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Phylogenetic system and classification of the family Scapaniaceae Mig. *emend*. Potemkin (Hepaticae)

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The phylogenetic system and classification of the family Scapaniaceae Mig. *emend*. Potemkin as a whole are presented for the first time. The classification of the family is significantly revised. Scapaniaceae is classified with 87 recent and one fossil species in 18 sections and three subgenera of one genus, *Scapania* (Dumort.) Dumort. *emend*. Potemkin. Subgenus *Scapania* has 82 species in 18 sections, subgenus *Macrodiplophyllum* (H. Buch) Potemkin has three species, and subgenus *Macroscapania* R.M. Schust. has two species. Earlier distinguished subgenera *Plicaticalyx* Müll. Frib. and *Ascapania* Grolle are merged in the sectio *Plicaticalyx* (Müll. Frib.) Potemkin, *comb*. *& stat*. *nov*., of the subgenus *Scapania*. The taxonomic composition of many sections is considerably revised, and the species composition of all infrageneric groups is listed in a systematic arrangement. Alteration of the species composition and/or species differentiation (including keys) of the sections *Ciliatae* Grolle*, Gracilidae* H. Buch, *Nemorosae* (Müll. Frib.) H. Buch, *Planifoliae* (Müll. Frib.) Potemkin, *Plicaticalyx, Scapania*, and *Verrucosae* Potemkin of the subgenus *Scapania* as well as of the subgenera *Macrodiplophyllum* and *Macroscapania* are provided. New sections are described for *Scapania karl-muelleri* Grolle (*Grolleoscapania* Potemkin, *sect*. *nova*) and for *S*. *schljakovii* Potemkin and *S*. *himalayica* Müll. Frib. (*Muelleria* Potemkin, *sect*. *nova*). A number of new synonyms and index for identification of taxonomic position of mentioned taxa of *Scapania* are provided.

Key words: classification, evolution, hepatics, phylogeny, *Scapania,* Scapaniaceae, taxonomy

Introduction

The paper presents a significantly revised phylogenetic concept of the monogeneric family Scapaniaceae Mig. *emend*. Potemkin. It comprises all known evolutionary trends of *Scapania* (Dumort.) Dumort. and provides a phylogenetic system and classification of the entire family.

The paper is based on studies of all but a few unavailable recognized species of *Scapania*. Over 90 types mostly of critical taxa of *Scapania* were analyzed. Circumscription of all species is based on a detailed analysis in about 60–100 morphological characters. The characters were evaluated from the viewpoints of the comparative, evolutionary and functional morphology, taking into account their dependence on ecological conditions and variability throughout their range. Analysis of functional morphology is pertinent because of comprehensive morpho-functional integration of the gametophyte resulting from its phenetically "developed" genotype. All these approaches have provided the basis to analyze evolution in *Scapania* on the basis of functions of the gametophyte (e.g., assimilation, water storage, light reflection, sporophyte protection, etc.) and establishing that these are becoming more effective in certain ecological conditions by means of an integral interaction of diverse structures of the gametophyte. Analysis of functional morphology has lead to understanding of evolutionary dynamics of characters within the genus, whereas approaches of evolutionary morphology together with data on ecology and distribution have completed the evolutionary comprehension of the group. Space constrictions do not permit full discussion of details of all these methodological approaches to help me understand microevolution as well as taxonomic entities in hepatics. They were already considered to some extent in my papers (Potemkin 1998a, 1998b, 1999a, 2000d) and will be further explored in forthcoming publications. General approaches of evolutionary morphology of plants were considered by Takhtajan (1954) and were applied to comprehension of macroevolution in hepatics by Schuster (1984a, 1984b).

Refinements in the phylogenetic system of *Scapania*

After previous publication of the classification of the genus *Scapania* (Potemkin 1998a) I assembled all available data on the genus and analyzed them from the viewpoints of morphology, ecology and distribution. Eight new species of *Scapania* were described (Potemkin 2000a, 2000b, 2000c, 2001), among which *S. koponenii* Potemkin was important for re-evaluation of relationships of the systematic groups of the genus. *Scapania koponenii* was segregated from plants distinguished earlier as Asiatic *S. aspera* M.&H. Bernet (Potemkin 1998a), and it was demonstrated that its position is among the primitive species of the sectio *Ciliatae* Grolle rather than in the sectio *Aequilobae* (Müll. Frib.) H. Buch, to which *S. aspera* belongs. This altered the idea of a polymorphous "root species" of the sectio *Aequilobae* and resulted in a delineation of the evolution of most sections of the subgenus *Scapania* from the common ancestor.

Earlier the sectio *Curtae* (Müll. Frib.) H. Buch was distinguished as the simplest and probably most primitive group of the genus (Potemkin 1998a, 1999c). However, despite being richest in the genus with regard to an ensemble of unspecialized character expressions, the species of the sectio *Curtae* have a number of advanced morphological characters (small size of plants, reduced paraphyses, general suppression of branching with sporadic formation of lateral intercalary branches) and, advanced for the genus, a comparatively broad distribution in territories with a continental climate. Moreover the distinctions of the species of the sectio *Curtae* are often uncertain. This lack of sharp delimitation of the species speaks for a comparatively young age of the group. On this basis I distinguish the sectio *Curtae* as a young neotenic sectio of *Scapania* with an origin probably induced by climatic changes of the Pleistocene.

Close relationships of the sections *Stephania* Amakawa & S. Hatt. *ex* Potemkin, *Umbrosae* H. Buch and *Nemorosae* (Müll. Frib.) H. Buch in their morphology and vicarious distribution pattern led me to merge them in one, sectio *Nemo-*

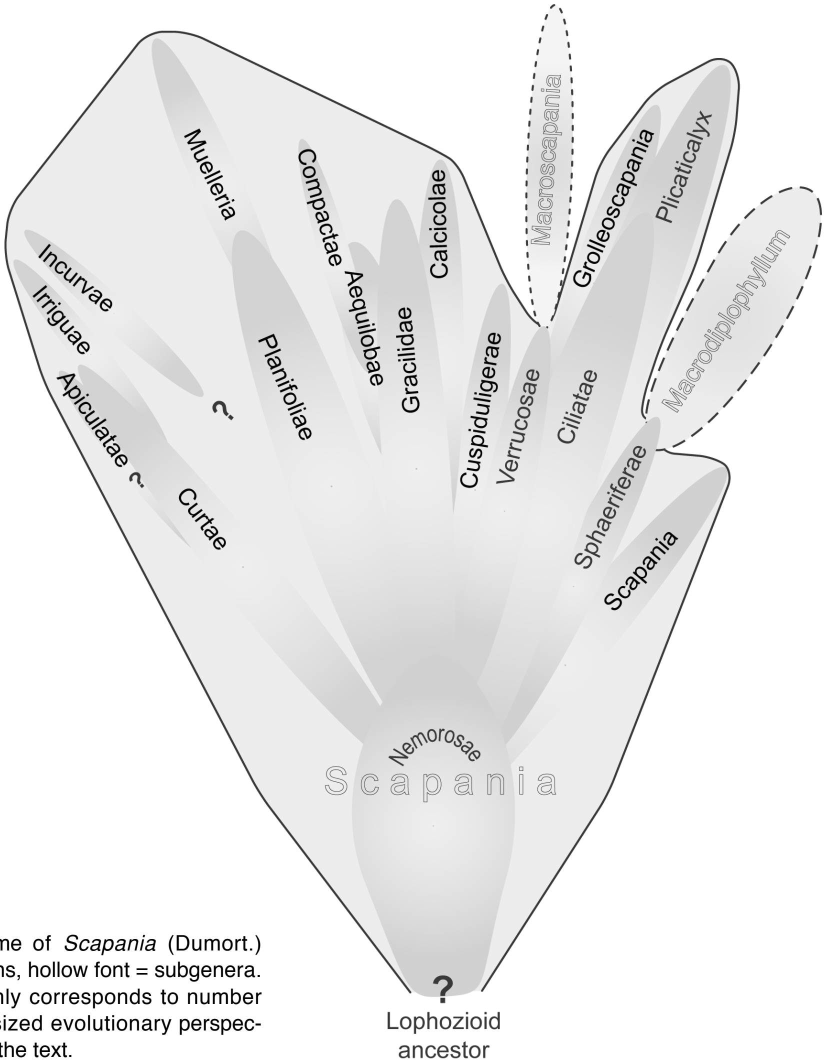

Fig. 1. Phylogenetic scheme of *Scapania* (Dumort.) Dumort. Solid font = sections, hollow font = subgenera. Area of the contours roughly corresponds to number of species in the hypothesized evolutionary perspective. Further explanation in the text.

rosae. This very much expands the scope of the *Nemorosae* which, circumscribed in this way, comprises the less specialized and probably most primitive recent species of the genus, *Scapania ligulata* Steph. *s. lato*, as well as some advanced species, including *S. nemorea* (L.) Grolle*, S. umbrosa* (Schrad.) Dumort., etc. This sectio appears to be a "root group" from which most of the other recent groups of *Scapania* might be derived.

Putting the sectio *Nemorosae* at the base of the phylogenetic system of the genus (Fig. 1) shows a hiatus between the *Nemorosae* and its presumably *Barbilophozia kunzeana*-like ancestor (Potemkin 1999c: p. 272). Among principal morphological characters forming this hiatus, distinctions in branching pattern, leaf structure and ability to produce amphigastria are the most important. It should be noted that the species of the sectio *Kunzeanae* (C.E.O. Jensen) Grolle, to which *Barbilophozia kunzeana* (Huebener) Müll. Frib. belongs, develop chiefly terminal and exceptionally ventral intercalary branches, whereas primitive species of *Scapania* sect. *Nemorosae* produce only ventral intercalary branches and no terminal ones. Species of

Scapania have a strongly fixed bilobed leaf condition and no underleaves while, on the contrary, *Barbilophozia kunzeana* and related species are flexible in leaf lobe number and freely develop underleaves. This hiatus should result from considerable age of the genus *Scapania*, which may extend to the age of Laurasia.

The concept of sectio *Nemorosae* as the most primitive group of the extant *Scapania*, as well as the idea of a considerable age of the genus, is supported by discovery of *S. hoffeinsiana* Grolle, the only known fossil Scapania, in Bitterfeld amber from Germany (Eocene, at least 50 m.y. BP) (Grolle & Schmidt 2001). This species appears to be close to *S. umbrosa*, an advanced species of sect. *Nemorosae*.

The phylogenetic system of the genus *Scapania* is based on an understanding of evolution of the genus by means of gradual specialization, on the one hand, and simplification of morphological organization via ontogenetic transformations on the other. It represents a "phylogenetic bush" with most sections derived from the sectio *Nemorosae* and mainly shows relationships of the groups. Within the phylogenetic bush the groups of sections close to the sections *Gracilidae* H. Buch, *Planifoliae*, *Ciliatae*, and *Curtae* are distinct. The sectio *Incurvae* Potemkin has probably an independent neotenic origin from an unknown east-asian ancestor. The subgenera *Macroscapania* and *Macrodiplophyllum* appear to be derived from the sections *Verrucosae* Potemkin and *Sphaeriferae* Müll. Frib. *ex* Konst. & Potemkin of the subgenus *Scapania* respectively.

Classification of *Scapania*

Potemkin (1998a) defined the subgenus *Scapania s. lato* and circumscribed most of its sections except some exotic southern groups. Afterwards relationships of those exotic groups with the subgenus *Scapania* were elucidated and the family Scapaniaceae was circumscribed with the only genus *Scapania*, including *Macrodiplophyllum* (H. Buch) Potemkin as a subgenus (Potemkin 1999c). That formed the basis for the following classification of the genus *Scapania*. Below are lists of recognized species of all recognized taxonomic groups, their new and recently introduced synonyms, frequently used synonyms of recognized sections, names of species unavailable for study (given in brackets), and taxonomic and systematic considerations. The order of the taxonomic groups and species in the classification reflects their relationships and their relative age. Distinction of sections of the subgenus *Scapania* often are not very sharply defined because of considerable overlap of their variability of separate characters (particularly the characters of the advanced species of large and closely related groups).

Subgenus *Scapania s. lato*

= subgen. *Ascapania* Grolle, *Buchiella* R.M. Schust., *Jensenia* S.W. Arnell, *Kaalaasia* H. Buch, *Plicaticalyx* Müll. Frib., *Protoscapania* Amakawa & S. Hatt., *Scapaniella* (H. Buch) Jørg.

Subgenus *Scapania* is the largest group of *Scapania* and includes 82 recent and one fossil species in 18 sections. It shows a high diversity of morphotypes. The most common morphotype of *Scapania* is characterized by leaves with distinctly smaller dorsal lobes and an acute keel from its base to sinus, an arcuate and often decurrent insertion at least of the ventral lobes, a strongly compressed and truncate perianth, nonpersistent oil bodies in all but occasional marginal leaf cells, ovoid gemmae, as well as moderately elongated elaters (length about 10–20 × the width) and ± slightly papillose spores. Such a morphotype is characteristic of most species of the sections *Ciliatae, Incurvae, Irriguae* (Müll. Frib.) H. Buch, *Nemorosae*, *Gracilidae*, *Planifoliae* (Müll. Frib.) Potemkin, *Scapania* and some species of *Curtae* and *Aequilobae*. These sections are distinct from each other in leaf shape, gemmae, oil-body characters, areolation, dentition and insertion of the leaves, and perianth mouth structure.

Principal deviations from the basic morphotype are in species of the following sections: (1) *Apiculatae* H. Buch (leaves not keeled and weakly sheathing basally, transversely inserted; plants very small and mostly xylicolous); (2) *Cuspiduligerae* H. Buch (leaves not keeled and sheathing basally, long-decurrent postically with a hyaline area of cells devoid of chloroplasts and oil bodies near the ventral leaf base; perianth compressed and truncate); (3) *Calcicolae* R.M. Schust. (perianth lophozioid, i.e,. an inflated and contracted to mostly lobulate ciliate-dentate mouth; leaves keeled, ± transversely inserted, with a hyaline area near the ventral lobe base and persistent large oil bodies); (4) *Compactae* H. Buch (leaves subequally bilobed, not keeled basally); (5) *Sphaeriferae* (sphaeric multicellular gemmae with intersecting internal walls; perianth ± compressed, irregularly plicate, with a lobulate-dentate mouth); (6) *Verrucosae* (angular gemmae).

Subgenus *Scapania* includes the species with a subcylindrical perianth, which were earlier attributed to the subgenus *Plicaticalyx*. These species were segregated in three groups, demonstrating closer relationships with the species of the sections *Ciliatae* and *Planifoliae* than with each other. These groups are distinguished as separate sections of the subgenus *Scapania* and they are *Plicaticalyx* (Müll. Frib.) Potemkin, *Grolleoscapania* Potemkin and *Muelleria* Potemkin. The sectio *Plicaticalyx* appears to be derived from a primitive species of sectio *Ciliatae*, *Scapania koponenii*. The sectio *Grolleoscapania*, with *S. karl-muelleri* Grolle, is probably derived from an advanced species of the sectio *Ciliatae*, *S. bhutanensis* Amakawa, and the sectio *Muelleria* Potemkin, with *S. himalayica* Müll. Frib and *S. schljakovii* Potemkin, from the sectio *Planifoliae*. Development of similar subcylindrical perianths in these three sections appears to be connected with ontogenetic deviation (Takhtajan 1954) of perianth development (abortion of the compression stage of development) resulted from the same environmental influence in Himalayas and adjacent territories. Besides the species of *Plicaticalyx, Grolleoscapania* and *Muelleria*, somewhat inflated perianths occur in some species of the sections *Curtae*, *Aequilobae* and *Compactae*. In those species the leaves are often not keeled at the base and the degree of bract keel development may correlate with compression of the perianth.

