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On the evolution and classification of *Scapania* (Hepaticae) — subgenus *Plicaticalyx*

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Subgenus *Plicaticalyx* (Müll. Frib.) H. Buch is a sharply defined group of *Scapania* (Dumort.) Dumort. delimited primarily on the stem and perianth characters. The species composition of *Plicaticalyx* is revised to include only three species, *Scapania ferruginea* (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees, *S. orientalis* Müll. Frib., and *S. ciliatospinosa* Horik. A key to the recognized species of *Plicaticalyx* with revised descriptions is provided. Phylogenetic relationships of *Plicaticalyx* with other *Scapania* are considered.

Key words: evolution, hepatics, *Scapania*, *Scapaniaceae*, *Plicaticalyx*, taxonomy

INTRODUCTION

Work on the classification of *Scapania* (Dumort.) Dumort. has shown that the subgenus *Plicaticalyx* (Müll. Frib.) H. Buch represents a sharply defined group of species (Potemkin 1998). It has two groups of characteristics otherwise unknown for the subgenus *Scapania s. lato* (Potemkin 1998): (1) stem with outer cortical cells more thin-walled than more interior cells and tending to form a hyalodermis. Formation of hylodermis correlates with development of more thin-walled marginal cells of lobe bases and rather broad rhizoids. These adaptations should be efficient for water absorption from the substrate through the outer cortical cells and subsequent transmission of water to the leaves. (2) Perianth subcylindric, ± polystratose and contracted to the mouth, with strongly thickened and light reflecting walls. Such a perianth, developed on plants with sharply keeled female bracts, appears to be a highly specialized device for sporophyte protection, which is somewhat similar functionally to a coelocaule. In contrast, inflated perianth development in the subgenus *Scapania* normally correlates with a weak development of the bract keel and/or orientation of lobes with respect to each other and their concavity. Otherwise, the shape of the perianth in *Plicaticalyx* is more advanced than in the subgenus *Scapania s. lato* and not dependent on the bract shape. These distinctive characters make *Plicaticalyx* more sharply defined from *Scapania* than those of any other historically recognized subgenus. The choice of perianth and stem characters in defining *Plicati-*

calyx more or less parallels the characters used to define the subgenus *Plectocolea* (Mitt.) Amakawa of *Jungermannia* L.

SPECIES COMPOSITION IN HISTORICAL PERSPECTIVE

Different authors have had different treatments of *Plicaticalyx*. These authors paid insufficient attention to stem anatomy and leaf tooth distribution. In this connection absence of data on perianth led to ambiguity of species attribution to the subgenera *Plicaticalyx* or *Protoscapania* (≡ sectio *Planifoliae* (Müll. Frib.) Potemkin of the subgenus *Scapania*).

Müller (1905: 295) mentioned that because of perianth shape, Gruppe *Plicaticalyx* requires higher taxonomic differention than the other groups recognized by him within *Scapania*. He considered the shape of perianth as a reason to include in *Plicaticalyx* even an unrelated species, *Scapania vexata* C. Massal., which is presently treated under the section *Scapaniella* (H. Buch) Potemkin of the subgenus *Scapania* (Potemkin 1998). Müller's approach was shared in different ways by Buch (1928), Amakawa and Hattori (1954), and Amakawa (1981). That resulted in assignment of unrelated species to this group. Buch (1928), raising Müller's Gruppe *Plicaticalyx* to subgeneric rank, synonymized with it Gruppe *Planifolia* with *Scapania ornithopoides* (With.) Waddell (*"ornithopodioides"*) and *S. nimbosa* Lehm., for which a perianth was unknown. Later, Amakawa and Hattori (1954) suggested the subgeneric name *Protoscapania* for Müller's Gruppe *Planifolia* but included in that subgenus an unrelated species of the subgenus *Plicaticalyx*, *Scapania ciliatospinosa* Horik., for which a perianth was unknown. Schuster (1974: 244) considered *Plicaticalyx* as an evolutionary step to *Protoscapania,* which is specialized in a different way. Amakawa (1981) provided detailed illustrations of many characters of the subgenus, including stem anatomy, but included in *Plicaticalyx Scapania maxima* Horik., which has a cortex and distinct basal tooth distribution typical of *Planifolia*. Earlier he (Amakawa 1964) erroneously considered *S. maxima* (as *S. pseudoferruginea* Amakawa) as a species closely related to *S. ferruginea*. Inoue (1972) and Potemkin (1998) transferred *S. maxima* to the sectio *Planifoliae*.

Study of extensive *Scapania* materials worldwide showed that only three species, *S. ciliatospinosa*, *S. ferruginea, and S. orientalis* Müll. Frib., may be attributed to *Plicaticalyx*.

TAXONOMIC ACCOUNT

Subgenus *Plicaticalyx* (Müll. Frib.) H. Buch *emend*. Potemkin

Scapania Gruppe *Plicaticalyx* Müll. Frib., Monogr. Lebermoosgat. *Scapania*: 295. 1905, *p. max. p. — Diplophyllum* Steph., Spec. Hep. IV: 108. 1910, *p. min. p. — Scapania* subgenus *Plicaticalyx* H. Buch, Soc. Sci. Fenn. Comm. Biol. 3(1): 160. 1928, *p. p.*; Amakawa, Hikobia Suppl. 1: 117–118. 1981, *p. max. p.* — Type: *Scapania ferruginea* (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees, Syn. Hepat. 72. 1844.

