

Circumscription of the family Scapaniaceae, with segregation of the new family Diplophyllaceae (Hepaticae)

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On the basis of phylogenetic analysis, the family Scapaniaceae Mig. is emended to include only the genus *Scapania* (Dumort.) Dumort. emend. Potemkin. The genus *Macro-diplophyllum* (H. Buch) Perss. is recognized as a subgenus in *Scapania*. The new combinations *Scapania* subgenus *Macro-diplophyllum* (H. Buch) Potemkin and *Scapania plicata* (Lindb.) Potemkin are provided. A new family, Diplophyllaceae Potemkin, with two genera, *Diplophyllum* (Dumort.) Dumort. and *Douinia* H. Buch, is segregated from the Scapaniaceae as a group of different origins resulting in a different morphology. *Douinia* is distinguished as a genus derived from *Diplophyllum* and its rank as a subfamily is rejected. The distinctive characters of *Delavayella* Steph. are discussed. Segregation of Delavayellaceae R.M. Schust. and Blepharidophyllaceae (R.M. Schust.) R.M. Schust. from the Scapaniaceae is supported.

Key words: Blepharidophyllaceae, *Blepharidophyllum*, *Delavayella*, Delavayellaceae, Diplophyllaceae, *Diplophyllum*, *Douinia*, evolution, hepatics, *Macro-diplophyllum*, *Scapania*, Scapaniaceae, taxonomy

INTRODUCTION

The family Scapaniaceae Mig. has in recent literature included two to four subfamilies. Grolle (1983) recognized within it four subfamilies, i.e. Scapanioideae, Douinioideae R.M. Schust., Blepharidophylloideae R.M. Schust., and Delavayelloideae (R.M. Schust.) Grolle. Schuster (1961, 1979, 1983) distinguished two of them as fami-

lies, Blepharidophyllaceae (R.M. Schust.) R.M. Schust. and Delavayellaceae R.M. Schust., and that resulted in the delimitation of the Scapaniaceae with two subfamilies, Scapanioideae, with the genera *Scapania* (Dumort.) Dumort., *Diplophyllum* (Dumort.) Dumort., and *Macro-diplophyllum* (H. Buch) Perss. (mostly distinguished as a subgenus of *Diplophyllum*) and Douinioideae, with only *Douinia* H. Buch.

Phylogenetic study of the genus *Scapania* led me to elucidate the relationships of the major entities of Scapaniaceae with its type genus, *Scapania*. Analysis of these relationships is provided below.

TAXONOMIC DISCUSSION

Scapania

The initial point for phylogenetic analysis of Scapaniaceae was definition of the basal genus. I consider *Scapania* as the basal genus of the family, since it demonstrates a greater diversity of evolutionary potential (Potemkin 1998). In that paper I assumed *Scapania* as a genus derived from the ancestral type intermediate between the family Jungermanniaceae Rchb. (subfam. Lophozioideae Macvicar) and the family Gymnomitriaceae H. Klinggr. A position close to the Gymnomitriaceae was concluded because of discovery of 2–3-spiral elaters and 2–3-stratose capsule walls in *Scapania praetervisa* Meyl. However, this may be not a sign of an ancestral type but a result of adaptation to harsh ecological conditions of growth on bare soil in an arctic and alpine environment. A similar structure of elaters is known for *Nardia breidlerii* (Limpr.) Lindb., *Prasanthus jamalicus* Potemkin, *Marsupella alpina* (Limpr.) Bern., *M. brevissima* (Dumort.) Grolle, *M. sparsifolia* (Lindb.) Dumort., and some other species of *Marsupella* Dumort., mostly characteristic of “difficult”, bare soil habitats. These features of the elaters were also observed in *Scapania scandica* (Arnell & H. Buch) Macvicar var. *argutedentata* H. Buch (Potemkin 1993) and *S. spitsbergensis* (Lindb.) Müll. Frib. (Potemkin 1994). The complete absence of gemmae in all known gymnomitrioid taxa supports the assumption of ecologically induced parallelism of elater structure. On this basis a lophozoid origin of *Scapania* seems most probable.

Relationships between Scapaniaceae and Lophozioideae have repeatedly been suggested (e.g., Buch 1928, Schuster 1951, 1974, Kitagawa 1965). These authors considered the genera *Tritomaria* Loeske and *Anastrophyllum* (Spruce) Steph. (Schuster 1951) as closest to Scapaniaceae. However, before Potemkin (1998), *Scapania*, as far as

I know, has never been placed as the basal genus of Scapaniaceae. The known interpretations of relationships of Scapaniaceae appear to be based on the concept of gradual transformation of the lophozoid ± indefinite keel and inflated perianth into the acute keel and compressed perianth of *Scapania*. Apparently, on this basis *Scapania* usually follows *Diplophyllum* in virtually all handbooks. I consider both genera as efficiently specialized in different ways.

Accepting in general the system of Lophozioideae suggested by Schuster (1951), with the section *Kunzeanae* R.M. Schust. (i.e. *Orthocaulis*) of *Orthocaulis* (H. Buch) R.M. Schust. as the basal group, I distinguish *Tritomaria* and *Anastrophyllum* as rather advanced groups to evolve from *Scapania*.