Sectio *Nemorosae* (Müll. Frib.) H. Buch

= sect. *Brevicaules* R.M. Schust., sect. *Curtae* (Müll. Frib.) H. Buch *p. min. p.*, sect. *Irriguae s.* Schuster (1974) *p. min. p.*, Gruppe *Rigida* Müll. Frib. *p. p.*, sect. *Stephania* Amakawa & S. Hatt. *ex* Potemkin, *syn. nov.*, sectio *Umbrosae* H. Buch *syn. nov.* — *Scapania ligulata* Steph. (= *S. stephanii* Müll. Frib., *syn. nov.*), *S. parvitexta* Steph. (= *S. parvidens* Steph., *syn. nov.* = *S. okamurana* Steph. *ex* Amak. & S. Hatt., *syn. nov., S. glaucoviridis* Horik., *syn. nov.*), *S. griffithii* Schiffn. (= *S. angusta* Mitt. *ex* Müll. Frib. (cf. Inoue 1972; Potemkin 1998a)), *S. integerrima* Steph. (= *S. kamimurae* Amakawa & S. Hatt., *syn. nov.*), [*S. hoffeinsiana* Grolle – fossil] (Grolle & Schmidt 2001), *S. umbrosa* (Schrad.) Dumort., *S. javanica* Gottsche (= *S. cuneifolia* Steph., *syn. nov., S. macgregorii* Steph., *S. paucidens* Steph., *syn. nov., S. spathulifolia* Steph. *ex* Warnst., *syn. nov.*), *S. rigida* Nees, [? *S. grossidens* Steph.], *S. brevicaulis* Tayl. (= *S. degenii* Schiffn. *ex* Müll. Frib. (Potemkin 1998a, 1999a)), *S. hedbergii* S.W. Arnell (? African derivative of *S. brevicaulis*), *S. nemorea* (L.) Grolle (= *S. crassiretis* Bryhn as subsp. *crassiretis* (Bryhn) Potemkin (1994)), *S. matveyevae* Potemkin (Potemkin 2000b). *Scapania simmonsii* Bryhn & Kaal., previously attributed to this section (Potemkin 1998a), is transferred to the sectio *Planifoliae* and considered under it.

Sectio *Nemorosae* comprises medium-sized to robust and small, predominantly brown pigmented species. They have ± arcuately inserted, ovate to oblong and reniform dorsal lobes and short to long decurrent lingulate to subrotund and lanceolate ventral lobes, with marginal teeth occurring mostly in their distal and often median portions. The median leaf cells are thin to thick-walled, with mostly 3–7 ± large oil bodies occluding mainly over half of cell lumen. The perianth mouth is non-lobulate, short to long, and dentate, normally with no additional basal teeth. The gemmae are 1–2-celled, mostly ± ovoid to (rarely) subspheric, bacilliform or ± angulate, and brown to/or colorless. In the case of the *Nemorosae* as well as of the *Gracilidae* I consider it unsound to segregate the section on the basis of the gemmae cell number. Gemmae cell number as well as any other character has its own way of establishment. As for gemmae, the 2-celled condition is considered as the basal condition and the 1-celled condition as derived. In this light occurrence of species of similar morphology, developing predominantly 1-celled or 2-celled gemmae within the section seems natural.

A considerable overlap of morphological variability, geographical ranges and ecological requirements of the species, which I attributed to the sections *Nemorosae* (*S. brevicaulis, S. grossidens, S. hedbergii, S. javanica, S. matveyevae, S. nemorea, S. rigida*), *Stephania* (*S. ligulata, S. parvitexta, S. integerrima*), and *Umbrosae* (*S. griffithii, S. umbrosa*), show their close relation to each other and persuade me to merge these three sections into one, *Nemorosae*. Some explanations are provided below.

A study of South East Asian representatives of the sections *Stephania* and *Nemorosae* showed their broad variability, which disregards the sectional distinctions. So, phases of *S. ligulata* with brown gemmae are difficult to differentiate from some forms of the malleable *S. javanica* and from *S. nemorea*.

Scapania griffithii, assigned to the *Umbrosae*, and *S. ligulata* of *Stephania* demonstrate an overlap of variability in gemma size, shape and cell number, leaf dentition and areolation, and perianth mouth structure, varying in *S. griffithii* from subentire to dentate like in *S. ligulata*. These facts, based on study of materials collected by Dr. David G. Long in Nepal and extensive collections of *S. ligulata* from diverse territories of SE Asia, confirm a close position of the species and disregard the sectional distinctions of sections *Stephania* and *Umbrosae*.

Taking into account that *Scapania umbrosa*, rather than *S. griffithii*, is the type species of the sectio *Umbrosae*, it is necessary to define relationships of *S. umbrosa* with the species assigned to the *Stephania*. As I have shown earlier (Potemkin 1998a) *S. umbrosa* shares a common habit with *S. integerrima* and *S. stephanii*. It is similar to those species in shape, insertion, areolation and serration of leaves, but distinct in having bacilliform, reddish brown, 2-celled gemmae and an entire perianth mouth; also, it often grows on rotten wood. These distinctions are considered as derived and persuade me to distinguish *S. umbrosa* as an advanced species in comparison with *S. stephanii* and *S. integerrima*.

Study of extensive materials of *Scapania stephanii* and *S. ligulata* from Hunan, SE China, as well as from other parts of their range showed that they cannot be distinguished as separate species. Their differences in size of plants, proportion and shape of leaves, as well as in cell size appear to be ecologically predetermined distinctions of small and robust expressions of one species. Both "species" have the same number and size of oil bodies, 2–5 per median cell, ca. 3–7 μm in diam. On this basis *S. stephanii* is considered as a synonym of *S. ligulata* at specific level. The infraspecific taxonomic status of *S. stephanii* should be clarified by a separate study.

Comparison of the holotype of *Scapania kamimurae* (25.VII.1941 *S. Hattori*, *NICH 57704*), which was assigned to the sectio *Curtae* by Amakawa and Hattori (1955), with all available materials of *S. integerrima* (7.IV.1906 *S. Okamura*, *G 25964*, holotype; Hep. Jap. Exsic.: ed. S. Hattori 297, 696; ed. S. Hattori & M. Mizutani 946, 896, all LE) showed that the taxa are identical in all principal criteria, including stem anatomy, leaf shape, insertion and areolation, perianth mouth and structure of androecia, as well as gemma characteristics. Gemmae of *S. kamimurae* (at first revealed in the type material) are broadly ovoid, 1–2-celled, colorless to brownish, thin- to somewhat thick-walled, rather small and similar to those of *S. integerrima*, 10–12 × 14–17 μm (secondary pigmentation of gemmae in *S. integerrima*, when present, apparently correlates with the color of gemmiparous leaves). Therefore *S. kamimurae* is excluded from the sectio *Curtae* and transferred to the sectio *Nemorosae* as a synonym of *S. integerrima*.

Scapania integerrima is not recognized in check-lists of Japanese Hepaticae and Anthocerotae (Mizutani 1984, Furuki & Mizutani 1994) and appears to be included as a synonym of *S. stephanii*. However, despite frequent similarity with mod. *angustifolia-parvifolia* of *S. ligulata* (= mod. *angustifolia* of *S. stephanii*) and very flexible perianth mouth structure, which cannot be distinguished from that of *S. ligulata* (cf. Amakawa & Hattori 1954: p. 106), *S. integerrima* appears to be distinct from *S. ligulata s. lato*. The former can produce narrowly lanceolate, rather coarsely serrate to entire ventral lobes, extensive pure purple pigmentation, usually somewhat larger and more collenchymatose leaf cells, and cortical cells in only 1–3 strata, with distinct deep pigmented middle lamellae and often rather large cavities, not characteristic of *S. ligulata*.

Scapania parvitexta is here broadly circumscribed, i.e., with inclusion of *S. parvidens, S. okamurana*, and *S. glaucoviridis,* which were all previously distinguished as separate species (Amakawa & Hattori 1954). All these species, in comparison with *S. ligulata*, show no serration of leaf margins and develop ± spinose marginal leaf teeth, stronger, thick-walled and mostly a little smaller median and particularly marginal leaf cells — (6–)8–10 × (8–)10–12(–14) μm vs. 10–16 × 11–17 μm — in distal sector of ventral lobe margin, and perianth mouth teeth similar or weaker than those of the leaf margins. For the perianth mouth of *S. parvitexta*, *see* original description of Stephani (1897: p. 107) rather than the subsequent faulty treatments by Stephani (1910) and Amakawa and Hattori (1954). Distinguishing *S. okamurana* as a separate species on the basis of broad keel wing and brown, partly 2-celled gemmae seems unreasonable because of a sporadic development of ± broad keel wing, instability of 1-celled gemmae condition, and of suppression of gemma pigmentation in all species of the sectio. I consider *S. okamurana* as a synonym of *S. parvidens* rather than of *S. glaucoviridis* as was suggested by Inoue (1972). *Scapania okamurana* is different from *S. glaucoviridis* primarily on the basis of considerably narrower dorsal (0.85–0.95 vs. 1.2–1.4 × as wide as long) and ventral (0.75–0.91 vs. 0.85–1.05 × as wide as long) leaf lobes. A considerable overlap of variability among *S. glaucoviridis, S. okamurana, S. parvidens* and *S. parvitexta*, and their differentiation from *S. parvitexta* on the basis of few ± unstable characters (primarily keel length and to less extent leaf shape, perianth mouth and leaf teeth) has led me to regard them as synonyms of *S. parvitexta*. The infraspecific taxonomic status of *S. glaucoviridis* and *S. parvidens* should be clarified in a separate study.

It is noteworthy that apparently all species assigned to the *Stephania* more or less frequently develop 2-celled gemmae. A similar inconsistency was observed in gemma color as well. Despite the fact that the section was originally described as having 1-celled, green gemmae (Amakawa & Hattori 1954), in every species there are forms with partly 2-celled as well as ± pigmented gemmae. Sometimes 2-celled gemmae prevail. Forms with mostly non-pigmented leaves and abundant pigmented gemmae are remarkable. Such forms are known in *Scapania ligulata* (as *S. javanica* var. *nipponica* S. Hatt. and apparently as *S. javanica* var. *osumiensis* S. Hatt., of which I have not seen any material) and in *S. parvitexta s. lato* (holotype of *S. glaucoviridis,* 20.VIII.1932 no collector no. *9222*, HIRO). They demonstrate no other significant distinctions from the typical forms of the species and probably resulted from some kind of inversion of gene expression. The above facts illustrate a strong plasticity of the species assigned to *Stephania* in gemma characters and many other characters. At the same time *Scapania griffithii s. lato* shows strong variability in gemma shape and size as well as in plant habit. It should be noted that smaller plants of this species (*S. angusta* phase) have much in common with the species of *Curtae*; medium-sized plants are similar to *S. ligulata* whereas larger expressions represent typical *S. griffithii*. All these forms may intergrade into one another (e.g. *Long 8130, 17040, 17168, 17331*, all LE, E). They develop 2-celled gemmae of different size and shape and range from small ± broadly ovoid gemmae indistinguishable from those of *S. ligulata* (seen in most observed specimens) to large bacilliform gemmae characteristic only of some robust yellowish brown plants; gemmae of both types occur sporadically in the same plant (*Long 8130*, LE). Variability of gemma size may be explained by environmental factors. Small gemmae, observed in smaller plants, are supposed to serve more long-distance dispersal from unfavorable habitats, whereas large gemmae, occurring only in well-developed plants, serve establishment of the population in favorable niches. These data provide the basis for re-evaluation of size, shape, cell number and pigmentation of gemmae as criteria for differentiation of the species of the sectio *Nemorosae*.

It is remarkable that sections *Nemorosae* and *Curtae* probably are rather closely related. This is indicated by frequent occurrence of 2-celled gemmae in the sectio *Nemorosae* as well as assignment of *Scapania integerrima* (as *S. kamimurae*) and *S. stephanii* to sectio *Curtae* (Amakawa & Hattori 1955, Müller 1905). Also of importance is the striking similarity of small forms of *S. griffithii* with the species of *Curtae* as well as similarity of some forms of *S. umbrosa* with *S. scandica*.

The considerable change of the species composition of sectio *Nemorosae* renders it necessary to provide a key to the recognized taxa.

1. Ventral lobe decurrent to level of keel insertion or almost not decurrent 2
1. Ventral lobe normally decurrent below level of keel insertion 4
2. Marginal teeth coarse, 2–3 cells at base and 2–4 cells

long; keel straight to indistinctly arched; gemmae unknown; cortex 5–6-stratose, of extremely thick-walled cells; plants to 5 mm wide and 50–70 mm long; Hawaii .... *S. grossidens*

2. Marginal teeth fine, 1–2 cells at base and 1–2 cells long; keel straight to strongly arched; gemmae usually present, 1-celled; cortex 1–3-stratose, of slightly to moderately strongly thick-walled cells; plants (0.5–)0.8–4(–4.4) mm wide and 5–50 mm long; arctic and along mountain ranges southward, Central and ?South Africa 3

3. Dorsal lobe 0.7–0.85 of ventral; antical margin of dorsal lobe often undulate proximally; cells 14–23 × 16–25(–28) μm along margins, 20–25 × 25–30(–35) μm medially; oil bodies 5–7 per median cell; cortex slightly defined, 1–2(–3)-stratose; Central and ?South Africa (Kenya, ?Lesotho) .... *S. hedbergii*

3. Dorsal lobe 0.5–0.75 of ventral; antical margin of dorsal lobe never undulate proximally; cells smaller, 15–20 × 17–22 μm along margins, 18–22(–26) × 22–24(–30) μm medially; oil bodies 3–5(–6) per median cell; cortex mostly well-defined, (1–)2–3-stratose; arcto-alpine circumpolar species with southernmost localities in Colorado, Italy, S. Siberia .... *S. brevicaulis*

4. Terminal cells of teeth in median and distal sectors of leaf margin to 2 × as long as wide or leaves subentire (in subentire leaves possible to find few teeth with slightly elongated terminal cells) 5

4. Terminal cells of teeth in median and distal sectors of leaf margin mostly 1.8–3 × as long as wide or leaves subentire (in subentire leaves it is possible to find a few teeth with rather strongly elongated terminal cells) .... *S. nemorea s. lato* 13

5. Ventral lobe ± narrowly lanceolate 0.5–0.71 × as wide as long, remotely coarsely or finely serrate to entire; dorsal lobe obliquely ovate to elliptic lanceolate, 0.5–0.8 × as wide as long; cortex 1–3(–4)-stratose, of moderately thick-walled cells mostly with rather distinct middle lamellae 6

5. Ventral lobe sublanceolate to ligulate and subrotund 0.6–1.05 × as wide as long, serrate to denticulate or entire; dorsal lobe obliquely ovate to reniform, 0.6–1.4 × as wide as long; cortex 2–5-stratose, of strongly thick-walled cells without distinct middle lamellae 8

6. Leaves coarsely serrate to entire, without horn-like tips resulting from gemma production; gemmae 1(–2)-celled, broadly ovoid, small 10–12 × 14–17 μm, 1.15–1.4 × as long as wide; perianth mouth dentate to lobulate dentate; deep purple pigmentation common .... *S. integerrima*