Plants 1–7 mm wide × 7–80 mm long, green to usually ± brown, sporadically with solitary ventral-intercalary branches. Stem cortex interrupted ventrally (i.e. with several tiers of cortical cells hardly thick-walled and slightly pigmented (Fig. 2: I)), formed of (2–)3–4 strata of more thick-walled intracortical cells and an outer layer of mostly lighter pigmented to bleached cortical cells with thinner walls and larger cavities, tending to form a ± distinct hyalodermis; stem cross section with a halo of mycorrhizal cells mostly in medullary cells adjacent to cortical cells and exceptionally with a central strand of bastlike cells with vestigial lumina. Rhizoids broad, 11–25 μm wide. Leaves spinose-dentate to ciliate, with ± suppressed dentition basally, with acute, straight to moderately arched keel, (0.02–)0.07–0.3(–0.45) the ventral lobe length. Dorsal lobe 0.25–0.6(–0.8) the ventral in area, ± oblique cordate, rectangular- or cordate-reniform, (0.7–)0.95–1.5(–1.65) as wide as long, subparallel or moderately divergent with stem, arcuately inserted to long decurrent. Ventral lobe ± oval to ovate, 0.6–1.05 as wide as long, arcuately inserted to long decurrent. Median leaf cells small to medium-sized, 14–28 × 17–33 μm, thin-walled, with acute to bulging trigones. Marginal cells smaller, in 1–3 rows ± thick-walled. Cuticle smooth to faintly papillose. Gemmae (1–)2-celled, ovoid to subspherical, yellowish to reddish brown, ± thin-walled, with more deeply pig-

mented internal walls. Dioicous. Perianth subcylindric, in outline ± oval or clavate, contracted to mouth, with 6–10 plicae mostly distal, more rarely (in some phases of *S. ciliatospinosa*) with plicae spreading to the proximal third, in cross-section normally polystratose at least in the proximal half, with mostly strongly thickened external and internal walls (thickness of the perianth wall varies greatly and seems to show much dependency on conditions of growth). Perianth mouth ciliate, the length of cilia correlating with length of marginal leaf cilia. Sporophyte characteristics known for *S. ferruginea* only (Amakawa 1981) and similar to other members of genus.

The following characters should be emphasized for delimitation of the subgenus: (1) perianth subcylindric and contracted to mouth; (2) outer cortical cells (a) with larger cavities than those of intracortical cells, (b) often lighter pigmented and (c) tending to form a distinct hyalodermis; (3) ± ring-like distribution of mycorrhiza in the medullary cells; (4) broad rhizoids; (5) cuticle smooth to faintly papillose; (6) subbasal tooth distribution, with marginal teeth or cilia freely developed in distal and median leaf sectors, gradually becoming more rare to leaf bases and usually absent on decurrent strips (in the species of *Plicaticalyx* at least dorsal decurrent strips remain entire).

Differentiation of the species

Despite the subgenus includes only three species, their differentiation is often problematic because of the strong variability. The main distinctive characters of the species are plant and cell size, degree of leaf dentition and length of teeth or cilia, stem anatomy peculiarities, and an absolute length of lobe decurrence. These depend much on the conditions of growth. That leads to considerable overlap of the variability of most characters and makes necessary their complex analysis and diverse approaches to species differentiation.

Key to the species of Plicaticalyx

1. Dorsal lobe decurrency shorter than or as long as ventral lobe; leaves spinose-dentate to short ciliate; terminal tooth cell usually slightly to moderately elongated, (11–)15–20 × (20–)30–80(–110) µm, 1.75–4.2(–6.0) as long as wide ..... *S. ciliatospinosa*
1. Dorsal lobe decurrency longer than ventral lobe; leaves mostly ciliate; terminal tooth cell usually moderately to strongly elongated, 14–25 × 45–200 µm, (2–)2.5–10 as long as wide 2
2. Leaves remotely ciliate to subentire, with (0–)20–40 cilia per ventral lobe; keel longer, 0.1–0.3(–0.45) ventral lobe; plants smaller, 1–3(–4.5) mm wide × 10–20(–45) mm long ..... *S. orientalis*
3. Leaves densely ciliate, rarely spinose-dentate, with over 50 cilia or teeth per ventral lobe; keel shorter, 0.11–0.2 ventral lobe; plants larger, 2–7 mm wide × 20–80 mm long ..... *S. ferruginea*

Scapania ferruginea (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees (Fig. 1)

Syn. Hepat. 72. 1844. — *Jungermannia ferruginea* Lehm. & Lindenb. in Lehmann, Nov. Strip. Pug. 4: 20. 1832. — *Diplophyllum ferrugineum* (Lehm. & Lindenb.) Steph., Spec. Hepat. 4: 115. 1910.

Scapania nepalensis Nees, Syn. Hepat. 71. 1844.

Scapania andreana Steph., Spec. Hepat. 6: 501. 1924.

Representative illustrations: Müller 1905: Taf. 47; Amakawa 1964: fig. 3(a–g); Amakawa 1981: fig. 1.

