coelophyllum*, it is clear that this species belongs to the genus *Hypnum*. The leaf margins are markedly revolute, up to more than 2/3 the leaf length and the leaf areolation are clearly different from that found in *Leptopterigynandrum*.

One of the distinguishing characteristics of *Garysmithia* is its short laminal cells covered with fine papillae (Buck 1980b). The peculiar type of papillosity ( verrucosity) was used to separate this taxon from *Pseudoleskeella tectorum* (Funk ex Brid.) Kindb. ex Broth. (Tan 1979). After examining the following species, *L. austro-alpinum*, *L. clavatum*, *L. decolor*, *L. stricticaule*, and *L. subintergum*, Buck (1980b) indicated that the papillae ( verrucae as suggested by Tan) were seen to be well developed in all species except that there is a
doubt in *L. stricticaule*. Under a higher power microscope the leaf cells of *L. stricticaule* exhibit faintly verrucose walls. Tan & Jia (1997) synonymized *L. stricticaule* with *L. austro-alpinum* with no explanation except for citing the specimens. The two species are very different. In *L. stricticaule* the stems and branches are attenuate with leaves usually coriaceous at bases and the leaf cells are elliptical to rounded-rhombic, often prorate at upper cell ends; while in *L. austro-alpinum* the stems and branches are not attenuate with leaves usually ovate at bases and the leaf cells are rhombic to elongate rhomboidal, never prorate at upper cell ends.

*Leptotepierygium clavatum* was described to be different from *L. austro-alpinum* by its clavate branch tips, broad and foliose pseudoparaphyllia, and oblong-ovate leaves (Buck 1980b). These characters are unreliable among specimens from South America. Both clavate branch tips and non-clavate ones can occur from the same collection in several instances; this may be related to wet habitats. The foliose pseudoparaphyllia and oblong-ovate leaves of *L. clavatum* are well within the range of variation expressed in *L. austro-alpinum*.


s.n. (NY); Vostocnyy Sayan Mts., July 27, 1961, Bardunov & Abramova s.n. (FH), USA. Alaska: Mt. McKinley National Park, Hermann 21533 (MICH, NY); Near mouth of Ogoturuk Creek, Steere 650721-12 (NY); Philip Smith Mts. Quad, just E of Galbraith Lake, Murray 76-290B, 77-612 (both in NY), Buck 8860 (NY).


*Type*: CHINA. Southeastern Tibet, Molo, Kongbo Prov., Lud/aw, She riff & Tay/or 4328 (holotype BMI), “*Leptopterigynandrum*", orthogr. pro.

Plants yellowish brown to brownish, in loose or loosely interwoven mats; leafy stems subjulaceous, elongate, slender, mostly 2.5–4.0 cm, up to 6(–7) cm long, 0.3–0.4 mm wide, irregularly to subpinnately branched, branch apices not tapering, filiform branches often present; sometimes with very slender and irregular branches; central strand weakly developed; pseudoparaphyllia foliose. Main stem leaves 0.8–1.0×0.4–0.5 mm, somewhat imbricately appressed when dry, erect-tumid when wet, ovate-lanceolate, cordate at base, slightly concave, shortly acuminate, slightly serrulate and reflexed or secund at apex; costa thin, double, often forked slightly above the base; upper leaf cells irregularly elliptical, 16–18×6–7 μm; median cells elliptical, 14–18×5–7 μm, verrucose, often strongly prorate at upper cell ends, very thick-walled; basal juxtapostomal cells rounded-quadrangular to irregularly quadrate, ca. 4–6 μm wide; alar cells quadrative or rounded-quadrangular, in 5–7 rows toward costa, forming a distinct alar group; branch leaves similar to stem leaves, but smaller. Autoicous. Perichaetial leaves broadly ovate-lanceolate, ca. 1.8 mm long, singly costate. Setae 1.2–1.3 cm long, smooth, twisted near the capsule neck; capsules erect, oblong-ovoid to short-cylindrical, 2.3–2.5×0.9–1.0 mm; exothecial cells irregularly pentagonal, moderately thick-walled, not collenchymatous; stomata few, in the neck of capsules, superficial; annuli somewhat differentiated, in 5–6 rows of small, subquadrate to oblate, thick-walled cells; peristome double, exostome teeth yellowish, lanceolate, 0.3–0.4 mm high, papillose throughout, outer surface with a median zig-zag line, inner surface strongly trabeculate; endostome segments linear, somewhat perforate, shorter than the teeth, 0.18–0.25 mm high; basal membrane 60–80 μm high; cilia absent. Spores 19–23 μm in diameter, papillose. Calyptrae not seen.

Illustrations. Figs. 28–46.

Etymology. The name *autoicum* (Latin autoicus) refers to the autoicous sexual condition.

Habitat. On soil, tree trunks; alt. 3460–3880 m.

Distribution. China and India; Fig. 47.