6. Leaves finely serrate to entire, occasionally with horn-like tips resulting from gemma production; gemmae (1–)2-celled, bacilliform to/or ovoid, 7–19 × 15–38 μm, 1.5–2.5 × as long as wide; leaf modified from gemma production occasionally with horn-like tips; perianth mouth remotely dentate to/or entire; deep purple pigmentation mostly absent 7

7. Gemmae reddish brown, bacilliform to narrowly ovoid, small, 7–11 × 15–27 μm; leaf modified from gemma production without horn-like tips; perianth mouth entire; on rotten wood, rocks and soil; warm and temperate territories of Europe and North America with suboceanic climate .... *S. umbrosa*

7. Gemmae colorless, ovoid to bacilliform, small to rather large, 8–19 × 23–38 μm; leaf modified from gemma production often with horn-like tips; perianth mouth remotely dentate to entire; on rocks and soil; SE Asia ... . *S. griffithii*

8. Leaf cells 6–16 × 10–17 μm along margins and 10–18 × 12–25 μm in median sector of ventral lobes, walls tend to be ± thick-walled along margins and in median portion of leaf; SE Asia 9

8. Leaf cells mostly 10–32 × 14–48 μm along margins and 17–34 × 20–45 μm in median sectors of ventral lobes, walls invariably thin-walled in median portion of leaf; subequatorial archipelagos of Pacific Ocean, High Arctic 11

9. Ventral lobes ± denticulate to dentate and subentire with usually spinous terminal tooth cells; median leaf cells with indistinct trigones, ± thick-walled, 10–14 × 12–15(–20) μm; marginal cells normally thick-walled and forming distinct border, (6–)8–10 × (8–)10–12(–14) μm .... *S. parvitexta s. lato*

9. Ventral lobes ± serrate with largely triangular, nonspinous terminal tooth cells; median leaf cells with ± distinct trigones, thin- to slightly thick-walled, (11–)13–18 × 15–30 μm; marginal cells occasionally thick-walled, 10–16 × 11–17–23 μm 10

10. Leaf modified from gemma production often with horn-like tips; gemmae (1–)2-celled, large bacilliform to narrowly ovoid and elliptical, 11–19 × 26–41 μm .... *S. griffithii*

10. Leaf modified from gemma production without horn-like tips; gemmae 1–2-celled, ± ovoid, ca. 11–14 × 17–23 μm .... *S.ligulata*

11. Leaf lobes very broad, dorsal lobe (1.13–)1.2–1.6 × as wide as long; ventral lobe 1.0–1.35 × as wide as long; cells large, marginal cells 17–32 × 20–48 μm, median cells 20–34 × (20–)25–38(–45) μm; oil bodies (5–)8–11(–16) per median cell, nonpersistent; gemmae (1–)2-celled, often with slightly to moderately projecting angles; East Siberian High Artic (Severnaya Zemlya Archipelago) .... *S. matveyevae*

11. Leaf lobes narrower, dorsal lobe 0.65–0.95–1.15 × as wide as long; ventral lobe 0.6–0.85 × as wide as long; cells smaller, marginal cells 10–20 × 13–25 μm, median cells 16–25(–28) × 18–28(–33) μm; oil bodies fewer, 3–7(–8) per median cell, sporadically persistent; gemmae 1–2-celled, without projecting angles 12

12. Plants usually greenish yellow; both leaf lobes regularly dentate, with terminal tooth cells in distal leaf sectors 1.6–2.0 × as long as wide; perianth mouth dentate, with terminal tooth cells 1.8–2.4 × as long as wide; gemmae constantly produced, 1(–2)-celled, usually cinnamon-brown to sometimes largely colorless to brownish; Philippines (as *S. spathulifolia*), Sumatra, Java, New Guinea, Samoa, Solomon Isls., Hawaii (as *S. paucidens*) .... *S. javanica*

12. Plants olive green to fuscous; leaves with remote teeth mostly on ventral lobes (dorsal lobes entire or with a few teeth near apex), with terminal cells in distal leaf sector 0.77–1.2 × as long as wide; perianth mouth sinuate,

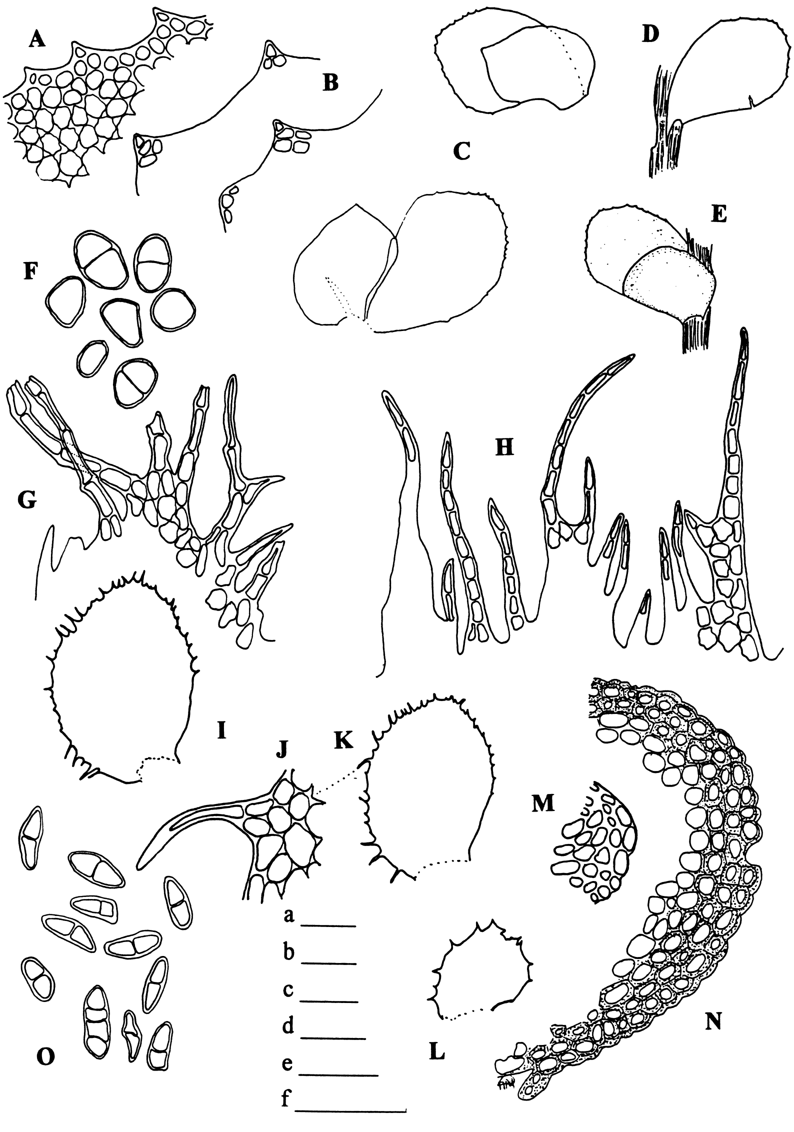

Fig. 2. *Scapania rigida* Nees (**A**–**F**; from holotype, *Hasskarl s. n.*, STR), *S. ornithopoides* (With.) Waddell (**G**; from *Flora Japonica* as *S. subnimbosa*, Kai, Mt. Komagatake, 17.VII.1910, no collector, LE), *S. simmonsii* Bryhn & Kaal (**H**; from *Steere 76575*, LE), *S. nepalensis* Nees (**I**–**M**; from holotype, Nepal, *cum Herpetis alternifolius*, STR)), *S. karl-muelleri* Grolle (**N**; from *Iwatsuki 1182*, H), *S. ciliata* Sande Lac. subsp. *hawaica* (Müll. Frib.) Potemkin (**O**; from 1876 *Baldwin*, H). — **A**: Sector of postical margin of ventral lobe. — **B**, **G**, **H**: Sectors of perianth mouth. — **C**: Leaves. — **D**: Leaf on stem, postical aspect. — **E**: Leaf on stem, antical aspect. — **F**, **O**: Gemmae. — **I**, **K**: Ventral lobes. — **J**: Sector of postical margin of ventral lobe from **K**. — **L**. Dorsal lobe. — **M**, **N**: Lateral sectors of stem cross sections. — Scale bars: a: 50 *µ*m (**A**, **B**, **G**, **H**). b: 20 *µ*m (**F**). c: 0.4 mm (**I**–**L**). d: 30 *µ*m (**O**). e: 50 *µ*m (**J**, **M**, **N**). f: 1 mm (**C**–**E**).

remotely denticulate, with terminal tooth cells 1.0–1.35 × as long as wide; gemmae sporadically produced, (1–)2-celled, green with admixture of yellowish; Java ... . *S. rigida* (Fig. 2A–F)

13. Marginal teeth slender, mostly 1-celled at base, occurring mostly in distal portion of leaf; oil bodies mostly persistent; cells usually with coarse, bulging trigones; dorsal lobe not or slightly decurrent; circumpolar Arctic subspecies, known southward only in Asia to Altay Mtns., Amur River Basin and N Japan ....*S. nemorea* subsp. *crassiretis*

13. Marginal teeth firm, mostly 1–3-celled at base, occurring

frequently from distal to proximal portions of leaf; oil bodies mostly nonpersistent; cells with small, acute to medium-sized, bulging trigones; dorsal lobe usually distinctly decurrent; E North American–Western European subspecies of warm and temperate climates .... *S. nemorea* subsp. *nemorea*

Sectio *Gracilidae* H. Buch

= sect. *Nemorosae p. min. p.*, sect. *Stephania s.* Potemkin 1998a, *p. min. p.* — *Scapania bolanderi* Austin, *S. nipponica* (Amakawa & S. Hatt.) Amakawa, *S. subnimbosa* Steph. (= *S. caudata* Steph., *S. robusta* Horik.), *S. gracilis* Lindb. (= *S. recurva* Steph.), *S. amplita* Steph.

Selection and subsequent study of the lectotypes of *Scapania subnimbosa* (VIII.1905 *Faurie 1800*, G 11475), *S. caudata* (*Faurie 772*, G) and of the holotype of *S. robusta* (26.VII.1928 *Noguchi*, HIRO) showed they cannot be distinguished at the species level and apparently deserve the status of a variety of *S. subnimbosa* at most. While *S. subnimbosa* and *S. caudata* were described at the same time, I suggest usage of the name *subnimbosa* because the type material is better, which would provide less reasons for different interpretations. All these species, distinguished as synonyms of *S. subnimbosa*, are distinct from *S. bolanderi* in (1) larger plant size and (2) mostly larger cells, (3) more numerous oil bodies, (4) shorter keel of leaves, (5) tooth distribution to dorsal and ventral leaf bases; (6) producing of spinose, (7) fragile and (8) deep brown pigmented marginal teeth even in nonpigmented leaves.

Inoue (1972), arguing for specific segregation of *Scapania robusta*, cited a number of its characters as distinct from *S. bolanderi*. These characters, which do not agree with the type, were very dense and regular marginal leaf teeth; ventral lobes about as wide as long; broadly rounded apices of dorsal lobes, which are very broad (1.3–1.6 × as wide as long). The holotype of *S. robusta*, as cited by Inoue (1972), differs from this description in the more narrow leaf lobes and dorsal lobes mostly triangularly narrowed in sharp apices.

Study of the holotype of *S. bolanderi* var. *nipponica* Amakawa & S. Hatt. (*Kodama 4634*, NICH) showed that interpretation of *S. nipponica* as a taxon resembling small *S. bolanderi* with rather long decurrent ventral lobes and leaves without dorsal appendages (Amakawa 1967) is not correct. Studied plants have much in common (short keel and spinose fuscous marginal teeth particularly) with *S. subnimbosa* rather than with *S. bolanderi*. The main distinctions from *S. subnimbosa* are the considerably smaller size of plants and cells; the tooth distribution chiefly in distal and median leaf sectors and the less elongated terminal tooth cells, 1.5–1.7 × as long as wide.

The inclusion of *Scapania ampliata* in the sectio *Nemorosae s. stricto* (Amakawa & Hattori 1954, Schuster 1974) or *Stephania* (Potemkin 1998a) appears erroneous because of its regularly lobulate dentate perianth mouth, broad-based marginal leaf teeth, and, to a lesser extent, the very rarely produced gemmae, atypical of the other species of *Nemorosae s. lato*. The peculiar, regularly lobulate dentate perianth mouth of *S. ampliata* is very different from the mouth of all other species of the section.

The position of *Scapania ampliata* within sectio *Gracilidae* seems natural because of the regularly lobulate dentate-ciliate perianth mouth; broad-based marginal leaf teeth; frequent development of a tooth near the dorsal lobe base of female bracts and of some leaves even when the antical margin of dorsal lobes is subentire; marginal leaf teeth with terminal cells more thin-walled and occasionally darker pigmented like in *S. nipponica* and *S. subnimbosa*; 2–3 large oil bodies per leaf cell; and the chiefly colorless gemmae. Description of the gemmae of *S. ampliata* as brown and 1-celled (Amakawa & Hattori 1954) appears to be incorrect because of apparent considerable dependence of gemma color on intensity of light. In only two specimens in which the perianths and gemmae were found (*Inoue 20708, 20709*, both in TNS), the gemmae are predominantly colorless and 1-celled with some brown-tinged and a few 2-celled.

The above-mentioned misinterpretations of the infrageneric position of *Scapania ampliata* resulted from a puzzling mixture of basal and advanced features that characterize the species. On the one hand, the species has a ± moderately compressed perianth with a lobulate ciliate-dentate mouth, with lobules strongly resembling distal portions of leaf lobes. Such a perianth appears to be the most simply organized in the *Gracilidae*. Similarity of shape of the perianth mouth lobes and the distal portion of leaf lobes indicates an origin of the lobulate perianth mouth from a fusion of the leaf lobes. On the other hand, small cells, leaves coarsely dentate at least to the base of the postical margin, and largely 1-celled gemmae are indicative of considerable specialization of the species.

Sectio *Aequilobae* (Müll. Frib.) H. Buch

Scapania aspera M.&H. Bernet, *S. aequiloba* (Schwägr.) Dumort.

Sectio *Compactae* (Müll. Frib.) H. Buch

= sect. *Nemorosae s.* Hong (1980) *p. min. p.* — *Scapania compacta* (Roth) Dumort.

Scapania hollandiae W.S. Hong, ascribed earlier to this section (Potemkin 1998a), is transferred to the sectio *Ciliatae*.

Sectio *Calcicolae* R.M. Schust.

= subgen. *Kaalaasia* H. Buch *s.* Schuster (1974). — *Scapania calcicola* (Arnell & J. Perss.) Ingham (with *S. ligulifolia* R.M. Schust. as subsp. *ligulifolia* (R.M. Schust.) Damsholt & D.G. Long (Potemkin 1999a)), *S. pseudocalcicola* R.M. Schust., *S. gymnostomophila* Kaal.