Plants 2–7 mm wide × 20–80 mm long, yellow-brown to green. Stem cortex (3–)4–5-statose, with outer cortical cells with the cavities larger than or similar to those of adjacent intracortical cells, with mostly slightly thickened and lighter pigmented walls, mostly flattened tangentially, not forming a distinct hyalodermis; central strand unknown. Dorsal lobe 0.3–0.5 the ventral, cordate–reniform, 1–1.47 as wide as long, obliquely inserted, with a very long decurrent strip (considerably longer than that of ventral lobe); ventral lobe ± oval to ovate, 0.6–0.8(–0.95) as wide as long, decurrent a little below keel insertion; keel 0.11–0.17 the ventral lobe length. Leaves ± densely ciliate to spinose-dentate, except lobe bases; marginal cilia 1–6-celled, with 1–2(–3)-celled uniseriate ends, 1–2-celled at base, with terminal cell 14–25 × (25–)45–200 µm, (2–)2.5–10 as long as wide. Median cells thin-walled, 14–25 × 17–32 µm; marginal cells thin- to moderately thick-walled, 10–25 × 10–25 µm. Cuticle smooth to faintly papillose on cilia and leaf margins. Gemmae 2-celled, yellowish to brown, 13–23 × 17–32 µm. Perianth ± oval, multistratose towards base, remaining 2-stratose to the middle third.

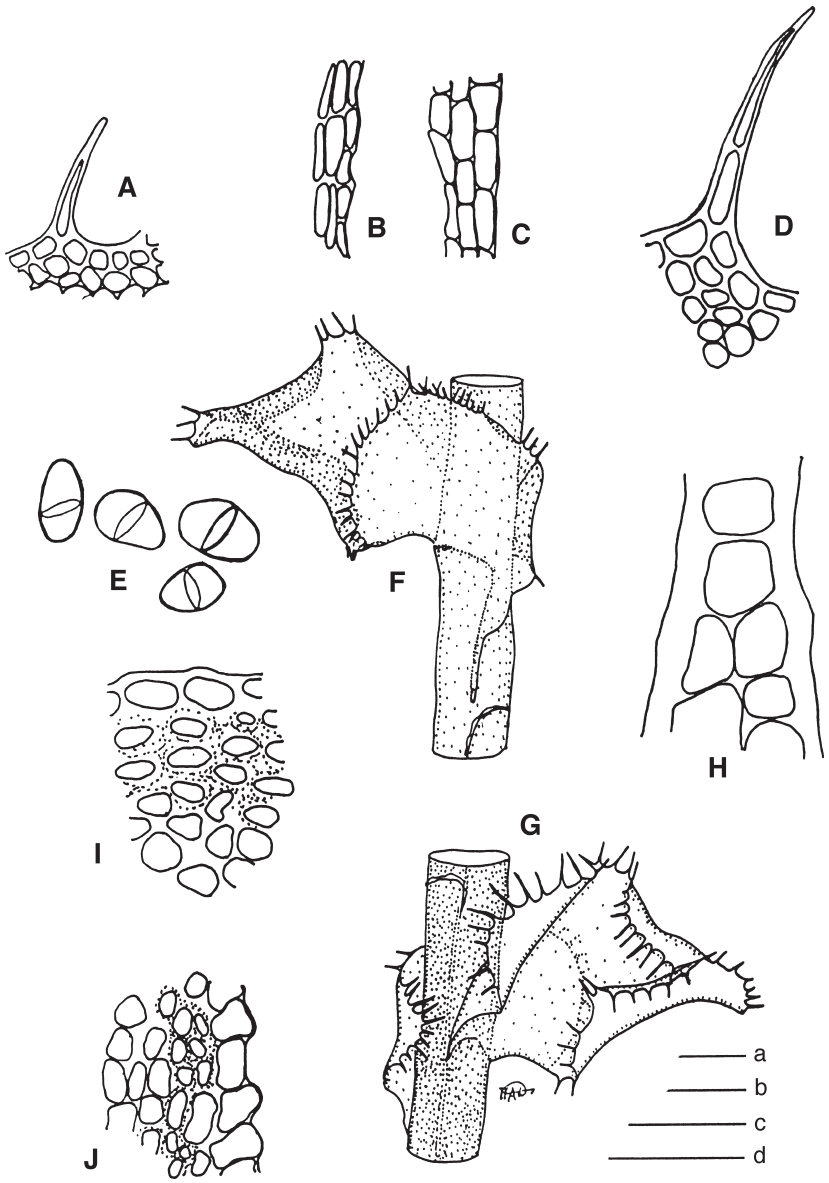

Fig. 1. *Scapania ferruginea* (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees. — A, D: Distal sectors of ventral lobe margin. — B, C: Marginal sectors of ventral lobe base. — E: Gemmae. — F: Leaf on stem, antical aspect. — G: Same leaf on stem, postical aspect. — H: Sector of perianth cross section, medially. — I, J: Sectors of stem cross sections of robust and small plant respectively. — A, B, F, G, I, J drawn from Herb. Griffith 972 (LE); C–E from Herb. Lehmannianum Pug. IV-20 (LE); H from *Sichuan group 446* (PE, LE). — Scale bars: — a: 400 μm (F–G); — b: 20 μm (E); — c: 80 μm (A–D); — d: 40 μm (H–J).