*Leptopterigynandrum autoicum* was described by Gangulee & Vohra (Gangulee 1978), based on an unpublished name of Dixon and two specimens deposited in BM. Although a full description of the species was provided, no distinctive character was given to separate it from other species of the genus, which was at that time comprised of seven species, as indicated by the authors. Interestingly, Gangulee (1978) did not recognize *Leptopterigynandrum decolor*, but rather considered it to be a species of *Pterigynandrum*. Besides their differences in sexual condition (autoicous in *L. autoicum* and dioicous in *L. decolor*), he did not think there was any relationship between them nor to any other species of
Figs. 28–46. *Leptopterigynandrum autoicum*. [28, habit; 29, branch; 30–32, stem leaves; 33–35, branch leaves; 36, pseudoparaphyllia; 37, apical leaf cells; 38–39, median leaf cells; 40, basal leaf cells; 41, perichaetial leaf; 42, capsule; 43, exothecial cells; 44, stoma; 45, peristome teeth (outer surface view); 46, spores]. Scales in mm: bar=4.16 (28); bar=1.04 (29); bar=0.50 (30–35, 41); bar=0.083 (36); bar=0.056 (37–40, 43–44); bar=1.25 (42); bar=0.125 (45); bar=0.084 (46). Figures 28–46, from Ludlow et al. 4328 (BM).
the genus. *Leptopterigynandrum autoicum* is characterized by the elliptical, distinctly prostrate leaf cells, and relatively robust plants.

Specimens examined. **CHINA.** Sichuan: Ba Tang Co., Zhong Za District, S. He 31347, 31342, 31354, 31380b (all in MO); Dao Cheng Co., Ju Long District, S. He 31681, 31684a, 31690, 31726, (all in MO); Ya Jiang Co., Mt. Jian Zi Wan, S. He 31981, 31982c (both in MO). Xizang (Tibet): Kongbo, Ludlow, Sheriff & Taylor 4416 p.p. (BM). Yunnan: Dschungdien (Chungtien), Bodo (Peti), Handel-Mazzetti 4550 (H); Dokerla, Handel-Mazzetti 8053 (G, S); Dali Co., Handel-Mazzetti 6480 (G, S), Diancang Mt. Range, Redfearn et al. 1524 (MO). **INDIA.** Southern India, collector ignotus s.n. (H).


Type: **PAKISTAN.** Waziristan, Datta Khel to Suidar Peak, on bark of tree, alt. 7000 ft., Stewart 536 (holotype BM), "brevirete", orthogr. pro.

Plants very small, yellowish brown, in loose mats; leafy stems very slender, mostly less than 1.0(−2.0) cm long, 0.20−0.25 mm wide, irregularly branched; pseudoparaphyllia filamentous to very slenderly foliose; central strand poorly developed. Main stem leaves ovate-lanceolate, 0.7−0.8(−0.9)×0.35−0.40(−0.45) mm, slightly concave and incurved at margins below, slenderly acuminate above; margins entire, crenulate above; costae short, unequally forked above the base; upper and median leaf cells similar, irregularly rounded-rhombic, 16−19×6−8 μm, verrucose; basal juxtacostal cells rounded-quadrate to rounded-rhombic, 4−6 μm wide; alar cells quadrate or subquadrate, in 5−6 rows toward costa, form-
Figs. 48–66. *Leptopterigynandra*um *brevirete*. (48, habit; 49, branch; 50–53, stem leaves; 54–57, branch leaves; 58, pseudoparaphyllia; 59, apical leaf cells; 60–61, median leaf cells; 62, basal leaf cells; 63, perichaetial leaf; 64, capsule; 65, exothecial cells; 66, stoma). Scales in mm: bar=4.16 (48); bar=1.04 (49); bar=0.50 (50–57, 63); bar=0.083 (58); bar=0.056 (59–62, 65–66); bar=1.25 (64). Figures 48–66, from Stewart 536 (BM).
ing a distinctly alar group; branch leaves smaller. Dioicous. Perichaetal leaves oblong-ovate at base, gradually acuminate at apex, ecostate. Setae 8–10 mm long, smooth, twisted above; capsules erect, oblong-ovoid, 1.7–1.9×1.1–1.2 mm; exothecial cells irregularly rectangular, thick-walled, not collenchymatose; stomata superficial; annuli weakly differentiated, in 4–5 rows of small, thick-walled, subsquare cells; peristome broken, not in whole, yellowish, inserted below the mouth, cross-striate at base; opercula and calyptrae not seen. Spores not seen.

Illustrations. Figs. 48–66.

Etymology. The name brevirete, combining brev- (Latin, short) and rete (Latin, network), refers to leaf cells that are short.

Habitat. On tree trunks; alt. 2100–3520 m.

Distribution. Pakistan and new to China.; Fig. 67.