Sectio *Planifoliae* (Müll. Frib.) Potemkin

= subgen. *Protoscapania* Amakawa & S. Hatt., sect. *Nemorosae* subsect. *Simmonsiae* R.M. Schust., *syn. nov.* — *Scapania nimbosa* Taylor *ex* Lehm., *S. zhukovae* Potemkin (Potemkin 2000c), *S. simmonsii* Bryhn & Kaal., *S. rotundifolia* Nicholson, *S. maxima* Horik., *S. ornithopoides* (With.) Waddell (= *S. handellii* Nicholson, *S. sakumae* Amakawa; both may deserve rank of varieties of *S. ornithopoides*), *S. secunda* Steph., *S. harae* Amakawa, *S. davidii* Potemkin (Potemkin 2001)

Scapania simmonsii is excluded from sectio *Nemorosae*, to which it was assigned earlier (Potemkin 1998a), and included in the *Planifoliae* on the basis of considerable similarity of its lobulate and ciliate perianth mouth with that of *S. ornithopoides* (Fig. 2G and H) and rather similar leaf shape with *S. nimbosa*. Moreover, *S. simmonsii* has coarsely nodulose trigones, an irregularly coarsely papillose cuticle, strongly convex subequal leaf lobes, and suppression of perianth and gemma formation that are characteristic of some of the other species of the *Planifoliae*. A dissimilar perianth mouth and leaf margin dentition of *S. simmonsii* have possibly resulted from very rare perianth formation. This has led to minimal influence of selection pressure on the perianth mouth and preservation of the ancestral condition. Leaf dentition was probably suppressed because it is apparently less efficient for keeping capillary water than strongly convex, subequally bilobed, recurved leaves. *Scapania simmonsii* represents a very isolated member of the *Planifoliae* and is the only arctic species of the section. It probably split from some basal species of the section and isolated in the Arctic. This agrees with Schuster's (1974: p. 612) assumption that *S. simmonsii* is "a remnant of the... essentially nonarctic flora that has persisted in some loci (chiefly not or imperfectly glaciated) in high arctic regions". *Scapania simmonsii* is distinct from the other species of the section in the considerably longer keel (0.25–0.5 vs. 0–0.2 ventral lobe length).

Re-evaluation of the section composition, description of *Scapania davidii* and *S. zhukovae* (Potemkin 2000c, 2001) and insufficient data on its Asiatic taxa render it necessary to provide a key to the species.

1\. Keel 0.25–0.5 of ventral lobe; leaves denticulate distally, with triangular (not spinose) marginal teeth (terminal cells to 1.5 × as long as wide); plants usually fuscous, with strongly convex, mostly subequal lobes (dorsal 0.7–0.95 the ventral), which are about as wide as long; ventral lobes strongly recurved; arctic .... *S. simmonsii*

1\. Keel to 0.2 of ventral lobe; marginal teeth at least sporadically occur near leaf base, spinose (terminal cells usually considerably over 1.5 × as long as wide); nonarctic areas 2

2\. Dorsal lobes moderately to ± hemispherically convex, subrotund (varying from broadly cordate and reniform to broadly oblong, obovate, and broadly ellipsoid); ventral lobes about as wide as long, turned backward so strongly that lobes of opposite leaves situated one over the other and ± perpendicular to stem and virtually forming one ventral row; plants slender, 0.75–1.8 mm wide 3

2\. Dorsal lobes plane or moderately convex, exceptionally

± hemispherically convex (some phases of *S. secunda*), mostly narrowly to broadly cordate or ovate; ventral lobes largely longer than wide, ± turned backward; lobes of opposite leaves as a rule not situated one over the other and not perpendicular to the stem, chiefly not forming one ventral row (except some phases of *S. secunda* and *S. harae*); plants broader, 2–8 mm wide 4

3. Leaf lobes of sterile leaves ± hemispherically convex and subequal in area (dorsal lobe mostly 0.85–0.95 of ventral); leaf margins regularly spinose dentate, with teeth and often marginal cells fuscous when leaves ± yellowish brown; leaf teeth distally and medially 1–2 cells long, with terminal cells (2–)3–4.5 × as long as wide; dorsal lobe subrotund (varying to broadly oblong, broadly ovate, and broadly ellipsoid), rather long decurrent; ventral lobes ovate to broadly ellipsoid, (0.85–)0.95–1.0 × as wide as long; plants 1.5–1.8 mm wide; China (Yunnan), Himalaya (E Nepal, Sikkim) .... *S. davidii*

3. Leaf lobes of sterile leaves moderately, never hemispherically convex, unequal in area (dorsal lobe 0.35–0.5(–0.75) the ventral); leaf margins remotely spinose dentate, with teeth and marginal cells not differentiated in color; leaf teeth distally and medially 1(–2) cells long, with terminal cells 1.5–2.5 × as long as wide; dorsal lobe subrotund (varying to broadly cordate and reniform), ± short decurrent; ventral lobes obovate, subrotund or ovate, broader, 1.0–1.2 × as wide as long; plants 0.75–1.0(–1.5) mm wide; China (Yunnan), Himalaya (Nepal) .... *S. rotundifolia*

4. Dorsal lobe 0.6–1.0 of ventral, distinctly divergent with stem; leaf margins remotely ciliate with broad-based (ca. 2–4 cells at base) cilia/teeth occurring mostly distally, with a few teeth near lobe bases or remotely spinose ciliate everywhere; Europe (Norway, UK), China (Yunnan), Himalaya (Nepal, Sikkim) .... *S. nimbosa*

4. Dorsal lobe 0.35–0.6 the ventral, chiefly subparallel to stem; leaf margins mostly regularly spinose dentate or ciliate everywhere with narrow based teeth/cilia, 1–2 cells at base or subentire with a few teeth near lobe bases (except for *S. zhukovae* with distant rather broad based teeth, 1–3 cells long at base) 5

5. Ventral lobe ± plane, not turned backward; dorsal lobe moderately convex; marginal cells of leaves normally thin-walled 6

5. Ventral lobe moderately convex, ± turned backward; dorsal lobe moderately to strongly convex; marginal cells of leaves normally thick-walled 8

6. Dorsal lobe long decurrent, with long ciliate appendage on decurrent strip; marginal cells 20–25 μm where subisodiametric; leaf margin very long ciliate with terminal cells of cilia 4.5–10.5 × as long as wide; gemmae yellowish brown; cuticle smooth; plants robust, 5–8 mm wide; China (Taiwan, Xizang, Yunnan), Humalaya (Bhutan, Nepal, Sikkim) .... *S. maxima*

6. Dorsal lobe ± short decurrent, without long ciliate appendage on decurrent strip; marginal cells 14–20 μm where subisodiametric; leaf margin spinose dentate to rarely dentate-ciliate with terminal tooth cells 1.5–4 × as long as wide; gemmae deep brown to deep purple; cuticle smooth to coarsely papillose, plants medium-sized, 1.2–4.5 mm wide 7

7. Plants 1.5–4.5 mm wide and 30–150 mm long; leaves densely spinose-dentate to rarely dentate-ciliate, with over 15 teeth on antical and over 20 teeth on postical leaf margin; cortex 3–5-stratose; mycorrhiza absent or diffuse in ventral medullary cells; SE Asia, oceanic Europe (UK, Norway, the Faeroes), oceanic Western North America (Aleutian and Queen Charlotte Isls.) .... *S. ornithopoides*

7. Plants 1.2–2.3 mm wide and 10–15 mm long; leaves distantly spinose dentate, with to 15 teeth on antical and to 20 teeth on postical leaf margin; cortex 1-stratose; mycorrhiza circular, diffuse in external medullary cells; Himalaya (Nepal) .... *S. zhukovae*

8. Dorsal lobe narrowly ovate, entire or almost entire, except basal sector; cuticle ± smooth; keel wing unknown; China (Xizang, Yunnan), Himalaya (Nepal, Sikkim) .... *S. secunda*

8. Dorsal lobe mostly broadly ovate, spinose dentate; cuticle with compound papillae at the middle of every cell; keel wing often broad; China (Yunnan), Himalaya (Bhutan, Nepal, Sikkim) .... *S. harae*

Sectio *Muelleria* Potemkin *sect. nova*

= sect. *Planifoliae p. min. p.* (named after Karl Müller, the first monographer of the genus *Scapania*, the author of *S. himalayica*)

Sectio Muelleria differt a sectione Plicaticalyx lobis foliorum non decurrentibus, incrassione parietum cellularium foliorum, carina brevissima, possibiliter parietibus cellularum medianarum fortiter incrassatis; differt a sectione Planifoliae perianthium subcylindricum multustratosum, incrassione parietum cellularium foliorum, non decurrentibus lobis ventralibus foliorum.

Type: *Scapania schljakovii* Potemkin

The section includes two species, *S. himalayica* Müll. Frib. (Herzog 1939) and *S. schljakovii* Potemkin (Potemkin 2001) and appears to be derived from the sectio *Planifoliae*. Perianth is known only in *S. schljakovii*, but the species share a similar leaf form and areolation, a vestigial keel, an arcuate and virtually non-decurrent insertion of leaf lobes, the presence of a specific area of elongated cells at the middle of lobe bases, spinose marginal teeth, as well as peculiar thickenings of leaf cells with ± concave central and bulging distal portions. They differ as follows.

Scapania schljakovii (Potemkin 2001: fig. 3G–P). Leaves with both lobes regularly spinose dentate to the base; marginal cells and teeth form deep brown border; outer cortical cells with smaller cavities and thicker walls than adjacent intracortical cells; leaf trigones moderate to small; intermediate thickenings of cell walls common in basal leaf sector; marginal leaf cells somewhat thick-walled in distal leaf sector; N Sikkim.

Scapania himalayica (Herzog 1939: fig. 6, Potemkin 2001: fig. 3A–F). Leaves entire or irregularly spinose dentate distally, the dorsal lobes entire or with single denticulations; marginal cells and teeth not differentiated in color or sporadically bleached; outer cortical cells with larger cavities and thinner walls than adjacent intracortical cells; leaf trigones exceedingly to moderately large; intermediate thickenings of cell walls rather rare in basal leaf sector; marginal leaf cells thin-walled; Sikkim, E Nepal.

Sectio *Ciliatae* Grolle

= sect. *Compactae p. p.* (Potemkin 1998a), sect. *Gracilidae p. min. p.*, sect. *Rufidulae p. p.* (Potemkin 1998a), sect. *Lepidae* R.M. Schust., *nom. inval.* — *Scapania koponenii* Potemkin (2000a), *S. hirosakiensis* Steph., *S. ciliata* Sande Lac. (= *S. hawaica* Müll. Frib. as *S. ciliata* subsp. *hawaica* (Müll. Frib.) Potemkin *comb. & stat. nov.* Basionym: *S. hawaica* Müll. Frib., Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 83: 160. 1905), *S. sandei* Schiffn. *ex* Müll. Frib., *S. lepida* Mitt., *S. bhutanensis* Amakawa, *S. americana* Müll. Frib., *S. hollandiae* W.S. Hong, *S. spitsbergensis* (Lindb.) Müll. Frib.

Scapania hirosakiensis was previously attributed to synonyms of *S. parvitexta*. According to investigated type materials (Hirosaki, 4.VI.1897 *Faurie 24,* G 11520, 11520A, 026914) *S. hirosakiensis* is distinct from *S. parvitexta* (one representative part of syntype with gemmae and perianth studied — *Faurie 15123*, G 24072; the other part — *Faurie 14262* — was not seen) as well as from all species ascribed to the *Stephania* in the coarsely papillose cuticle; lobulate ciliate perianth mouth; stronger elongated terminal tooth cells similar to those of some other species of the *Ciliatae*; and enlargement of basal leaf teeth (all characters not found in the *Stephania*). *Scapania hirosakiensis* appears to be most close to *S. koponenii*, from which it is distinct in the often spinose apiculated dorsal lobes; frequent lobulate spinous appendage near dorsal lobe base; generally coarser, bleached marginal teeth 1–5 cells at base and 1–3(–4) cells long with terminal cell 2–3 × as long as wide; not sharply defined marginal border of many (normally over 3) rows of strongly evenly thick-walled cells; and rather irregularly and coarsely papillose cuticle.

Scapania hawaica Müll. Frib. apparently represents a derivative of the widespread *S. ciliata*, which became distinct from the latter due to rather long isolation in Hawaii. Its most remarkable distinction is the larger (23–32(–39) × 11–15 μm), narrowly ovoid (2–3(–3.5) × as long as wide), chiefly thick-walled and sporadically 3–4-celled gemmae (Fig. 2O). I recognize *S. hawaica* as a subspecies of *S. ciliata*.

The poorly known *Scapania bhutanensis* (Fig. 3L–Q), described by Amakawa (1975), is distinct from *S. ciliata* primarily in dorsal lobes (1) ovate to cordate (vs. oblong, reniform or obliquely cordate); (2) often larger (0.4–0.75 vs. 0.35–0.5(–0.6) ventral lobe); (3) distinctly convex (vs. plane to hardly convex); (4) slightly divergent with stem at angle 10–30° (vs. 30–60°); (5) with longer and often branched cilia basally (vs. normally ± suppressed basal cilia); (6) ventral lobes broader (width mostly 0.75–1.0 vs. 0.6–0.8 the length); (7) keel shorter (0.09–0.2 vs. 0.2–0.3 the ventral lobe) and (8) ± arched; (9) irregularly coarsely papillose cuticle not obscuring leaf areolation; (10) brownish (11) broader gemmae ((13–)14–19 × 16–30 μm vs. 10–14(–17) × 17–25(–39) μm), × 1.0–1.6 vs. 1.2–2.1(–3.5) as long as wide; (12) common development of brown pigmentation (vs. common absence of pigmentation).