Variation and differentiation

Scapania ferruginea varies much in the plant size and cell size as well as in the length of the marginal cilia. Because of the ciliate leaf margin it may be confused with *S. maxima* and *S. ornithopoides*. *Scapania ferruginea* differs from both species in that the outer cortical cells have a larger lumen than those of adjacent intracortical cells and in the subcylindric perianths. Although a perianth is unknown for *S. maxima,* the other characters support its position within the section *Planifoliae* with a compressed truncate perianth (Potemkin 1998).

Moreover *Scapania ferruginea* differs from *S. maxima* in the usually entire dorsal decurrent strips always devoid of long ciliate appendages. It is distinct from *S. ornithopoides* by having long decurrent dorsal lobes.

Specimens examined. — **Bhutan.** Herb. Griffith 972 (LE). **India.** Sikkim-Himalaya, 13 Apr. 1899 *Decoly &*

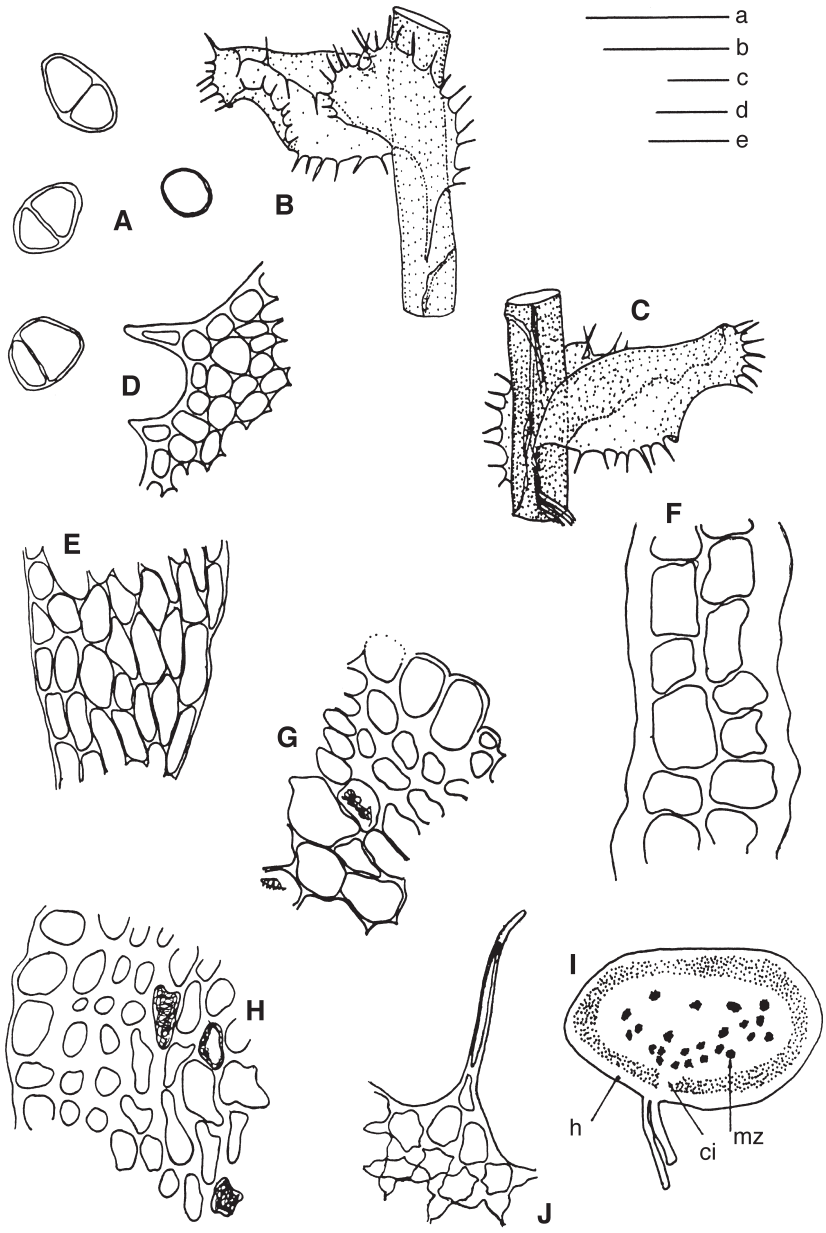

Fig. 2. *Scapania orientalis* Müll. Frib. — A: Gemmae. — B: Leaf on stem, antical aspect. — C: Same leaf on stem, postical aspect. — D: Distal sector of ventral lobe margin, mod. *parvidens-mesoderma-marginata*. — E: Sector of decurrent strip of ventral lobe. — F: Sector of perianth cross section, medial. — G: Dorsal sector of stem cross section (left cell of hyalodermis with destroyed outer wall). — H: Lateral sector of stem cross section. — I: Stem cross section, with a distinct mycorrhiza (mz) distribution pattern, cortex ventral interruption (ci) and hyalodermis (h). — J: Distal sector of ventral lobe margin, mod. *ciliata-pachyderma-submarginata*. — A–C, I drawn from *Poelt H190* (JE); J from Bhotan, Oongar, 6000´, *Griffith s. n.* (NY); others from Oct. 1882 *Duthie 18345* (G, holotype?). — Scale bars: — a: 40 μm (A, F–H); — b: 80 μm (D–E); — c: 400 μm (B–C); — d: 100 μm (I); — e: 40 μm (J).