Dixon provided the description of *Leptopterigynandr um brevirete* ("brevirette"), but it was only validly published by Blatter & Fernandez (1931). In Dixon’s description, this species was considered to be very near *Heterocladium subintegrum* Mitt. (= *Leptopterigynandr um subintegrum*), but differs from the latter species by having longer, more rigid, less branched stems, more closely imbricate leaves with shorter points, and the longer leaf cells that are more rhomboidal, thin-walled, very smooth, shorter, and subsquare at the margins. Dixon did not mention the verrucose leaf cells in both species, but described them as having smooth cells. The major differences between them are in the length of their costae, the sizes of their leaves, and the shape of leaf cells. *Leptopterigynandr um brevirete* has
shorter costae, extending about 1/4–1/3 the leaf length, smaller leaves (0.7–0.8×0.35–0.40 mm), and elliptical to rounded-rhombic leaf cells (16–19×6–8 µm); while L. subintergum has longer costae, reaching about 2/5–1/2 the leaf length, larger leaves (0.8–1.0×0.4–0.5 mm), and elongate rhomboidal leaf cells (35–43×8–9 µm). Among three species in the genus (L. autocium, L. brevirete, and L. stricticaule) that have elliptic to rounded-rhom­bic leaf cells, L. brevirete is the only one whose cells are not prorate. Leptopterigynandrum brevirete is also characterized by having filamentous or very slenderly foliose pseudoparaphyllia, while all other species in the genus have foliose ones.

Specimens examined. CHINA. Sichuan: Ba Tang Co., Zi La (Yi Dun) District, S. He 31483 (MO); Nan Ping Co., Jiu Cai Gou District, S. He 30169, 30197a, 30259 (all in MO).

       Entodon decolor (Mitt.) C. Müll., Linnaea 42: 435. 1879.
       Leptopterigynandrum decolor (Mitt.) Buck, Bryologist 83: 460. 1980b, nom. hom.

Plants small to medium-sized, dull yellowish to yellowish brown, in loose mats; leafy stems julaceous, (1.0–)2.0–2.5 cm long, 0.40–0.45 mm wide, irregularly and remotely branched; branches short, straight; in cross section consisting of 2–3 layers of small, thick-walled epidermal cells, a cortex of enlarged, hyaline, thin-walled cells, and a weakly developed central strand; pseudoparaphyllia foliose. Main stem leaves cordate at base, slightly concave, more or less symmetric, abruptly acuminate toward slender, slightly reflexed at apex, ending in a point 2 cells long, 1.2–1.4×0.6–0.8 mm; margins slightly incurved below, entire to subentire; costae ca. 1/3 the leaf length, double or forked slightly above the base; apical leaf cells elongate rhomboidal, 40–50×6–9 µm; median cells rhomboidal, 35–40×8–10 µm, verrucose, not prorate; basal juxtacostal cells rhombic to irregularly oblate; alar cells quadrate to subquadrate, in 4–6 rows toward costa; branch leaves similar in shape, smaller in size. Dioicous. Perichaetial leaves oblong-lanceolate or ovate-lanceolate, ca. 4.5 mm long, ecostate. Setae 0.9–1.1 cm long, smooth, not twisted above; capsules erect, oblong-ovoid, 1.8–2.0×0.7–0.8 mm; exothecial cells nearly pentagonal, evenly thick-walled; stomata immersed; opercula shortly conic, ca. 0.5 mm high; annuli weakly differen-
tiated, in 3–4 rows of small, subquadrate, thick-walled cells; peristome double; exostome teeth dark brown, lanceolate, inserted well below the mouth, 0.35–0.40 mm long, faintly papillose throughout, outer surface with a median zig-zag line, inner surface trabeculate; endostome segments slenderly lanceolate, shorter than the teeth, ca. 0.3 mm long; basal membrane ca. 0.14 mm high; cilia absent. Spores 14–19 μm in diameter. Calyptrae not seen.

Illustrations. Figs. 68–87.

Etymology. The name decolor from Latin refers to plants losing their natural color.

Habitat. On rocks; alt. 3000–3900 m.

Distribution. China and Sikkim; Fig. 88.

Brotherus (1907) transferred Stereodon decolor to the genus Pterigynandrum, but later he (Brotherus 1925) followed Fleischer (1923) by placing it in Leptopterigynandrum. Gangulee (1980) continued to follow Brotherus’ earlier treatment of this species by recognizing it in Pterigynandrum. It appeared that both Mitten (1859) and Brotherus (1907) indirectly considered that there was a similarity between Leptopterigynandrum and Pterigynandrum. Mitten (1859) related Stereodon decolor to Pterigynandrum filiforme Hedw., although they are quite different. Buck (1980b) stated that Leptopterigynandrum decolor differed from Pterigynandrum filiforme by its entire margins and acuminate leaf apices. More significantly, the peristome of L. decolor consists of an elongate exostome and an endostome arising from a well developed basal membrane. The leaf cells of P. filiforme are strongly prorate abaxially from projections of the upper cell ends, whereas those of L. decolor are verrucose over the entire adaxial surface, more distinct in those cells near the re-
Fleischer (1917) introduced *Pterigynandr um brandisii* C. Müll., nom. nud. and suggested that it might be a species of *Leptopterigynandrum*. Gangulee (1980) listed this name under *Pterigynandr um decolor*; however, Buck (1980b) considered the plants with this name are assignable to *Eurohypnum leptothalmum* (C. Müll.) Ando.