The poorly known *Scapania hollandiae* (Hong 1980), as I understand it on the basis of examined collections from western North America (British Columbia, *Schofield et al. 97820, 98042, 98137*; Wyoming, *Potemkin 952801, 953802, 955201*, all LE), represents an isolated species of sectio *Ciliatae*. It is different from the other species in the subentire to faintly denticulate leaves with spinose, bleached teeth formed mostly by projections of marginal cell walls; arcuately inserted, not or hardly decurrent ventral lobes; subequal leaf lobes; fleshy stem (unique for *Scapania*);

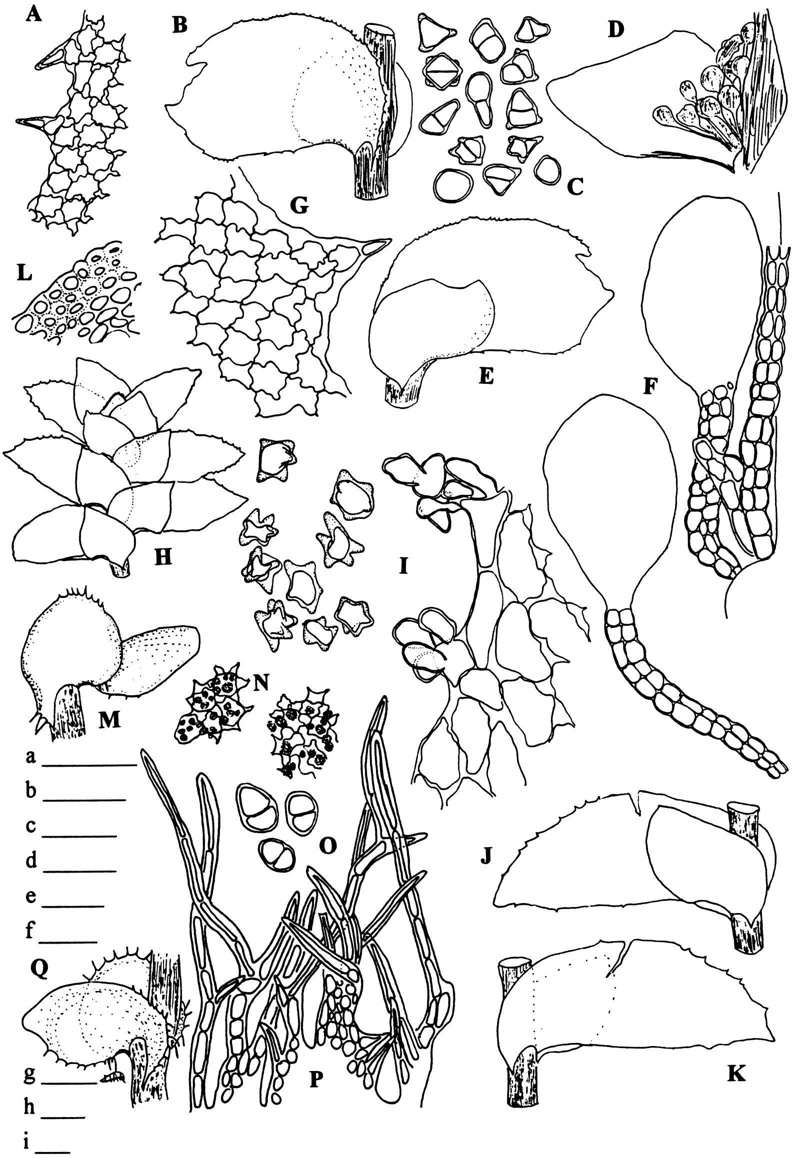

Fig. 3. *Scapania portoricensis* Hampe & Gottsche (**A**–**F**; **A**, **B**, **D**–**F** from *Schwanecke s.n.*, type of *S. portoricensis*, BM; C from *Frahm et al. 719*, H), *S. geppii* Steph. (**G**–**K**; from holotype, *Elliot s.n.,* G 11508), *S. bhutanensis* Amakawa (**L**–**Q**; **L**, **N** from holotype, 26.V.1967 *H. Kanai et al.*, NICH; **M**, **O**–**Q** from *Long 23891*, LE). — **A**, **G**: Sectors of postical margin of ventral lobes. — **B**, **K**, **Q**: Leaves on stem, postical aspect. — **C**, **I**, **O**: Gemmae (I with sector of gemmiparous lobe). — **D**: Axil of male bract with antheridia and paraphyses. — **E**, **M**, **J**: Leaves on stems, antical aspect. — **F**: Antheridia, antheridial stalk, and paraphysis**.** — **H**: Apical sector of gemmiparous shoot. — **L**: Dorsal sector of stem cross section. — **N**: Median cells of ventral lobe with papillae. — **P**: Sector of perianth mouth. — Scale bars: a: 2 mm (**H**). b: 1 mm (**B**, **E**). c: 50 *µ*m (**A**, **G**, **L**, **N**). d: 0.5 mm (**D**). e: 30 *µ*m (**O**). f: 0.5 mm (**J**, **K**, **M**, **Q**). g: 50 *µ*m (**P**). h: 20 *µ*m (**I**). i: 20 *µ*m (**C**).

suppression of gemma production and of secondary pigmentation. The formation of bleached spinose marginal leaf teeth, suppression of secondary pigmentation and similarity of habit of *S. hollandiae, S. ciliata* and *S. americana* support the placement of *S. hollandiae* within sect. *Ciliatae* rather than *Compactae* as presumed earlier (Potemkin 1998a). I believe that the development of a fleshy, succulent stem in *S. hollandiae* is an alternative to formation of a ciliate leaf margin as a device to resist desiccation. Therefore, I consider the development of such a stem resulted in suppression of leaf dentition in this species.

Type material of *Scapania hollandiae* cannot be found at present and is unavailable for study (W.S. Hong, pers. com.). Original description and illustrations of the species (Hong 1980) include characters considered above (except the fleshy stem) and some features of *S. americana* (leaves dentate to the base, with longer teeth and shorter keels, etc.). It is therefore uncertain if the type of *S. hollandiae* corresponds to the species characterized above or represents an atypical form of *S. americana*.

The following key is provided because the species composition of sectio *Ciliatae* has been altered and insufficient data exist to differentiate the species.

1. Leaf margin swollen, 2–3-stratose; leaf margin and cilia deep brown pigmented, internal leaf sectors lighter pigmented; N Borneo, Ceylon .... *S. lepida*
1. Leaf margin never swollen, always 1-stratose; leaf margin and/or cilia bleached or not differentiated in color from internal leaf sectors 2
2. Leaf margin regularly ciliate, with usually bleached cilia with terminal cells (3–)4–7(–9.5) × as long as wide 3
2. Leaf margin spinose dentate to short ciliate or faintly denticulate and subentire, with frequently not bleached teeth with terminal cells ca. 1.6–4 × as long as wide or even less elongated 4
3. Dorsal lobe mostly ovate to cordate, moderately convex, often subparallel to stem (lobe-stem angle ca. 10–30°); keel very short, 0.09–0.2 ventral lobe, often arched; marginal cilia near dorsal lobe base long and sporadically branched; gemmae brown ca. 14–19 × 16–30 μm, 1.0–1.6 × as long as wide; cilia of perianth mouth branched; China (Yunnan), Himalayas (Bhutan, Nepal) .... *S. bhutanensis* (Fig. 3L–Q)
3. Dorsal lobe mostly oblong to reniform, slightly convex or plane, distinctly divergent with stem (lobe-stem angle ca. (20–)30–60°); keel longer, 0.2–0.3 ventral lobe, straight to indistinctly arched; marginal cilia near dorsal lobe base short or absent, never branched; gemmae normally green, smaller and narrower, ca. 10–14(–17) × 16–25(–30) μm to in subsp. *hawaica* ca. 11–15 × 23–32(–39) μm, 1.2–2.0(–2.5) × to in subsp. *hawaica* 2–3(–3.5) × as long as wide; perianth mouth cilia unbranched; widespread in SE Asia with isolated subsp. *hawaica* in Hawaii .... *S. ciliata s. lato*
4. Ventral lobe broad, 0.85–1.15 × as wide as long; keel usually with broad dentate wing; paroicous. Arctic and adjacent mountain ranges southward .... *S. spitsbergensis*
4. Ventral lobe narrower, mostly 0.55–0.85(–0.95) × as wide as long; keel never with broad dentate wing; dioicous 5
5. Dorsal lobe ovate to cordate, rather slightly divergent with stem (lobe-stem angle ca. 20–40°); keel short, 0.09–0.25 ventral lobe, indistinctly to strongly arched; terminal tooth cells 3–4 × as long as wide; Java, Sumatra .... *S. sandei*
5. Dorsal lobe obliquely ovate, cordate, rounded rectangular, and reniform, distinctly divergent with stem (lobe-stem angle ca. (30–)45–60°); keel longer, 0.24–0.6 ventral lobe, straight to moderately arched; terminal tooth cells at the most 1.6–3 × as long as wide 6
6. Dorsal lobe 1.0–1.4 × as wide as long, broadly reniform and rounded rectangular, mostly broadly rounded at apex, 0.4–0.85 ventral; cuticle moderately papillose to smooth; temperate W North America 7
6. Dorsal lobe mostly narrower, 0.75–1.0 × as wide as long, often obliquely ovate to cordate, more rarely rounded rectangular and reniform, usually slightly to spinose pointed at apex, 0.45–0.55 ventral; cuticle coarsely papillose; E. Asia 8
7. Leaves spinose dentate everywhere except often dorsal bases, with (1–)2–3-celled teeth; stem never fleshy; ventral lobes long decurrent below the keel insertion, 0.55–0.75 × as wide as long; dorsal lobes mostly 0.4–0.75 the ventral in area; gemmae occasionally present; low elevations, 0–1500 m .... *S. americana*
7. Leaves usually faintly denticulate distally to subentire; stem mostly fleshy; ventral lobes not decurrent or hardly decurrent below the keel insertion, broader, (0.65–)0.75–0.95(–1.1) × as wide as long; dorsal lobes larger, mostly 0.55–0.85 the ventral in area; gemmae unknown; mostly higher elevations, 1200–2500 m .... *S. hollandiae*
8. Marginal teeth spread to leaf base; dorsal lobe base frequently with lobulate spinose appendage; marginal cells in many rows evenly thick-walled and bleached; dorsal lobe often spinose apiculated; terminal tooth cells 2–3 × as long as wide; Japan .... *S. hirosakiensis*
8. Marginal teeth usually not spread to leaf base; dorsal lobe base without lobulate spinose appendage; marginal cells in 1–2 rows slightly thick-walled or thin-walled, not bleached; dorsal lobe never spinose apiculated; terminal tooth cells (1.45–)1.6–2.0 × as long as wide; SE China (Fujian, Guangdong, Hunan, Jiangxi, Zhejiang) .. .. *S. koponenii*

Sectio *Scapania*

= sect. *Undulatae* H. Buch, sect. *Rufidulae* Grolle *p. p.* (Potemkin 1998a) — *Scapania subalpina* (Nees *ex* Lindenb.) Dumort., *S. obscura* (Arnell & C.E.O. Jensen) Schiffn., *S. undulata* (L.) Dumort. (= ? *S. purpurea* Kashyap & R. Chopra), *S. serrulata* R.M. Schust., *S. rufidula* Warnst., *S. komagadakensis* Amakawa, *S. gigantea* Horik., *S. uliginosa* (Lindenb.) Dumort. (= *S. paludosa* Müll. Frib. (Potemkin 1999a))

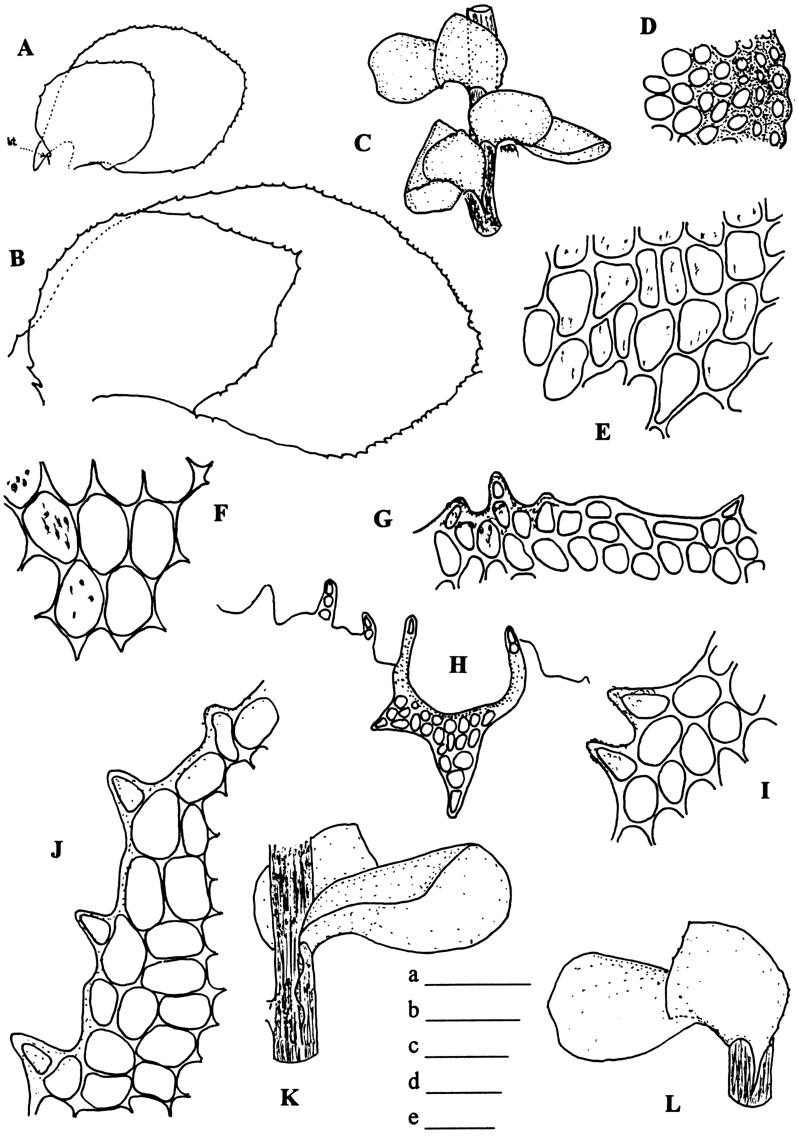

Fig. 4. *Scapania gigantea* Horik. — **A**, **B**: Leaves with distinct teeth near dorsal lobe base (bt). — **C**: Shoot sector. — **D**: Stem cross section, lateral sector. — **E**, **F**: Median cells of ventral lobes with shown papillae. — **G**, **H**: Sectors of perianth mouths. — **I**, **J**: Marginal sectors of ventral lobes. — **K**: Leaf on stem, postical aspect. — **L**: Leaf on stem antical aspect. — **A**, **F**, **G**, **I** from *Koponen 16473* (H); others from IX 1930 *Horikawa* (mater. orig., H). — Scale bars: a: 50 µm (**D**, **E**–**G**, **I**, **J**). b: 2 mm (**C**). c: 1 mm (**A**, **K**, **L**). d: 100 µm (**H**). e: 0.5 mm (**B**).

The taxonomic composition of the type section of the genus seems to be rather obscure. This results from a very broad concept of *Scapania undulata*, including many earlier separate species as synonyms. The variability of *S. undulata* through its range and along ecological gradients is almost undecipherable. This has lead to inclusion of a number of taxa in its synonymy, but some of the synonymizations appear doubtful. *Scapania gigantea* and *S. komagadakensis* in my opinion are such “false” synonyms. I distinguish these species as parallel steps to establishment of *S. uliginosa s. lato* morphotypes in sectio *Scapania*. They all are characterized by ± triangularly narrowed dorsal lobe apices of mature leaves and stable decurrency of dorsal lobe not characteristic of *S. undulata*. The main distinctive characters of *S. komagadakensis, S. gigantea, S. undulata*, and *S. uliginosa s.lato* are defined below.

Scapania komagadakensis. Plants yellowish brown; cortex 2–3-stratose, brown, of ± thick-walled cells with deeper pigmented middle lamellae; leaves finely dentate distally and medially, without teeth on decurrent strips. Dorsal lobe distinctly decurrent, ovate to cordate with obtuse apex, mostly slightly divergent with stem (the lobe-stem angle ca. 10–30°). Ventral lobe with ± undulate margins, 0.8–1.05 × as wide as long. Leaf trigones small to moderate, acute to bulging; marginal border rather weakly defined even in forms with moderate trigones of median cells. Cuticle punctate papillose. Gemmae unknown. The above is based on study of the holotype (3.VIII.1967 *Sakuma*, NICH) and an analysis of the original description and illustrations (Amakawa 1968).