Schaul (H); Sikkim, Herb. Ind. Or. *Hook. fil. & Thomson 1443* (LE). **Nepal.** *Wallich* (isotype of *Jungermannia ferruginea*, BM). Between Topke Gola and Shewaden, *Iwatsuki 1839* (H); between Hile and Chitre, *Iwatsuki 269* (H); near Sete, *Noordijk 112* (L); near Chukhung, *Noordijk 21* (L, LE); Kathmandu Valley, Mt. Shivapuru, *Schmutz 7229A, 7214C, 7178* (L, LE). **India. "**Herb. Gen. Väinö Krohn" (H). **China.** Yunnan, *Wang Qi-wu 6387, 6389, 6940, 7233, 7242* (PE), *7259* (PE, LE). Sichuan, *Sichuan group 4406* (PE, LE); *Wang Fa-zhan 2378* (PE); *Wu Zhong-lun 12357* (PE); unknown collector 10.VI.1958, *2384* (PE). Xizang, *Wang Mei-zhi 8505* (PE). Locality unknown: Herbarium Lehmannianum Pugile IV-20 (LE).

Scapania orientalis Steph. ex Müll. Frib. (Figs. 2–3)

Bull. Herb. Boissier (ser. 2) 1: 606. 1901. [= Vorarb. Monogr. *Scapania*: 14]. — *Diplophyllum orientale* (Müll. Frib.) Steph., Spec. Hepat. 4: 115. 1910.

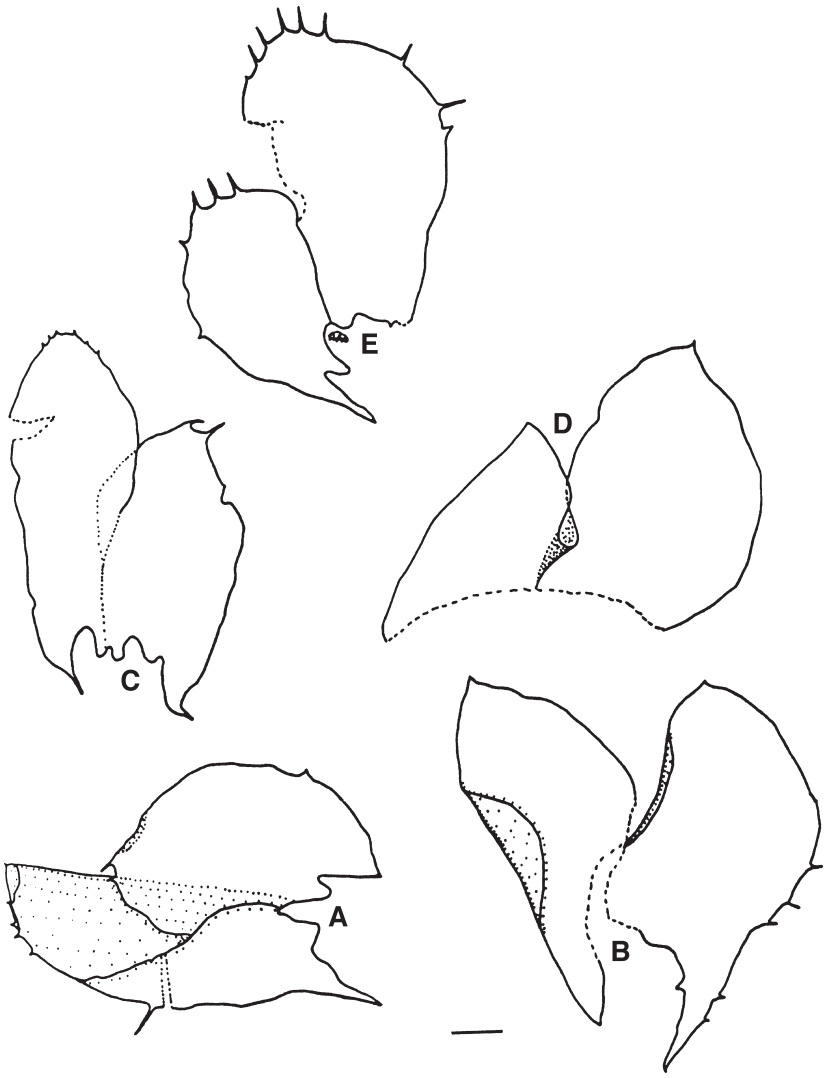

Fig. 3. *Scapania orientalis* Müll. Frib. — A–E: Leaves. — All drawn from *Poelt H190* (JE). — Scale bar: 300 µm.

Scapania ferruginea var. *flaccida* Müll. Frib., Beih. Bot. Centralbl. 11: 545. 1902, *syn. nov*.

Scapania ferruginea var. *longispina* Amakawa, J. Hattori Bot. Lab. 46: 390. 1979.

Representative illustrations: Müller 1905: Taf. 46; Amakawa 1964: fig. 2(j–n); Kashyap & Chopra 1932: pl. XI(5–9); Amakawa 1981: fig. 4.