Buck (1980b) suggested that *L. decolor* might be the same as *L. austro-alpinum*, awaiting a worldwide review of the genus. The present study indicates that they are two different species. *Leptopterigynandrum decolor* differs from *L. austro-alpinum* by its typically cordate leaf bases, slenderly acuminate, nearly entire and weakly secund leaf apices, larger leaf cells (35–40 µm×8–10 µm), oblong-ovoid capsules, and ecostate perichaetial leaves. *Leptopterigynandrum austro-alpinum* generally has ovate leaf bases, shortly acuminate, serrulate and strongly secund leaf apices, smaller leaf cells (28–32 µm×7–8 µm), cylindrical capsules, and costate perichaetial leaves. In addition, *L. decolor* has a much narrower distribution, restricted to Sikkim and reported here new to China.

Specimens examined. CHINA. Sichuan: Ba Tang Co., Zi La (Yi Dun) District, S. He 31596 (MO); Song Pan Co., Near Hong Long Temple, S. He 31536b (MO); Xiang Cheng Co., Mt. Wu Ming, S. He 31795 (MO).


Type: CHINA. Northwestern Yunnan province, Dschungdien (Chungtien), Piepun, Handel-Mazzetti 4743 (holotype H!; isotypes FH!, SI).

Plants grayish green to yellowish green, or pale yellowish brown, in loose mats; leafy stems less than 1.5–2.5 cm long, 0.45–0.55 mm wide, more or less subjulaceous, irregularly or subpinnately branched, often toward one side; branches strongly incurved or circinate; stems in cross section with 2–3 layers of small, thick-walled epidermal cells, a cortex of enlarged, hyaline, thin-walled cells, a central strand poorly developed; pseudoparaphyllia foliose or slenderly lanceolate. Main stem leaves oblong-ovate, slightly concave, distinctly asymmetric, suddenly slenderly acuminate, 1.3–1.5×0.5–0.7 mm; margins entire to subentire, costae forked above the base, reaching ca. 1/2 the leaf length, in cross section stereid cells not differentiated; apical and median leaf cells rhomboidal, 24–32×6–8 µm, verrucose, not prorate; basal juxtacostal cells rhombic, 12–16 µm wide; alar cells quadrate to oblate, in 4–5 rows toward costa; branch leaves similar in shape, smaller in size. Dioicus. Perichaetial leaves oblong-lanceolate, ca. 2.0 mm long, singly costate. Setae ca. 1.1 mm long, smooth, not twisted above; capsules suberect, oblong-ovoid, 1.7–1.8×0.8–0.9 mm; exothelial cells irregularly pentagonal; stomata superficial; opercula conic, 0.4–0.5 mm high, not rostrate; annuli weakly differentiated, in 5–6 rows of small, subquadrate to oblate, thick-walled cells; peristome double; exostome teeth inserted well below the mouth; other features of the peristome similar to those of *L. decolor*. Spores 14–19 µm in diameter. Calyptrae not seen.

Illustrations. Figs. 89–109.

Etymology. The name *incurvatum* from Latin *incurvatus*, meaning curved inwards, refers to stems and branches that are incurved.

Habitat. On tree trunks; alt. 2850–3850 m.
Distribution. Endemic to China; Fig. 110.

Leptopterigynandrum incurvatum is typically characterized by its circinate branches and oblong-ovate, asymmetric stem leaves. Additional characters used to distinguish it from other species include suberect capsules, shortly conic operculae, and usually very slender pseudoparaphyllia.


6. Leptopterigynandrum piliferum S. He, sp. nov.

Species nova Leptopterigynandro decolor (Mitt.) Fleisch. affinis, sed foliis piliferis, ramis non julaceus differt. Type: MONGOLIA. Khangai: Ts. Tsegmed 2660 (holotype NY!).

Plants medium-sized, elongate, grayish green or dull green, in loose mats; leafy stems ca. 4.0 cm long, 0.4–0.5 mm wide, pinnately branched, subjulaceous, sometimes flagelliform branches present; stems in cross section consisting of 3–4 layers of small, thick-walled epidermal cells, a cortex of enlarged, hyaline, thin-walled cells, and a diminutive central strand; pseudoparaphyllia foliose. Main stem leaves ovate-lanceolate, 1.2–1.4 × 0.5–0.6 mm, not concave, abruptly ending in piliferous apices (hair-points 5–10 cells long); margins slightly incurved below, entire; costae double or forked near the base, reaching 1/4–1/5 the leaf length; hair-pointed cells rectangular, subapical leaf cells elongate-rhomboidal, 35–45 × 6–8 μm; median cells rhomboidal, 30–35 × 8–10 μm, verrucose, moderately thick-walled, not prorate; basal juxtacostal cells rhombic or subquadrat, 10–12 μm wide; alar cells quadrate, in 5–6 rows toward costa; branch leaves similar in shape, smaller in size. Dioicous? (only archegonia found). Sporophyte not seen.

Illustrations. Figs. 111–124.

Etymology. The name piliferum from Latin, meaning bearing hairs, refers to leaves that are piliferous.

Habitat. On thin soil over rock; alt. 2240–3040 m.

Distribution. China and Mongolia; Fig. 125.