Scapania gigantea (Fig. 4). Plants deep purple to brownish purple; cortex 3–6-stratose, purple to purplish brown, of ± thick-walled cells with deeper pigmented middle lamellae; leaves finely dentate distally and medially, at least sporadically with some or many teeth on dorsal and occasionally ventral decurrent strips; larger tooth at base of dorsal lobe decurrent strip usually observed on some leaves. Dorsal lobe distinctly long to short decurrent, ellipsoid to ovate and obliquely reniform, triangulary narrowed in mostly acute apex and often distinctly divergent with stem (ca. 15–80°); ventral lobe largely with not undulate margins, rather narrow, 0.66–0.76 × as wide as long. Leaf trigones vestigial to small, acute; marginal cells in several rows slightly thick-walled. Cuticle punctate to striolate papillose. Gemmae in small amount on juvenile, not exposed leaves, 1-celled, thin-walled, broadly to narrowly ovoid, at least with one broadly rounded end, in studied specimens colorless. The description is based on: Japan, Honshui: IX.1930 *Horikawa* (*materia originalis*, H), *Koponen 16473* (H); China, Yunnan *Wang Qi-wu 7197, 7204, 7214* (LE, PE)

Scapania undulata. Plants grassy green to fuscous and purplish; cortex mostly 2–3-stratose and brown, of ± thick-walled cells with usually not differentiated middle lamellae; leaves variably dentate to entire, never with larger tooth on decurrent strip of dorsal lobe. Dorsal lobe subtransversely inserted to variably decurrent, rounded quadrangular to oblong and obliquely ovate, broadly rounded to rarely triangulary pointed at apex, mostly distinctly divergent with stem (the lobe-stem angle ca. 25–55°). Ventral lobe with frequently ± undulate margins, 0.7–1.0 × as wide as long. Leaf trigones normally vestigial to small acute (larger trigones occur in var. *oakesii* (Austin) H. Buch and phases attributed to *S. purpurea*, type unavailable)*;* marginal border often absent in mod. *leptoderma-integrifolia-viridis*, strongly defined in mod. *lepto- vel mesoderma-dentata*. Cuticle ± smooth**.** Gemmae 2-celled, broadly ovoid, colorless to purplish in sun. The description is based on numerous specimens throughout the species range, mainly from LE, H, NY, WTU, F, and UBC.

Scapania uliginosa s. lato. Plants green to purple and fuscous; cortex 1–2-stratose, of ± thick-walled cells with usually not differentiated middle lamellae; leaves entire to denticulate usually distally and medially; larger tooth at base of dorsal lobe decurrent strip unknown. Dorsal lobe invariably distinctly decurrent, cordate, rounded quadrangular and reniform, triangulary narrowed in rounded to obtusely pointed apex and predominantly subparallel to stem; ventral lobe with not undulate margins, broad, 0.8–1.45 × as wide as long. Leaf trigones vestigial to rather large in *S. paludosa* var. *papillosa* Müll. Frib. phases; marginal cells in several rows thick-walled to thin-walled. Cuticle punctate papillose to smooth. Gemmae 1-celled, thin-walled, narrowly ovoid to subspherical, colorless to purplish. The description is based on numerous specimens throughout the species range, mainly from LE, H, NY, WTU, F, and UBC.

Sectio *Sphaeriferae* Konst. & Potemkin (1994)

= sect. *Umbrosae s.* Grolle (1983), *p. p.* — *Scapania sphaerifera* H. Buch & Tuom.

Sectio *Verrucosae* Potemkin

= sect. *Aequilobae p. min. p.* — *Scapania verrucosa* Heeg (= *S. manina* Steph., typ. error for "*mauina*", *syn. nov.*; *S. parva* Steph.; *S. verrucifera* C. Massal.), [*S. udarii* S.C. Srivastava & A. Srivastava].

Although material of *Scapania udarii* was unavailable for study, a detailed analysis of its description and illustrations (Srivastava & Srivastava 1993) revealed the following significant distinctions from the related *S. verrucosa*: (1) presence of purple to vinaceous (vs.

brown) secondary pigmentation of plants; (2) stronger divergent leaf lobes with the dorsal lobe divergent from the stem at an angle of 25–40° (vs. 40–65°) and the ventral 75–105° (vs. 35–60(–80°)); (3) almost invariably sharply angular (vs. rounded to blunt) leaf lobes; (4) keel shorter, 0.2–0.25 vs. 0.3–0.5 the ventral lobe and (5) distinctly arched (vs. straight to slightly arched); (6) leaf areolation with marginal cells in more than four rows evenly thick-walled (vs. less than in four rows) and (7) median cells with coarse, bulging (vs. small, mostly acute) trigones; (8) regularly finely (vs. coarsely) papillose cuticle; (9) gemmae with strongly (vs. slightly) projected and (10) thickened angles; (11) development of lateral (vs. ventral) intercalary branches; (12) shorter decurrent ventral lobes and (13) narrower dorsal lobes.

Sectio *Cuspiduligerae* H. Buch

= subgen. *Buchiella* R.M. Schust. — *Scapania cuspiduligera* (Nees) Müll. Frib.

Sectio *Cuspiduligerae* is close to the primitive species of sectio *Ciliatae* and to sectio *Plicaticalyx,* and derived from them. It appears to be a line of development parallel to these sections. This idea is based on the following characters of *Scapania cuspiduligera*, confirming its relationships with some primitive species of the sections *Ciliatae* (C) and *Plicaticalyx* (P): constantly bordered leaves (C) with ligulate ventral lobes (P); production of atavistic spinous teeth on female bracts (C, P); inability to develop large angular thickenings of median leaf cells (C, P); ability to form a coarsely papillose cuticle with strongly flattened, apparently rudimentary papillae (C, P); suppression of secondary pigmentation (C); formation of leaves not keeled proximally (P), brown gemmae (P), and a dorsiventrally flattened perianth (C).

Formation of a dorsiventrally flattened perianth on plants with non-keeled sheathing leaves suggests origin of the sectio *Cuspiduligerae* from plants with keeled leaves and flattened perianths. The following characters of *S. cuspiduligera* appear to be advanced: leaves with subequal lobes and sheathing non-keeled bases, few large oil-bodies, formation of a hyaline area without chloroplasts and oil-bodies near the ventral lobe base.

Sectio *Plicaticalyx* (Müll. Frib.) Potemkin, *comb. & stat. nov.*

Basionym: *Scapania* subgen. *Plicaticalyx* Müll. Frib., Bull. Herb. Boiss., sér. 2, 3: 36. 1902 (= subgen. *Ascapania* Grolle, *syn. nov.*). — *Scapania hians* Steph. *ex* Müll. Frib. (= *S. delavayi* Steph., *syn. nov.*, *S. papillosa* Müll. Frib.), *S. contorta* Mitt. (= ? *S. oblongifolia* Steph., *syn. nov.*), *S. pseudocontorta* Potemkin (Potemkin 2000c), *S. spiniloba* Potemkin (Potemkin 2000c), *S. orientalis* Steph. *ex* Müll. Frib. (= *S. ferruginea* var. *flaccida* Müll. Frib.), *S. ferruginea* (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees, *S. sinikkae* Potemkin (Potemkin 2001), *S. ciliatospinosa* Horik.

Sectio *Plicaticalyx* includes two rather distinct groups of species assigned earlier to subgenera *Plicaticalyx* and *Ascapania*. The reason to merge these two groups is the discovery of *Scapania spiniloba*, which possesses shared characters of *S. orientalis,* of *Plicaticalyx* and of *S. hians* of *Ascapania* (Potemkin 2000c).

The first group of species is related to *Scapania ferruginea*, the type of the sectio *Plicaticalyx*, and includes *S. ciliatospinosa*, *S. ferruginea*, *S. orientalis*, and *S. sinikkae*.

The correct name for plants treated as *Scapania orientalis* remains questionable. Study of a single plant that constitutes the holotype of *S. nepalensis* Nees (Nepal, *cum Herpetis alternifolius* — the only specimen in STR, considered as holotype; Fig. 2I–M), usually ascribed to synonyms of *S. ferruginea*, showed that this plant seems to be *S. orientalis* rather than *S. ferruginea*. Its distinctive features are (1) small size of plants, ca. 1.5 cm long and 1.5–2 mm wide; (2) very remotely dentate-ciliate dorsal lobes; (3) fewer marginal cilia of ventral lobes than in the related *S. ferruginea* (to 34–36 per lobe); (4) ± distinct hyalodermis. Moreover it corresponds to the original description of the species by Nees (Gottsche *et al.* 1844), who differentiated *S. nepalensis* and *S. ferruginea* on the basis of density of marginal leaf teeth, i.e. the principal criterion to distinguish *S. orientalis* from *S. ferruginea* (Potemkin 1999b). Attribution of this plant to a juvenile form of *S. ferruginea* from wet habitats by Müller (1905) contradicts my opinion of its

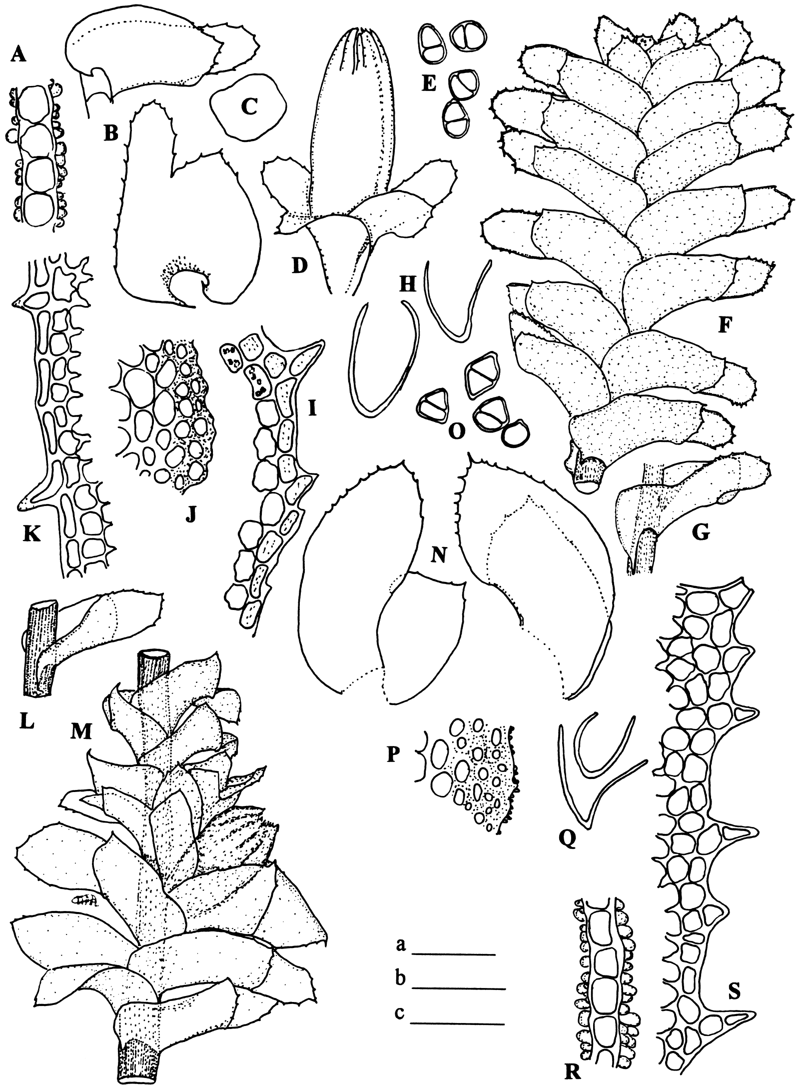

Fig. 5. *Scapania contorta* Mitt. (**A**–**K**; **A**, **E**–**K** from *Long 16930*, LE; **B**–**D** redrawn from Mitten's drawings of *S. contorta*, Chongtam, lectotype, NY), *S. hians* Müll. Frib. (**L**–**S**; from *Long 18923*, LE). — **A**, **R**: Sectors of leaf cross sections. — **B**, **N**: Leaves. — **C**: Perianth cross section. — **D**: Apical shoot sector with perianth. — **E**, **O**: Gemmae. — **F**: Apical sector of gemmiparous shoot. — **G**, **L**: Leaf on stem, postical aspect. — **H**, **Q**: Leaf cross sections in basal and distal portions. — **I**, **S**: Postical margin of ventral lobes in apical portion. — **J**, **P**: Lateral sectors of stem cross section. — **K**: Postical margin of ventral lobe in proximal portion. — **M**: Sector of shoot with axillary unfertilized perianth. — Scale bars: a: 2 mm (**F**, **G**, **L**, **M**). b: 50 μm (**A**, **E**, **I**–**K**, **O**, **P**, **R**, **S**). c: 0.5 mm (**H**, **N**, **Q**).

taxonomic position. The exceedingly scant type of *S. nepalensis*, which does not allow definitive taxonomic interpretations, persuades me to retain the nomenclature unchanged to avoid further confusion.

The second group of species includes *Scapania contorta, S. hians,* and *S. pseudocontorta. Scapania contorta* and *S. hians,* previously considered conspecific, can be distinguished by the following characters.

Scapania contorta (Fig. 5A–K): Plants (1.7–)1.9–2.5 mm wide, with marginal leaf teeth ± regularly developed to the proximal third of ventral lobe margin and often ± spinose (their terminal cells 1.2–2.5(–3) × as long as wide); ventral lobe with ± parallel margins, mostly broadly rounded distally; dorsal lobe of mature leaves chiefly broader than the ventral (its width, when measured near sinus base, perpendicularly to keel, (1.1–)1.2–1.6 the width of ventral lobe); stem surface smooth to slightly papillose in forms with extremely papillose leaves; hyalodermis-like layer of outer cortical cells unknown; mycorrhizal infection absent or postical; median cells of leaf base form a small to moderate area of lax tissue; plants usually ± brown, occasionally with purple only at leaf bases; marginal leaf teeth and adjacent marginal cells of ventral lobes usually deeper pigmented than median portions of leaves and form a fuscous border.

Scapania hians (Fig. 5L–S; Müller 1905: tab. 30a; Herzog 1939: fig. 7; Godfrey & Godfrey 1978: figs. 1–30): Plants 1–1.7 mm wide, with leaves entire to irregularly dentate in distal and occasionally median portions and marginal teeth with mostly triangular, nonspinose terminal cells (1–1.5 × as long as wide); ventral lobe mostly gradually ± triangularly narrowed to a ± acute apex; dorsal lobe of mature leaves mostly not broader than the ventral (its width, when measured near sinus base, perpendicularly to keel, 0.8–1(–1.1) the width of ventral lobe); stem surface ± distinctly papillose (more papillose when outer cortical cells thin-walled); outer cortical cells sporadically form hyalodermis-like layer; mycorrhizal infection diffuse, developed circularly, or absent; median cells of leaf base form an extensive area of lax tissue; plants green, brown or purple; pigmentation of marginal leaf teeth and adjacent marginal cells similar to pigmentation of the other portions of leaves.

The leaves in *Scapania hians* and *S. contorta* are broadened to the base and the keel is broadly rounded proximally. These characters show considerable variability. Forms with leaves not broadened at the base and a keel acute from near the leaf insertion to the sinus occur sporadically. They are characteristic of plants with short keels and smaller dorsal lobes respectively. Such atypical forms of *S. contorta* are probably *S. oblongifolia* (type too scant to be certain). The forms of *S. hians* with short acute keels and smaller dorsal lobes were described as *S. delavayi*. The latter shows much convergence with *S. koponenii*, the primitive species of the sectio *Ciliatae*. Being sterile, *S. hians* is distinct from *S. koponenii* in the brown gemmae, nonspinose marginal teeth and a more weakly defined cortex.