Plants 1–3(–4.5) mm wide × 10–25(–45) mm long. Stem cortex 3–4-stratose, with outer cortical cells ± bleached or not, thin- to moderately thick-walled, sporadically tangentially flattened, often forming a distinct hyalodermis; central strand unknown. Dorsal lobe 0.4–0.6(–0.8) the ventral, oblique rectangular-reniform to cordate, (0.7–)1.0–1.4 as wide as long, obliquely inserted and considerably longer decurrent than ventral lobe; ventral lobe ± oval, 0.7–0.85 as wide as long, decurrent a little below the keel insertion; keel 0.1–0.3(–0.45) the ventral lobe length. Leaves ± remotely ciliate with (0–)20–40 cilia per ventral lobe; marginal cilia 1–4(–8)-celled, 1–2(–4)-celled at base, with terminal cell 17–25 × (50–)100–175 µm, (2.5–)5.5–7.0 as long as wide. Median cells thin-walled, 17–28 × 20–30 µm, mostly with sharply defined bulging trigones; marginal cells thin to moderately thick-walled, 14–23 × 17–25 µm, often elongated tangentially, to 35 × 20 µm. Gemmae (1–)2-celled, yellowish brown to reddish, 17–21 × 20–32 µm. Perianth ± fusiform (Oct. 1882 *Duthie*; Kashyap & Chopra 1932: Pl. XI(5)) to

clavate (according to Müller 1905), 2-stratose to the upper half, with many (about 10 or more) plicae near mouth.

Variation and differentiation

Scapania orientalis varies much in size of plants, development of leaf cilia, keel length, and degree of marginal border development. It is mostly 1.5–2.5 mm wide and 10–20 mm long but occasionally the plants are considerably larger (*Miehe 9094*), to 4.5 mm wide and 4.5 cm long. Plants collected by Miehe are atypical, have a short keel, about 0.1 the ventral lobe length, and multicellular cilia, to 4 cells basally. Despite the considerable variability, the keel of *S. orientalis* is mostly rather short, about 0.15–0.2 the ventral lobe length. Its length may vary from leaf to leaf on the same plant and occasionally attain 0.45 the ventral lobe length. The number of the marginal cilia and their length vary also from leaf to leaf and in plants of the same tuft, but number usually around 20–35. Leaves with fewer cilia or even without them occur sporadically (*Poelt H190*). Marginal cells are mostly thin- to slightly thick-walled and rather large, mostly about 17–20 × 20–25 µm. Tangentially elongated cells, 18–20 × 25–35 µm, often occur. According to Amakawa (1981) some plants may develop small marginal cells, to 10 × 10 µm, and narrow-based cilia, 12–14 µm broad. Such plants have not been seen during this study. Outer cortical cells vary considerably from thin-walled and bleached to rather thick-walled and pigmented. They occasionally are ± tangentially flattened. Gemmae in *S. orientalis* are more broadly ovoid to subspheric and partly 1-celled in comparison with the other species of the subgenus. In the type specimen and plants illustrated by Kashyap and Chopra (1932) the perianth is ± fusiform rather than clavate as it was described by Müller (1905). This discrepancy probably reflects variability in shape.

Scapania orientalis may be confused with *S. ciliatospinosa* because of similar size and stem anatomy. It differs from *S. ciliatospinosa* in that dorsal lobes are considerably longer decurrent than ventral lobes, and in having fewer and longer marginal cilia and often larger leaf cells. When the species grow together (*Griffith s.n.*), *S. orientalis* is distinct on the basis of the long and remote cilia. Similar leaf insertion and long cilia make robust phases of *S. orientalis* similar to *S. ferruginea*, from which they are distinct in having much fewer cilia per ventral lobe.

Specimens examined. — **India.** NW, Ganges Valley above Jalla 11–12 000 ft. Inter radices Senecionis … Oct. 1882 *J. F. Duthie* [as *Diplophyllum orientale*, labelled by J. Vána as holotypus (G n. 18345). Despite the strong similarity of label with original description, the year of collecting is different, 1882 rather than 1881. This probably is an error of label rewriting]. Darjeeling, Senchal Range, 8 000 p., 29.XI.1900 *Hartless* (isosyntype of *Scapania ferruginea* var. *flaccida*, BM). **Nepal.** *Griffith s. n.* (LE, NY), *Poelt H190* (JE), *Miehe 9094* (JE). **Bhutan.** *Grierson & Long 590b* (JE).

Scapania ciliatospinosa Horik. (Fig. 4)

J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 2: 222. 1934.

Scapania nepalensis sensu K. Müller (*non* Nees in Gottsche *et al*., 1844), Nova Acta Acad. Caes. Leop.-Carol. 83: 300. 1905. — *Diplophyllum nepalense* (Nees) Steph., Spec. Hepat. 4: 116. 1910. (descr. and comb. based on Müller's 1905 (*non* Nees in Gottsche *et al*., 1844) comprehension of *S. nepalensis*).

Scapania ferruginea var. *minor* Amakawa, J. Hattori Bot. Lab. 27: 9. 1964.

Scapania schiffneri Grolle, J. Jap. Bot. 40: 215. 1965.

Representative illustrations: Müller 1905: Taf. 45; Horikawa 1934: pl. 18: 10–14; Amakawa 1964: figs. 3(h–l); Amakawa 1981: fig. 3; Inoue 1972: fig. 2: 1–4.