The short, double costae, rhomboidal leaf cells, quadrate to subquadrat alar cells forming a distinct triangular group, foliose pseudoparaphyllia, a diminutive central strand, and especially verrucose leaf cells all point to the genus Leptopterigynandrum. The new species is close to L. decolor, but differs by its piliferous leaf apices and more or less subjulaceous stems. The type specimen was determined as L. austro-alpinum (Tsegmed 2660, NY).

Figs. 89–109. Leptopterigynandrum incurvatum. (89, habit; 90, branch; 91–93, stem leaves; 94–96, branch leaves; 97, leaf cross section; 98, pseudoparaphyllia; 99, stem cross section; 100, apical leaf cells; 101–102, median leaf cells; 103, basal leaf cells; 104, perichaetal leaf; 105, capsule; 106, operculum; 107, exothecial cells; 108, stoma; 109, spores). Scales in mm: bar = 4.16 (89); bar = 1.04 (90); bar = 0.50 (91–96, 104); bar = 0.056 (97, 100–103, 107–108); bar = 0.083 (98–99); bar = 1.25 (105–106); bar = 0.084 (109). Figures 89–109. from Handel-Mazzetti 4743 (H).
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Fig. 110. Distribution of Leptopterigynandrum incurvatum.

Paratypes: CHINA. Sichuan: Nan Ping Co., Jiu Cai Gou District, S. He 30201, 30209 (both in MO).


Type: CHINA. Northwestern Yunnan, Chungtien (Zhongdien), Peipun, Handel-Mazzetti 4760 (lectotype FH!, designated here); southwestern Sichuan (Setschwan), Yenyuen, Handel-Mazzetti 2338 (syntypes FH!, H!, JE!, SI!).

Plants yellowish green, pale yellowish brown to yellowish brown, in loosely interwoven mats; leafy stems elongate, julaceous to subjulaceous, ca. 8 cm long, 0.5–0.6(–0.7) mm wide, rigid, irregularly branched; central strand poorly developed; branches attenuate at apex; branchlets 5–8 mm long, tips slightly curved and attenuate, sometimes elongate and slender; pseudoparaphyllia numerous, slenderly foliose. Main stem leaves cordate to broadly ovate at base, rather abruptly narrowed, slenderly acuminate at apex, 1.2–1.4×0.6–0.8 mm; margins slightly incurved below, entire nearly throughout or only crenulate near the apex; costae double, forked near the base, reaching up to 1/3 the leaf length; upper leaf cells irregularly rectangular or rhomboidal, 16–20×6–8 μm, filiform apices consisting of 2–3 cells; median cells elliptical to narrowly oval, 12–14×5–7 μm, verrucose, thick-walled, slightly to moderately prorate at upper cell ends; basal juxtacostal cells rounded-rhombic to oblate; alar cells quadrate, in 5–7 rows toward costa, forming a distinct alar group; branch leaves similar in shape, smaller in size. Dioicous. Sporophytes not seen.

Illustrations. Figs. 126–136.
Figs. 111–124. *Leptopterigynandrum piliferum*. (111, habit; 112, branch; 113–115, stem leaves; 116–118, branch leaves; 119, pseudoparaphyllia; 120, stem cross section; 121, apical leaf cells; 122–123, median leaf cells; 124, basal leaf cells). Scales in mm: bar=4.16 (111); bar=1.04 (112); bar=0.50 (113–118); bar=0.083 (119–120); bar=0.056 (121–124). Figures 111–124, from Ts. Tsegmed 2660 (NY).
Fig. 125. Distribution of *Leptopterigynandra* *piliferum*.

Etymology. The name *stricticaule*, combining *strictus* (Latin, very straight) and *caule* (Latin stem), refers to plants that have very straight stems.

Habitat. On tree trunks; alt. 3325–3800 m.

Distribution. China and India; Fig. 137.

*Leptopterigynandra* *stricticaule* is the most robust species in the genus with stems up to 8 cm long. It is characterized by having attenuate branches, generally cordate leaf bases with somewhat incurved margins, and rounded-rhombic to elliptic leaf cells with indistinct prorulae at upper ends. Tan and Jia (1997) reduced this species to be a synonym of *L. austro-alpinum*, with which this study disagrees. The differences between the two species were discussed earlier.


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Figs. 126–136. *Leptopterigynandrum stricticaule.* (126, habit; 127, branch; 128–129, stem leaves; 130–131, branch leaves; 132, pseudoparaphyllia; 133, apical leaf cells; 134–135, median leaf cells; 136, basal leaf cells). Scales in mm: bar = 4.16 (126); bar = 1.04 (127); bar = 0.50 (128–131); bar = 0.083 (132); bar = 0.056 (133–136). Figures 126–136, from Handel-Mazzetti 4760 (H).
Type: CHINA. Xizang (Tibet), Long-zi Xian (Co.), Zhun-ba, M. Zang 1215 (holotype WUK; isotype HKAS!).