SPECIMENS EXAMINED. — *Scapania contorta*. **India.** Chongtam, 6000 (NY, selected lectotype); Sikkim, Himalaya, regio temp., Chongtam, 6000 ped., *J.D.H. s.d., s.n.* (BM, selected isolectotype); part of syntype in G lost; *Long 7910* (NY), *16930*, *20644a*, *21127, 21519* (LE), 1942 *Chen*, JE. *Scapania delavayi*. **China.** Yunnan, Maculchan, *Delavay s.d., s.n.* (G 8171, type). *Scapania hians*. Aug. 1896 *Giraldi* (G 11519, holotype); *Long 18839, 18841, 18923, 20743, 22233, 22842* (all LE). *Scapania papillosa*. 1937 *Troll* (JE, isotype). *Scapania oblongifolia*. Himalaya, *Duthie s.d., s.n.* (G 8176, type).

Recent description of *Scapania pseudocontorta, S. sinikkae,* and *S. spiniloba* (Potemkin 2000c, 2001) and re-evaluation of *S. contorta* above render it necessary to provide a key to the recognized species of sectio *Plicaticalyx*.

1. Dorsal lobes ± arcuately inserted and short decurrent; cuticle coarsely papillose or, more rarely, smooth 2
1. Dorsal lobe ± obliquely inserted and long to short decurrent; cuticle ± smooth 4
2. Ventral lobes bordered by fuscous brown marginal teeth and often cells, ± strap-like, mostly rounded at apex; marginal teeth ± spinose, extending to proximal third of ventral lobe, their terminal cells 1.2–2.5(–3) × as long as wide. Dorsal lobes basally ± broader than ventral, normally extending beyond further edge of stem; China (Sichuan), Himalayas (Bhutan, Nepal, Sikkim) .... *S. contorta*
2. Ventral lobes not bordered, with ± similarly pigmented marginal and median sectors, distally mostly triangularly narrowed in a sharp apex; marginal teeth nonspinose, extending at most to median third of ventral lobe, their terminal cells 1.0–1.8 × as long as wide. Dorsal lobes about as wide as ventral, not or sporadically extending beyond further edge of stem 3
3. Plants *Scapania contorta*-like, 2–3.5 mm wide, fuscous to (in apical sectors) deep purple (blackish when dry); leaf cells with smooth cuticle, deeply pigmented middle lamellae, coarse nodulose often confluent parietal thickenings; teeth with terminal cells 1.2–1.8 × as long as wide; marginal denticulations spread at most to middle third of postical leaf margin; Himalayas (Nepal) .... *S. pseudocontorta*
3. Plants with scapanioid to marsupelloid habit, 1–1.7 mm wide, green, brown or purple; leaf cells with regularly coarsely papillose cuticle (or rarely almost smooth), never with deeply pigmented middle lamellae and coarse nodulose often confluent parietal thickenings; teeth with terminal cells 1–1.5 × as long as wide; marginal denticulations chiefly in distal third of ventral lobe; Canada (British Columbia), China (Shen-si, Yunnan), Himalayas

(Nepal, Sikkim) .... *S. hians*

4. Lobes of leaves not modified from gemma production ± abruptly spinose tipped, entire or with a few remote spinose teeth mostly in distal and medial portions; leaf keel longer, mostly 0.2–0.4 ventral lobe; plants often purple and brown pigmented; Himalayas (Nepal) .... *S. spiniloba*
4. Lobes of leaves without distinctive spinose tips, ciliate or spinose dentate to proximal portions; leaf keel shorter, mostly 0.1–0.2 ventral lobe; plants mostly yellowish brown 5
5. Both leaf lobes broadly long decurrent. Central strand of strongly thick-walled ± brown-pigmented cells consistently present (except occasionally absent in apical and prostrate basal stem sectors); China (Xizang, Yunnan) .. .. *S. sinikkae*
5. One of leaf lobes with a much shorter broad decurrent strip than other (occasionally in *S. ciliatospinosa* dorsal lobes inserted almost along stem and then their decurrent strips end at level of much longer ventral decurrent strip). Central strand unknown or, in some phases of *S. ferruginea*, hardly developed 6
6. Dorsal lobe short decurrent, ventral lobe broadly long decurrent. Perianth near mouth with sparse to rather copious spinose surface [perianth surface near mouth formed of ± elongated cells; terminal cells of cilia almost invariably strongly elongated, 6–7 × as long a wide]; China (Sichuan, Xizang, Yunnan, Taiwan), Himalayas (Bhutan, Nepal, Sikkim, NW India) .... *S. ciliatospinosa*
6. Dorsal lobe broadly long decurrent, ventral lobe broadly short decurrent. Perianth with smooth surface near mouth 7
7. Leaves remotely ciliate to subentire, with (0–)20–40 cilia per ventral lobe; plants 1–3(–4.5) mm wide × 10–20(–45) mm long; Himalayas (Bhutan, Darjeeling, Nepal, NW India) .... *S. orientalis*
7. Leaves densely ciliate, rarely dentate to subentire, with over 50 cilia or teeth per ventral lobe; plants larger, 2–7 mm wide × 20–80 mm long [perianth with surface near mouth formed of mostly subisodiametric cells; terminal cells of cilia variously elongated, 2–6.5 × as long a wide]; Himalayas (NW? (Long & Grolle 1990), Bhutan, Darjeeling, Nepal, Sikkim), China (Sichuan, Taiwan, Xizang, Yunnan) .... *S. ferruginea*

Sectio *Grolleoscapania* Potemkin, *sect. nova*

(named after Dr. Riclef Grolle, the author of *Scapania karl-muelleri*, with deep gratitude for diverse help in my studies on *Scapania*)

Sectio Grolleoscapania differt a sectione Plicaticalyx cuticula grosse papillata; carina brevissima; lobis foliorum similibus magnitudine, late cordatis, valde convexis & recurvatis; ciliis folii densis tenuibus decoloratisque.

TYPE: *Scapania karl-muelleri* Grolle.

This monotypic section includes only *Scapania karl-muelleri*, assigned earlier to the sectio *Planifoliae* (Grolle 1966, Potemkin 1998a). After description of the perianth the species was transferred to the subgenus *Plicaticalyx* without consideration of its distinctions from the other species of the subgenus (Wu *et al.* 1999). However, *S. karl-muelleri* is distinct from the species of *Plicaticalyx* in the following combination of characters: (1) coarsely papillose cuticle; (2) vestigial keel; (3) leaf lobes subequal, broadly cordate, strongly convex and recurved; and (4) dense slender and bleached marginal cilia, which are characteristic of the *Ciliatae*.

In parallel with the species of the sectio *Plicaticalyx*, *Scapania karl-muelleri* often develops ± bleached outer cortical cells with rather large cavities, which are frequently larger than those of adjacent intracortical cells (Fig. 2N).

Sectio *Curtae* (Müll. Frib.) H. Buch

= subgen. *Jensenia* S.W. Arnell. — *Scapania mucronata* H. Buch (with *S. praetervisa* Meyl. as subsp. *praetervisa* (Meyl.) R.M. Schust. (Potemkin 1999a)), *S. helvetica* Gottsche, *S. zemliae* S.W. Arnell (= *S. invisa* R.M. Schust. (Potemkin 1999a)), [*S. gamundiae* R.M. Schust.] (? Fuegian derivative of *S. zemliae*), *S. lingulata* H. Buch, *S. esterhuyseniae* S.W. Arnell (? African derivative of *S. lingulata*), *S. curta* (Mart.) Dumort. (= *S. perssonii* R.M. Schust. (Potemkin 1999a)), *S. obcordata* (Berggr.) S.W. Arnell (= *S. paradoxa* R.M. Schust. (Potemkin 1999a)), *S. diplophylloides* Amakawa & S. Hatt., *S. scandica* (Arnell & H. Buch) Macvicar (= *S. parvifolia* Warnst. (Potemkin 1999a)), [*S. fulfordiae* W.S. Hong] (position within the *Curtae* doubtful).

Sectio *Curtae* appears to be a young neotenic group of the genus and demonstrates relationships with sectio *Nemorosae*, which were considered under that section.

Sectio *Irriguae* (Müll. Frib.) H. Buch

— *Scapania irrigua* (Nees) Nees, *S. hyperborea* Jørg. (with *S. tundrae* (Arnell) H. Buch as var. *tundrae* (Arnell) Potemkin = *S. pulcherrima* R.M. Schust. (Potemkin 1995, 1999a)), *S. paludicola* Loeske & Müll. Frib.

Sectio *Irriguae* appears to be a derivative of sectio *Curtae*. Origin of sectio *Irriguae* may be associated with adaptation of plants to growth in swampy conditions.

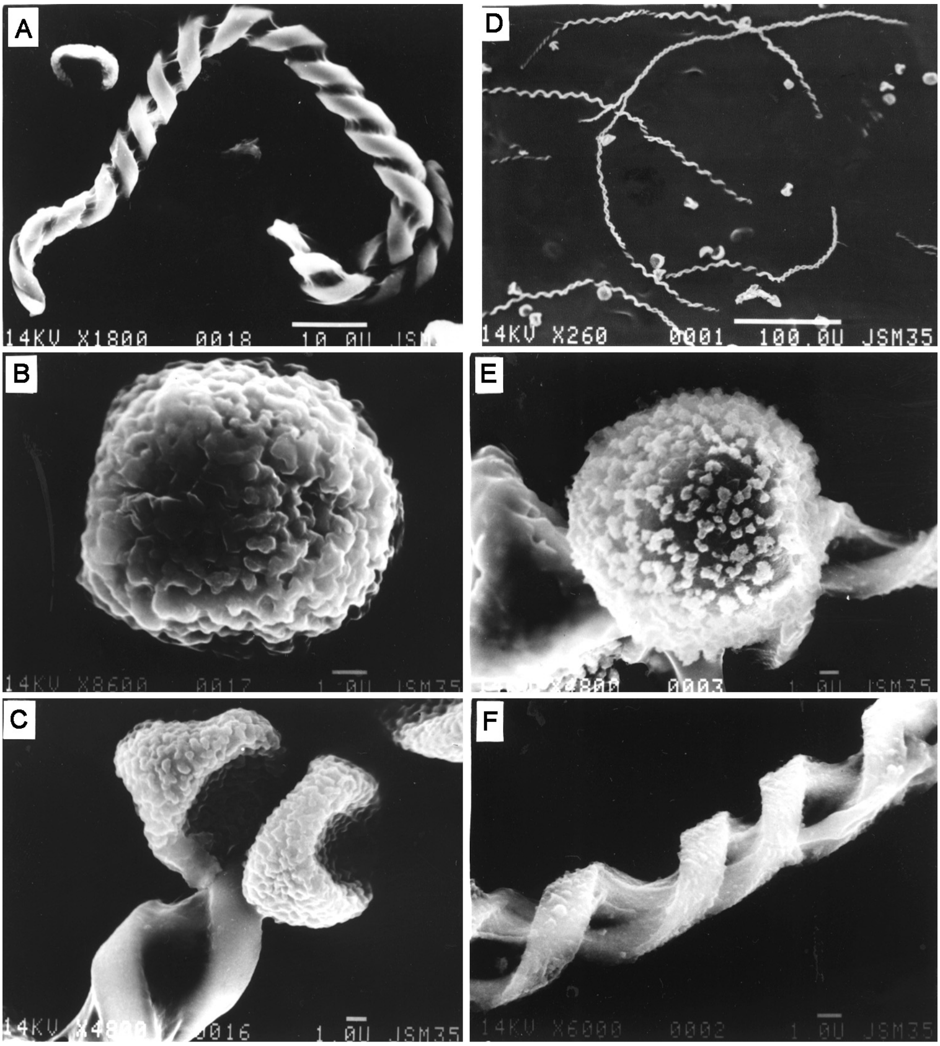

Fig. 6. *Scapania verrucosa* Heeg (**A**–**C**; from 3.VI.1997 *Wu*, LE), *S. portoricensis* (**D**–**F**; from 4.IX.1982 *Frahm et al.,* det. Gradstein 719, LE). — **A**, **C**, **D**, **E**. Elaters and spores. — **B**. Spore. — **F**. Sector of elater.

Sectio *Apiculatae* H. Buch

= sectio *Scapaniella* (H. Buch) Potemkin 1998a, *nom. illeg*., subgen. *Scapaniella* (H. Buch) R.M. Schust. — *Scapania glaucocephala* (Taylor) Austin (= ? *S. scapanioides* Grolle, ? *S.calciphila* R.M. Schust., with *S. saxicola* R.M. Schust. as var. *saxicola* (R.M. Schust.) Potemkin (Potemkin 1999a)), *S. carinthiaca* J.B. Jack *ex* Lindb. (= *S. massalongii* (Müll. Frib.) Müll. Frib. (Potemkin 1999a)), *S. apiculata* Spruce (= *S. ensifolia* Grolle)

Sectio *Apiculatae* appears to be a neotenic group of *Scapania* derived from sectio *Curtae* or from sectio *Cuspiduligerae*. Origin of sectio *Apiculatae* may be associated with adaptation of plants to growth on rotten wood.

Sectio *Incurvae* Potemkin

= sect. *Compactae* H. Buch *p. p.*, sect. *Irriguae s*. Schuster & Damsholt (1974) *p. p.*) — *Scapania kaurinii* Ryan.

Subgenus *Macroscapania* R.M. Schust.

Subgenus *Macroscapania* appears to be a Neotropical derivative of the subgenus *Scapania*. It shows some relationships with *Scapania verrucosa*, which is distributed southward to Mexico and Hawaii. The species of *Macroscapania* possess a number of features not characteristic of the other species of the genus, i.e., (1) exceedingly long elaters (width/length ratio ca. 1: 30–50); (2) peculiarly spinose punctate spore surface (Fig. 6); (3) dissemination of spores in large masses, being intermingled with elaters; (4) polygonal gemmae as well as (5) development of broad coarsely dentate ± decurrent keel wing on weakly dentate leaves; (6) formation in *S. portoricensis* of 2-seriate antheridial stalks otherwise unknown in *Scapania* (Fig. 3F) (except partly 2-seriate antheridial stalks mentioned by Amakawa (1981) for *S. ferruginea* (Lehm. & Lindenb.) Gottsche, Lindenb. & Nees); and (7) secondary reduction of paraphyses. Formation of short lax androecia and multiandrous (6–8-androus) bracts is characteristic for both species of the subgenus. They show, however, different sperm dispersal mechanisms. In *S. portoricensis* Hampe & Gottsche antheridia mature ± simultaneously in dense clusters. They have long (to 350 μm) mostly 2-seriate ± thick-walled and pigmented stalks. Their aggregated permanent stalks act like paraphyses. Scale-like paraphyses occur sporadically in this species. In *S. geppii* Steph. antheridia have longer (up to 350–450 μm), 1-seriate, also permanent stalks, bringing the body out of its dorsal lobe shelter, which is not much distinct from the dorsal lobes of sterile leaves. Antheridia in *S. geppii* mature individually and probably one after the other. Together with mature antheridia juvenile ones and stalks of antheridia with destroyed or withered bodies occur. Paraphyses are strongly reduced to stalked slime papillae.

Despite a considerable similarity in habit with the species of subgenus *Scapania*, *Macroscapania* appears to be subgenerically separate due to characters discussed above. It is similar to *Scapania verrucosa* in having angulate gemmae, leaf shape and dentition, but it has a very different spore surface as well as different elaters (Fig. 6). I consider *Macroscapania* as an example of rapid evolution in hepatics in the Neotropic (Schuster 1990).

Taxonomic composition

Scapania portoricensis Hampe & Gottsche (= *S. minutidens* Steph., *syn. nov.*), *S. geppii* Steph.

The two species of *Macroscapania* are distinguished as follows.