Plants 1–2.5 mm wide × 7–30 mm long, green to deep brown, occasionally with traces of purple near leaf bases. Stem cortex 3–5-statose, with outer cortical cells ± bleached, thin to slightly thick-walled, usually not flattened tangentially, mostly forming a distinct hyalodermis; central strand of bastlike cells occurs rarely. Dorsal lobe 0.25–0.6 the ventral, cordate-reniform, 0.95–1.5(–1.65) as wide as long, obliquely inserted, without or with a distinctly decurrent strip, which is at most about as long as that of ventral lobe; ventral lobe ± oval to ovate, 0.7–1.05 as wide as long, broadly to rather narrowly decurrent considerably below the keel insertion; decurrent strips of both lobes often bleached and formed of ± thin-walled cells; keel (0.02–)0.07–0.16(–0.2) the ventral lobe. Leaves ± densely spinose-dentate to short ciliate, except on the decurrent strips of dorsal and mostly ventral lobes; marginal teeth 1–3(–4)-celled, 1–2-celled at

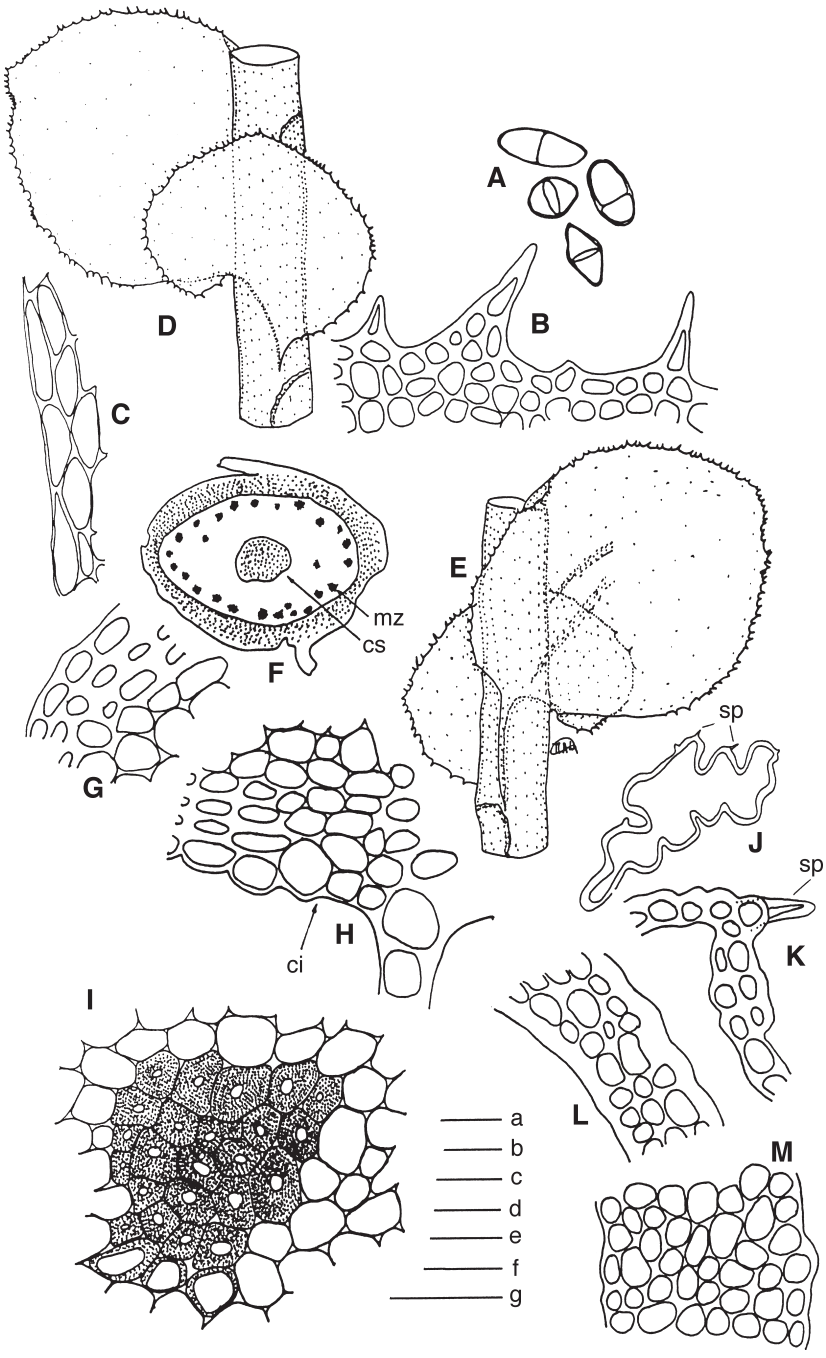

Fig. 4. *Scapania ciliatospinosa* Horikawa. — A: Gemmae. — B: Distal sector of ventral lobe margin. — C: Sector of decurrent strip of ventral lobe. — D: Leaf (with vestigial keel) on stem, antical aspect. — E: Same leaf on stem, postical aspect. — F: Stem cross section with distinct central strand (cs) and mycorrhiza (mz) distribution pattern. — G: Dorso-lateral sector of stem cross section. — H: Ventral sector of stem cross section with distinct cortex interruption of large thin-walled cells (ci). — I: Medullary sector of stem cross section with central strand. — J: Perianth cross section in the upper fifth with distinct surface spines (sp). — K: Sector of J. — L: Sector of perianth cross section, medially. — M: Sector of perianth cross section in the lower fifth. — A drawn from Bhotan, Oongar, 6000', *Griffith s. n.* (NY); B–C and F–I from *Xizang group 7583* (PE, LE); D–E from *Horikawa 9148* (holotype, HIRO); J–M from *Liang Kai-young 430a* (PE, LE). — Scale bars: — a: 400 μm (D, E); — b: 200 μm (J); — c: 20 μm (A); — d: 100 μm (F); — e: 40 μm (K–M); — f: 40 μm (B, C); — g: 40 μm (G–I).