Plants grayish green to yellowish green when young, yellowish brown when old, in loosely interwoven, or sometimes compact mats; leafy stems slender, julaceous, irregularly branched, ca. (1.0–)1.5–2.5(–3.5) cm long, 0.20–0.25 mm wide, sometimes with many branchlets or many flagelliform or filiform branches at young stage, less than 1 cm long; central strand diminutive; pseudoparaphyllia broadly foliose. Main stem leaves imbricate-appressed when dry, erect-tumid when wet, narrowly ovate-lanceolate, 0.8–1.0×0.4–0.5 mm, gradually acuminate, apices ending in a point 2 cells long; margins slightly incurved below, entire to subentire or somewhat serrulate at branch leaf apices; costae double or forked close to the base, relatively strong, reaching up to 1/2 the leaf length; apical leaf cells narrowly rhomboidal, 18–21×6–7 μm; median cells elongate-rhomboidal, 35–43×8–9 μm, verrucose, moderately thick-walled, not prorate at upper cell ends; basal juxta-costal cells irregularly rhombic to shortly rectangular; alar cells quadrate, in 5–7 rows toward costa, forming a distinct alar group; branch leaves similar in shape, smaller in size. Dioecious. Sporophytes not seen.

Illustrations. Figs. 138–155.

Etymology. The name subintegrum, combining sub- (Latin, somewhat) and integrum (Latin, entire), refers to leaves that have nearly entire margins.

Habitat. On tree trunks, base of trees, rotten woods, or rocks; alt. 2400–4700 m.

Distribution. India, China, Mongolia, Russia, USA (Alaska, Colorado), Bolivia, and South
Figs. 138–155. *Leptopterigynandrum subintegrum*. (138, habit; 139, branch; 140–142 & 146–148, stem leaves; 143–145 & 149–150, branch leaves; 151, pseudoparaphyllia; 152, apical leaf cells; 153–154, median leaf cells; 155, basal leaf cells). Scales in mm: bar=4.16 (138); bar=1.04 (139); bar=0.50 (140–150); bar=0.083 (151); bar=0.056 (152–155). Figures 138–145 & 151–155, from Thomson s.n. (BM); 146–150, from M. Zang 1215 (WUG).

Stark & Buck (1986) transferred *Forststroemia filiformis* M.-X. Zhang to the genus *Leptopterigynandrum* based on the short, often double costae, leaf areolation pattern, and a diminutive central strand. The morphology of densely and minutely roughened leaf cells was not used by the authors as a distinctive character for the placement of this taxon since the leaves were described as having smooth laminal cells. The leaf cells in *L. filiforme*, especially those from older leaves are verrucose, and most conspicuously so near the costae...
in the middle of leaves. They are similar to those observed in *L. subintegrum*. Other features of *L. filiforme* are identical to those of *L. subintegrum*, thus, making it a synonym of the latter species.

Weber (2000) reported that the plants of *L. austro-alpinum* from Colorado, U.S.A. were glaucous-green or dull blue-green when moist in the field. Many herbarium specimens from this region do appear to be very green, but the confirmation of this bluish green color needs to be tested in other geographic regions. All specimens named as *L. austro-alpinum* from Colorado have proven to be *L. subintegrum*. The plants are fairly small, with many short branchlets. The leafy stems are usually less than 1.5 cm long, 0.20–0.25 mm wide. The leaves have larger cells (35–40×8–9 μm). These characters contrast markedly from those of *L. austro-alpinum*, which generally has medium-sized leafy stems (2–4 cm long, 0.4–0.6 mm wide), and smaller leaf cells (28–32×7–8 μm). *Leptopterigynandrum subintegrum* appears to have a much wider distribution in the world than was previously thought (i.e. restricted to India and China).