Scapania geppii (Fig. 3G–K; Müller 1905: tab. 48): Dorsal lobe of sterile leaves 0.62–0.86 × as wide as long, ± obliquely narrowly cordate to lanceolate, almost triangular and subelliptical, ± flat 0.25–0.35 ventral and strongly divergent with it; ventral lobe lanceolate, triangulary narrowed in acute to cuspidate apex, 0.39–0.45(–0.52) × as wide as long, arcuately inserted, not decurrent or hardly decurrent below keel insertion; keel with broad entire wing; gemmae 1-celled, polygonal, with mostly strongly projected and thickened angles; antheridial stalks 1-seriate; Lesser Antilles (Dominica).

Scapania portoricensis (Fig. 3A–F; Herzog 1928: figs. 1–10; Müller 1905: tab. 18): Dorsal lobe of sterile leaves 0.8–1.3 × as wide as long, ± obliquely cordate to ovate, convex, 0.35–0.7 ventral, slightly divergent with it to subparallel; ventral lobe oblong to subelliptic, broadly rounded to rarely triangulary pointed at apex, 0.5–0.82 × as wide as long, arcuately inserted, ± decurrent below keel insertion; keel rarely with broad dentate to entire wing; gemmae 1–2-celled, ± angulate and polygonal to subspheric, with slightly to moderately projected and thickened angles; antheridial stalks mostly 2-seriate (sporadically 1-seriate and partly 3-seriate); tropical areas of Central and Southern America (Antilles, Bolivia, Brazil, Columbia, Ecuador, Peru).

Subgenus *Macrodiplophyllum* (H. Buch) Potemkin

= *Diplophyllum* (Dumort.) Dumort. subgen. *Macrodiplophyllum* H. Buch, *Macrodiplophyllum* (H. Buch) Perss.

Macrodiplophyllum is distinct from the other *Scapania* in the diplophylloid habit predetermined by leaves not keeled proximally and sheathing the stem, with characteristic ligulate-falcate lobes; and the slightly flattened, regularly pluriplicate perianth that gradually narrows to a densely lobulate-ciliate mouth. *Macrodiplophyllum* was included in *Scapania* on the basis of similar leaf areolation and dentition as well as 2–3(–4)-celled gemmae with intersecting internal walls and ± projecting angles similar to those of *S. sphaerifera* (Potemkin 1999c).

Taxonomic composition

Scapania microdonta (Mitt.) Müll. Frib. (= *Diplophyllum microdontum* (Mitt.) H. Buch, *Macrodiplophyllum microdontum* (Mitt.) Perss.), *S. plicata* (Lindb.) Potemkin (= *Diplophyllum plicatum* Lindb., *Macrodiplophyllum plicatum* (Lindb.) Perss.), *S. imbricata* M. Howe (= *Diplophyllum imbricatum* (M. Howe) Müll. Frib., *Macrodiplophyllum imbricatum* (M. Howe) Perss.). When sterile the species are distinct as follows.

1. Plants *Scapania*-like; cuticle regularly coarsely papillose; marginal teeth spinose, 1(–2)-celled, developed from distal to proximal sectors of leaves; dorsal leaf lobes ca. (0.6–)0.75–0.9(–1.0) × as wide as long, ± crossing beyond the further edge of stem; keel often rather strongly arched; gemmae green, ± thick-walled; northern amphipacific species with range extensions to continental areas of eastern Siberia and western North America .... *S. microdonta*
1. Plants ± *Diplophyllum*-like; cuticle irregularly slightly papillose to nearly smooth; leaf margins entire to variously dentate usually around lobe apices only, with nonspinose marginal teeth; dorsal leaf lobes mostly narrower, ca. 0.4–0.6 × as wide as long, not crossing beyond the further edge of stem; keel moderately to slightly arched; gemmae, if known, brown, thin-walled 2
2. Plants light green to yellowish brown, with leaf lobes unequal (dorsal 0.4–0.6 the ventral), entire to dentate distally; the stem not glistening and mostly brown, with very strongly thick-walled outer cortical cells; leaves decurrent antically and postically; marginal leaf cells 10–16 μm wide, slightly differentiated from intramarginal cells; northern Amphipacific .... *S. plicata*
2. Plants largerly olive brown to blackish (exceptionally yellowish brown), with leaf lobes subequal (dorsal 0.75–0.9 the ventral) and normally entire; the stem glistening and mostly blackish, with rather slightly thick-walled outer cortical cells; leaves nondecurrent postically and occasionally hardly decurrent antically; marginal leaf cells narrower, 8–13 μm wide, sharply differentiated from larger intramarginal cells; northern Pacific North America .... *S. imbricata*

Taxonomic summary

The family Scapaniaceae includes 87 recent and one fossil species arranged in one genus, three subgenera and 18 sections:

I. Subgen. *Scapania*
1. sect. *Nemorosae*: *S. ligulata, S. parvitexta, S. griffithii, S. integerrima, S. hoffeinsiana, S. umbrosa, S. javanica, S. rigida, ?S. grossidens, S. brevicaulis, S. hedbergii*, *S. nemorea, S. matveyevae*.
2. sect. *Gracilidae*: *S. bolanderi, S. nipponica, S. subnimbosa, S. gracilis, S. ampliata*.
3. sect. *Aequilobae*: *S. aspera, S. aequiloba*.
4. sect. *Compactae*: *S. compacta*.
5. sect. *Calcicolae*: *S. calcicola, S. pseudocalcicola, S. gymnostomophila*.
6. sect. *Planifoliae*: *S. nimbosa, S. zhukovae, S. simmonsii, S. rotundifolia*, *S. maxima, S. ornithopoides, S. secunda*, *S. harae, S. davidii*.
7. sect. *Muelleria*: *S. himalayica*, *S. schljakovii*.
8. sect. *Ciliatae*: *S. koponenii, S. hirosakiensis, S. ciliata, S. sandei, S. lepida, S. bhutanensis, S. americana, S. hollandiae, S. spitsbergensis*.
9. sect. *Scapania*: *S. subalpina, S. obscura, S. undulata, S. serrulata, S. rufidula*, *S. komagadakensis, S. gigantea, S. uliginosa*.
10. sect. *Sphaeriferae*: *S. sphaerifera*.
11. sect. *Verrucosae*: *S. verrucosa, S. udarii*.
12. sect. *Cuspiduligerae*: *S. cuspiduligera*.
13. sect. *Plicaticalyx*: *S. hians*, *S. contorta, S. pseudocontorta, S. spiniloba, S. orientalis, S. ferruginea, S. sinikkae, S. ciliatospinosa*.
14. sect. *Grolleoscapania*: *S. karl-muelleri*.
15. sect. *Curtae*: *S. mucronata, S. helvetica*, *S. zemliae, S. gamundiae, S. lingulata, S. esterhuyseniae, S. curta, S. obcordata, S. diplophylloides*, *S. scandica, ?S. fulfordiae*.
16. sect. Irriguae: *S. irrigua*, *S. hyperborea, S. paludicola*.
17. sect. *Apiculatae*: *S. glaucocephala, S. carinthiaca, S. apiculata*.
18. sect. *Incurvae*: *S. kaurinii*.

II. Subgen. *Macroscapania*: *S. portoricensis, S. geppii*.

III. Subgen. *Macrodiplophyllum*: *S. microdonta, S. plicata, S. imbricata*.

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References

Amakawa, T. 1967: *Scapania* sect. *Gracilidae* of the areas around the North Pacific Ocean. — *J. Hattori Bot. Lab.* 30: 315–327.

Amakawa, T. 1968: New or critical species of the genus *Scapania* of Japan 1. — *J. Hattori Bot. Lab.* 31: 94–100.

Amakawa, T. 1975. Scapaniaceae. — In: Ohashi H. (ed.), Flora of Eastern Himalaya, third report. Hepaticae (compiled by S. Hattori). — *Univ. Mus., Univ. Tokyo* 8: 226–228.

Amakawa, T. 1981: A revision of the subgenus *Plicaticalyx* of the genus *Scapania*. — *Hikobia Suppl.* 1: 117–127.

Amakawa, T. & Hattori, S. 1954: A revision of the Japanese species of Scapaniaceae. II. — *J. Hattori Bot. Lab.* 12: 91–112.

Amakawa, T. & Hattori, S. 1955: A revision of the Japanese species of Scapaniaceae. III. — *J. Hattori Bot. Lab.* 14: 71–90.

Buch, H. 1928: Die *Scapanien* Nordeuropas und Sibiriens 2. Systematischer Teil. — *Soc. Sci. Fennica, Comm. Biol.* 3(1): 1–177.

Furuki, T. & Mizutani, M. 1994: Check-list of Japanese Hepaticae and Anthocerotae, 1993. — *Proc. Bryol. Soc. Japan* 6(5): 75–83.

Godfrey, J. D. & Godfrey, G. A. 1978: *Scapania hians* in Schensi, China and British Columbia, Canada. — *Bryologist* 81: 357–367.

Grolle, R. 1966: Die Lebermoose Nepals. — *Ergebn. Forsch.-Unternehmen Nepal Himalaya* 1(4): 262–298.

Grolle, R. 1983: Hepatics of Europe including the Azores: an annotated list of species, with synonyms from the recent literature. — *J. Bryol.* 12: 403–459.

Grolle, R. & Schmidt, A. 2001: A fossil *Scapania* (Hepaticae) with perianth and capsule in Bitterfield amber (Eocene) from Germany. — *Bryologist* 104: 362–366.

Gottsche, C. M., Lindenberg, J. B. G. & Nees ab Esenbeck, C. G. 1844: *Synopsis Hepaticarum.* — sumptibus Meissnerianis, Hamburgi. 834 pp.

Herzog, Th. 1928: *Scapania portoricensis* Hpe & G. — *Ann. Bryologici* 28: 91–112.

Herzog, Th. 1939: Zwei Bryophytensammlungen aus dem Sikkim-Himalaya. — *Ann. Bryologici* 12: 71–97.

Hong, W. S. 1980: The genus *Scapania* in western North America. II. Taxonomic treatment. — *Bryologist* 83: 40–59.

Inoue, H. 1972: Studies on Formosan Hepaticae. 1. Introduction and Scapaniaceae. — *Jap. J. Bot.* 20: 311–327.

Konstantinova, N. A. & Potemkin, A. D. 1994: Studies on *Scapania sphaerifera* (Hepaticae). — *Ann. Bot. Fennici* 31: 121–126.

Long, D.G. & Grolle R. 1990: Hepaticae of Bhutan II. — *J. Hattori Bot. Lab.* 68: 381–440.

Mizutani, M. 1984: Check-list of Japanese Hepaticae and Anthocerotae, 1983. — *Proc. Bryol. Soc. Japan* 3(10): 155–162.

Müller, K. 1905: Monographie der Lebermoosgattung *Scapania* Dum. — *Nova Acta Acad. Caes. Leop.-Carol.* 83: 1–312.

Potemkin, A. D. 1994: Studies on *Scapania*, Hepaticae. Sectio *Rufidulae* and sectio *Nemorosae*. — *J. Hattori Bot. Lab.* 77: 273–285.

Potemkin, A. D. 1995: Contribution to the knowledge of the liverworts of North America. — *Fragm. Flor. Geobot.* 40: 323–338.

Potemkin, A. D. 1998a: On the origin, evolution and classification of the genus *Scapania* (Dum.) Dum. (Scapaniaceae, Hepaticae). — *J. Hattori Bot. Lab.* 85: 33–61.

Potemkin, A. D. 1998b: On evaluation of liverwort taxonomic characters and species concept. — In: *Problems of the botanical sciences at the boundary of XX and XXI centuries*. Abstracts, presented to the II(X) Congress of the Russian Bot. Soc. (26–29 May, 1998, St. Petersburg) 2: 141–142.

Potemkin, A. D. 1999a: An analysis of the practical taxonomy of some critical northern species of *Scapania* (Scapaniaceae, Hepaticae). — *Bryologist* 102: 32–38.

Potemkin, A. D. 1999b: On the evolution and classification of *Scapania* (Hepaticae) — subgenus *Plicaticalyx*. — *Ann. Bot. Fennici* 36: 127–136.

Potemkin, A. D. 1999c: Circumscription of the family Scapaniaceae, with segregation of the new family Diplophyllaceae (Hepaticae). — *Ann. Bot. Fennici* 36: 271–283.

Potemkin, A. D. 2000a: Bryophyte flora of Hunan Province, China. 2. *Scapania koponenii sp. nova* (Scapaniaceae, Hepaticae). — *Ann. Bot. Fennici* 37: 41–44.

Potemkin, A. D. 2000b: An updated list of liverworts of the Severnaya Zemlya Archipelago (East Siberian High Arctic) with description of new species, *Scapania matveyevae*. — *Arctoa* 9: 95–100.

Potemkin, A. D. 2000c: Three new species of *Scapania* (Hepaticae) collected by Dr. David G. Long in Nepal. — *Arctoa* 9: 115–122.

Potemkin, A. D. [Потемкин, А. Д.] 2000d: [An evolutionary approach to segregation of genera and families in hepatics]. — In: *Mycology and cryptogamic botany in Russia: traditions and modern state*. Proceedings of the international conference devoted to 100th anniversary of investigations on mycology and cryptogamic botany in V.L. Komarov Bot. Inst. RAS (St. Petersburg, April 24–28, 2000): 525–528. [In Russian].

Potemkin, A. D. 2001: Three new species of *Scapania* (Hepaticae) from India and China. — *Ann. Bot. Fennici* 38: 83–89.

Schuster, R. M. 1974: *The Hepaticae and Anthocerotae of North America east of the hundredth meridian*. Vol. III. — Columbia Univ. Press, New York, London. xiv + 880 pp.

Schuster, R. M. 1984a: Comparative anatomy and morphology of the Hepaticae. — In: Schuster, R. M. (ed.), *New manual of bryology* 2: 760–891. Hattori Bot. Lab., Nichinan.

Schuster, R. M. 1984b: Evolution, phylogeny and classification of the Hepaticae. — In: Schuster, R. M. (ed.), *New manual of Bryology* 2: 892–1092. Hattori Bot. Lab., Nichinan.

Schuster, R. M. 1990: Origins of Neotropical leafy Hepaticae. — *Trop. Bryol.* 2: 239–264.

Schuster, R. M. & Damsholt, K. 1974: The Hepaticae of West Greenland from ca. 66° N to 72° N. — *Meddel. Groenland* 199: 1–373.

Srivastava, S. C. & Srivastava, A. 1993: A remarkable *Scapania* (Scapaniaceae) from Manali (Himachal Pradesh: Western Himalaya). — *J. Indian. Bot. Soc.* 72: 237–240.

Stephani, F. 1897: Hepaticae Japonicae. — *Bull. Herb. Boiss.* 5: 76–108.

Stephani, F. 1910: *Species Hepaticarum.* Vol. 4. — Georg & C^{ie}, Libraires-Éditeur, Géneve & Bale. 824 pp.

Takhtajan, A. L. [Тахтаджан, А. Л.] 1954: [*Problems of evolutionary morphology of plants*]. Leningrad, Leningrad Univ. Press. 215 pp. [In Russian].

Wu, Y., Cao, T. & Fu, X. 1999: *Scapania harae* and *S. karl-muelleri* (Hepaticae) new to China and the infrageneric position of *S. karl-muelleri*. — *Bryologist* 102: 317–319.

Index for identification of taxonomic position of mentioned taxa of *Scapania* with numerical references to the taxonomic summary above (names accepted for species or higher taxa are italicised).