base, with terminal cell (11–)15–20 × (20–)30–80(–110) μm, 1.75–4.2(–6.0) as long as wide. Median cells thin-walled, with rather large, ± bulging and occasionally confluent to medium-sized acute trigones, from 14–17 × 17–20 μm to 14–25 × 17–33 μm; marginal cells moderately thick- to thin-walled, from (6–)9–15 × 9–17 μm to 10–20 × 12–23 μm. Gemmae usually reddish brown, rarely yellowish or purplish, 2-celled, 14–20 × 17–28 μm. Perianth ± clavate, often bistratose almost

to the mouth and with short spines on its surface near the mouth.

Variation and differentiation

Scapania ciliatospinosa is characterized by a definite geographical variability in size of leaf cells. Plants of western populations, known as *S. nepalensis* Nees *sensu* Müll. Frib. or *S. schiffneri* Grolle, are characterized by smaller leaf cells (14–17 × 17–20 µm medially and (6–)9–15 × 9–17 µm along leaf margins). On the basis of this character these populations are distinct from the other species of the subgenus. Eastward, from Xizang, China, to Taiwan, plants with larger cells occur (14–25 × 17–33 µm medially and 10–20 × 12–23 µm along leaf margins). It is impossible to differentiate them from the other species of the subgenus on the basis of cell size. They should be distinguished on the basis of the characters mentioned in the key.

The studied plants of *Scapania ciliatospinosa* from Xizang and Yunnan, China, may develop a very remarkable central strand of exceedingly thick-walled medullary stem cells. Manifestation of this character, however, is not stable and shows no clear correlation with the other characters of those plants. This persuades me to consider that development of the central strand in *S. ciliatospinosa* to be induced by conditions of growth and not to be taxonomically significant.

Dorsal lobe insertion of *Scapania ciliatospinosa* varies from oblique and not decurrent to oblique and long decurrent. Plants with long decurrency of dorsal lobe much resemble *S. ferruginea* from which they differ in similarly long decurrent ventral lobe and shorter cilia.

Specimens examined. — **Nepal.** *Lachoong, Jongri,* and others with unclear labels, totally 6 specimens as *S. nepalensis* (NY); Kathmandu Valley, *Schmutz 7214C, 7226B* (L, LE); East Nepal, *Hara et al. 236086* (TNS). **Bhutan.** Oongar, *Griffith s. n.* (6 specimens as *S. nepalensis,* NY); *Long 8038, 8474, 8728 (*NY). **India.** Brit. Sikkim, Darjeeling, 28 Oct. *Hartless s. n.* (NY); Sikkim-Himalaya, prope Kurseong, Sonada, May 1899 *Decoly & Schaul* (NY). **China.** Yunnan, *Wang Qi-wu 6697,7259* (PE), *Xie Hui-fang 2065* (PE, LE). Sichuan, *Liang Kai-yong 430a* (PE, LE). Xizang, *Ni Zhi-cheng 128* (PE), *Xizang group 7583* (PE, LE). Taiwan, Prov. Tainan, Mt. Morrison, Numano-daira-Tataka-Mayeyama-Niitaka-shita, 19.VIII.1932 *Y. Horikawa 9148* (holotype HIRO, isotype H).

Relationships and evolution of *Plicaticalyx*

Taking into account the approaches to comprehension of *Scapania* evolution (Potemkin 1998), I consider a possible origin of *Plicaticalyx* from entities related to the primitive species of the sections *Ciliatae* Grolle and *Aequilobae* (Müll. Frib.) H. Buch which share with it leaf shape and insertion pattern, spinose-dentate to ciliate leaf margin, and ± bordered leaves. Such an ancestor should have outer cortical cells variable in size, spinose-dentate leaves with subbasal or distal tooth distribution, smooth or slightly papillose cuticle, and perianth rather variable in degree of compression and contraction to the mouth.

Among the three species of *Plicaticalyx* there is none to consider basal for the evolution of the subgenus. *Scapania ferruginea* is less specialized in stem and perianth structure but advanced in the long ciliate leaf margin. *Scapania orientalis* and *S. ciliatospinosa* represent the two different trends in the leaf evolution. The former is specialized in remotely long ciliate leaves whereas the latter is specialized in having leaves densely spinose-dentate to their bases. Despite quite advanced stem anatomy of both species, *S. ciliatospinosa* seems to be the most advanced species because of the ability to develop a shorter keel, smaller leaf cells, central strand and multistratose perianth bearing spines near the mouth surface.

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