Specimens examined. **BOLIVIA.** Chuquisaca: Prov. Nor Cinti, 20°36'S, 64°45'W, Lewis 84-1945 (NY); Prov. Sur Cinti, 20°55'S, 64°49'W, Lewis 84-1878 (NY). La Paz: Ancoma, Cordillera Real, 15°46'S, 68°33'W, Troll s.n. (JE, NY). Potosi: Prov. Quijarro, Lewis 79-384A (FH, GOET). Tarjia: Prov. Mendez, Lewis 79-696 (H). **CHINA.** Qinghai: Yushu Pref. Nangqen Co., 31°55'N, 96°27'E, B. C. Tan 95-179, 95-185 (both in FH, NY), Sichuan: Ba Tang Co., Zhong Za District, S. He 31383, 31395, 31427 (all in MO); Dao Cheng Co., Ju Long District, S. He 31682, 31707 (both in MO), Sang Dui District, S. He 31814a, 31822, 31823 (all in MO); Markham Co., Zuo Ke Ji District, S. He 31267 (MO), ca. 15 km S of Zhuokeji, Allen 7011 (MO); Nan Ping Co., Jiu Cai Gou District, S. He 30095b, 30096, 30157e (all in MO), at km 142, Huangshengguan to Zhangia, Allen 7077 (MO), at km 36 marker, from Zhangla to Jiucaigou, Redfearn 35376 (FH); Ya Jiang Co., Mt. Jia Zi Wan, S.
He 31961 (MO). Xizang: Cha Yu (Zayü) Co., Z.-C. Ni 7 (MO); Takpo Prov., Kongbo La (southern Tibet), Ludlow, Sherriff & Taylor 189b (BM). Yunnan: Haba et Dugwantsun, Dschungdien (Chung-tien), Handel-Mazzetti 6993 (BM, S). INDIA. Simla, Aug. 1848, Thomson s.n. (NY). MONGOLIA. Khangai: Ts. Tsegmed 2916 (H); Khovd: Ts. Tsegmed 3622 (S). RUSSIA. Altai Mts., Ignatov 9/32 (MO), Kurkure Range, Ignatov 8159 (MO); Karakem River Valley, between Kobiguayuk and Ayu­lyuyuyuk Creeks; 50°30'N, 89°10'E, June 20, 1989, Ignatov s.n. (NY). SOUTH AFRICA. Lesotho, along cliff just E of Chalete at Sani Pass, alpine grassland, Magill 7126 (as L. austro-alpinum, MO, S); igneous cliffs S of Sani Pass border post, alpine meadow, Magill 7094 (as L. austro-alpinum, MO), 7095 (as L. austro-alpinum, MO, S). USA. Alaska: Philip Smith Mts. Quad, N of Atigun Canyon, 68°29'N; 149°25'W, Lewinsky 2570, 2577, 2792 (all in MICH). Colorado: Hinsdale Co., San Juan Mts., Hermann 27839 (B, G, MICH, MO, NICH, NY, S), Cebolla Creek, Cebolla Camp­ground, 15 miles East Lake City, Hermann 27230 (MICH, NY, US), along Squaw Creek Trail, Rio Grande Wilderness area, Hermann 27874 (MICH, NY); Boulder Co., Boulder Canyon, 1.5 mi above and west of Boulder Falls, Weber B-35817 (NY), Little Royal Gorge of Como Creek, Weber & Wittmann B-110617 (MO); Clear Creek Co., 3.5 miles SW Idaho Springs, along Chicago Creek, Hermann 28020 (MICH, S); Fremont Co., Cheney s.n. (NY); Larimer Co., Rocky Mountain National Park, 1 mile North of Indianhead branch, 40°26'45"N, 105°30'15"W, Rolston 84175 (MICH, NY).

Type: China. Sichuan (Setschwan), Muli Co. alt. 3600–3700 m, Handel-Mazzetti 7365 (holotype H!).

Plants green, or yellowish green to brownish green, in loosely interwoven mats; leafy stems soft, very slender, subjulaceous, usually 1.0–2.0 cm long, occasionally reaching 4.0 cm long, 0.20–0.25 mm wide, irregularly and remotely branched, sometimes with many short branchlets, 3–5 mm long; central strand of stems not clearly developed; pseudopara­phyllia slenderly foliose. Main stem leaves appressed when dry, erect-tumid when wet, 0.8–1.0×0.2–0.3 mm, narrowly lanceolate, slenderly acuminate to filiform, ending in a point 4 cells long; margins plane, entire to subentire, slightly serrulate near the apex; costae double, short, or forked near the base, reaching up to 1/4–1/3 the leaf length; upper leaf cells rectangular; lower cells and median leaf cells similar, elongate rhomboidal, 30–40×6–7 μm, verrucose, moderately thick-walled, not prorate at both ends; basal juxtacostal cells irregularly rectangular to rhomboidal; alar cells quadrate, in 4–6 rows toward costa, forming a distinctly alar group; branch leaves similar in shape, smaller in size. Dioicous. Sporophytes not seen.

Illustrations. Figs. 157–169.

Etymology. The name tenellum from Latin, delicate, refers to plants that are small, slender, and thin.

Habitat. On tree trunks; alt. 1900–4200 m.

Distribution. China, Mongolia, Russia, and Bolivia; Fig. 170.

The slender, subjulaceous stems and narrowly lanceolate leaves with filiform leaf apices of 4 cells long, and slender pseudoparaphyllia mixed with foliose ones are characteristics of L. tenellum. Two Bolivian specimens were annotated with an unpublished name as Leptopterigynandrum angustatum Buck, and these proved to be L. tenellum. Besides this, the species originally described from China now extends its distribution range to Mongolia and Russian Altai Mountains as well.

Specimens examined. BOLIVIA. In Felslochern des Pinasgebietes, Herzog 2614 (JE, NY, S, an-
notated as *Leptopterigynandrum angustatum* Buck, *nud. nud*.). CHINA. Sichuan: A Ba Co., Mai Er Ba District, S. He 31041 (MO); Li Co., Redfearn et al. 34978, 34988b (both in MO); Song Pan Co., Near Huang Long Temple, S. He 30518 (MO). MONGOLIA. Khentei: Ts. Tsegmed 2448 (NY); Khovd: Tsegmed 376 (NY). RUSSIA. Altai Mts., Ignatov 0/681, 8/152 (both in MO).

10. **Leptopterigynandrum tenuicaule** (R. S. Williams) S. He, *comb. nov.*


Plants dull yellowish to pale brown or yellowish brown, somewhat compact or in
loosely interwoven mats; leafy stems subjulaceous to more or less julaceous, slenderly elongate, 1.5–2.5 cm, sometimes to 5–6 cm long, (0.2–)0.3–0.5(–0.6) mm wide; irregularly branched, branch tips straight to slightly curved, sometimes with flagelliform branches or short branchlets, ca. 3–4 mm long; central strand diminutive, with several slightly smaller and thin-walled cells; pseudoparaphyllia lanceolate-foliaceous. Main stem leaves imbricately appressed or loosely imbricate when dry, erect-tumid when wet, 1.1–1.3×0.6–0.7 mm, ovate to oblance-ovate, slightly concave, rather abruptly narrowed, slenderly acuminate at apex, often ending in a point 3–4 cells long; margins somewhat incurved on one side and nearly entire below, subentire near the apex; costae double, reaching beyond 1/2 the leaf length, often forked above the base; upper and median leaf cells similar, linear-rhomboidal, 40–50(–55)×6–7 μm, moderately thick-walled, distinctly verrucose, not prorate at upper cell ends; basal juxta-costal cells irregularly rhombic to subquadrate; alar cells quadrate, in 5–6 rows toward costa, forming a distinct alar group; branch leaves similar in shape, smaller in size. Autoicous. Perichaetial leaves oblanceolate, singly costate. Setae 8–10(–12) mm long, smooth, not twisted above; capsules erect, cylindrical, 2.4–2.6×0.7–0.8 mm; opercula conic, ca. 0.45 mm high; annuli weakly developed, in 3–4 rows of small, pentagonal, thick-walled cells; exothecial cells pentagonal, moderately thick-walled, not collenchymatous; stomata superficial; peristome double; exostome teeth dark brown, lanceolate, inserted well below the mouth, 0.45–0.50 mm high; endostome segment linear, 0.30–0.35 mm high; basal membrane ca. 0.15 mm high; cilia absent. Spores 15–19 μm in diameter. Calyptrae not seen.

Illustrations. Figs. 171–189.

Etymology. The name *tenricula*, combining *tenui-* (Latin, slender) and *caule* (Latin, stem),
Figs. 171–189. *Leptopterigynandrum tenuicaule*. [171, habit; 172, branch; 173–174, stem leaves; 175–177, branch leaves; 178, pseudoparaphyllia; 179, apical leaf cells; 180–181, median leaf cells; 182, basal leaf cells; 183, perichaetal leaf; 184, capsule; 185, operculum; 186, exothecial cells; 187, stoma; 188, peristome teeth (outer surface view); 189, spores]. Scales in mm: bar = 4.16 (171); bar = 1.04 (172); bar = 0.50 (173–177, 183); bar = 0.083 (178); bar = 0.056 (179–182, 186–187); bar = 1.25 (184–185); bar = 0.125 (188); bar = 0.084 (189). Figures 171–182, from *Bües 1057* (NY); 183–189 from *Herzog 3456* (JE).
refers to slender stems.

Habitat. On tree trunks, branches, or rocks; alt. (1200–)3000–4400 m.

Distribution. Mexico, Bolivia, and Peru; Fig. 190.

Williams (1928) described *Erythrodon tium tenuicaule* without providing any justification for its generic position. It was described as dioicous, but the fruiting plants of the type specimens clearly show an autoicous sexual condition. *Erythrodon tium tenuicaule* was synonymized with *Leptopterigynandrum austro-alpinum* by Buck (1980b), probably based on a much broader concept of the latter species. The two species clearly differ in the following aspects. *Leptopterigynandrum austro-alpinum* is characterized by the shortly acuminate leaf apices that are often clearly serrulate or serrate, ending in a point 1–2 cells long, shorter costae extending ca. 1/3 to less than 1/2 the leaf length, shorter median leaf cells (28–32×7–8 μm), alar cells in 6–9 rows toward costa, immersed stomata, and dioicous sexual condition. In contrast, *L. tenuicaule* is characterized by the slenderly acuminate leaf apices that are subentire or near so, often ending in a point 3–4 cells long, longer costae mostly reaching beyond 1/2 the leaf length, longer median leaf cells (40–55×6–7 μm), alar cells in 5–6 rows toward costa, superficial stomata, and autoicous sexual condition. The most distinctive features of *L. tenuicaule* are slenderly acuminate leaf apices and elongate-rhomboidal leaf cells. These features were excellently illustrated by Herzog (1916, Fig. 65) based on specimens from Bolivia and by Sharp et al. (1994, Fig. 637) based on specimens from Mexico. The Bolivian and Mexican expressions are identical to the type expression of *Erythrodon tium tenuicaule* from Peru; however, they have until now been treated as identi-
cal to *L. austro-alpinum* in Mexico and tropical America. The typical expression of *L. austro-alpinum* in tropical America was well illustrated by Buck (1980b) and Gradstein et al. (2001). It is apparent that there are two species in this complex, *L. austro-alpinum* and *L. tenuicallle*, in tropical America. There is only one species, *L. tenuicallle*, in Mexico.


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**LITERATURE CITED**


Williams, R. S. 1928. Some apparently undescribed mosses from Peru, also new combinations. Bry-