Barbilophozia kunzeana (Huebener) Müll. Frib. is exceedingly variable in width of ventral merophyte, cuticle papillosity, leaf shape (occurrence of arctic forms with bilobed almost conduplicate leaves and reduced underleaves is remarkable), its 3–4-stratose capsule wall combined with many other characters, to convince me that *Scapania* is a genus derived from an ancestor related to this species. *Barbilophozia kunzeana* itself, however, is different from *Scapania* in the somewhat angulate gemmae, inflated perianths, mostly regular development of underleaves, and some other characters. I think the gemma shape was apparently not strongly fixed at the base of the evolution of Lophozioideae, and this led to appearance of ovoid gemmae in two evolutionary lineages of Lophozioideae (*Lophozia heterocolpos* (Hartm.) M. Howe and *L. capitata* (Hook.) Macoun s. lato) and in *Scapania*. On the basis of the high plasticity of the *Barbilophozia kunzeana*-like ancestor, the idea of perianth compression correlated with leaf keel development seems possible.

Analysis of the present distribution of *Scapania* shows that the highest endemism and richest representation of diverse taxonomic groups is in SE Asia. The few species known from the Southern Hemisphere (except the highly advanced subgenus *Macroscapania* R.M. Schust.) are more or less advanced representatives of the northern groups. Therefore *Scapania* is considered as a genus of Laurasian origin.

Macrodiplophyllum

The genus *Macrodiplophyllum* (H. Buch) Perss. (\equiv *Diplophyllum* subgen. *Macrodiplophyllum* H. Buch in most modern treatments) is considered to be closest to *Scapania*. It includes three species, *M. imbricatum* (M. Howe) Perss., *M. microdontum* (Mitt.) Perss., and *M. plicatum* (Lindb.) Perss., occurring mostly in the area of the North Pacific Arc. All species of *Macrodiplophyllum* have a scapanioid leaf dentition (if any), areolation, and insertion (short decurrent to arcuate), as well as ventral intercalary branching (characteristic of many Asian *Scapania*), that provide reason to associate them with *Scapania* rather than with *Diplophyllum*.

Distinctions of *Macrodiplophyllum imbricatum*, *M. microdontum*, and *M. plicatum* are not equivalent. If *M. microdontum* has a \pm scapanioid appearance and stands close to *S. sphaerifera* H. Buch & Tuom., the two other species resemble a robust *Diplophyllum* due to the leaf bases long sheathing the stem, and more narrow lingulate falcate ventral lobes.

I hypothesize evolution of *Macrodiplophyllum* through *Scapania sphaerifera*-*Macrodiplophyllum microdontum* "bridge" (which is considered below). *Macrodiplophyllum microdontum* is a species with a less specialized "macrodipliphylloid" morphology, a broader range and probably a greater ecological amplitude than the two other species. The morphological hiatus between *M. microdontum* and the *M. plicatum*-*imbricatum* complex resulted from suppression in the latter of the basal leaf dentition and cuticle papillosity characteristic of *M. microdontum*, as well as from their leaf bases longer sheathing the stem and more narrow lingulate falcate ventral lobes. Suppression of the dentition and papillosity has probably resulted from adaptations of these species to humid conditions in rock crevices and similar sites in oceanic areas of the North Pacific Arc. Enhancement of the diplophylloid morphology (formation of longer sheathing leaf bases particularly) seems to be a device to compensate the suppression of basal tooth distribution.

It is necessary to define the distinctions between *Macrodiplophyllum microdontum* and *Scapania sphaerifera*

to elucidate a possible evolution of *Macrodiplophyllum* through *S. sphaerifera*-*Macrodiplophyllum microdontum* "bridge". *Scapania sphaerifera* resembles *M. microdontum* in (1) \pm sheathing and rounded leaf bases, (2) acute distal keel sectors, (3) shape of ventral lobes, (4) spinous terminal cells of marginal leaf teeth and distribution of teeth to the leaf base, (5) leaf areolation, (6) cuticle structure, (7) multicellular gemmae with intersecting internal walls, (8) pattern of modification of gemmiparous leaves with characteristic elongation of marginal cells, (9) stem anatomy with frequent occurrence of ventral mycorrhiza infection, and (10) pluriplicate perianths slightly contracted to the mouth, with the mouth lobulate-ciliate (cf. Figs. 1 and 2; Buch 1928: fig. VI, Konstantinova & Potemkin 1994: fig. 2). Moreover, they have similar ecological requirements and were collected together in the Verkhojansky Range (9.VII.1998 Akimova, LE). The character of special significance connecting *S. sphaerifera* and *M. microdontum* is the 3–4-celled gemmae with intersecting internal walls. Regular production of multicellular gemmae with intersecting internal walls is known within Scapaniaceae only in these species.

The principal distinctions of *Macrodiplophyllum microdontum* from *Scapania sphaerifera* are (1) \pm falcate ventral and particularly dorsal lobes, (2) stronger arched commissura, greater sheathing of the stem, (3) more slightly flattened and very regularly plicate perianths (vs. more flattened, irregularly plicate perianths of *S. sphaerifera* (cf. Buch 1928: fig. VI, Konstantinova & Potemkin 1994: fig. 2), (4) ability to develop very crowded, branched, long ciliate lobules of the perianth mouth, (5) shorter, at base mostly 1-celled marginal teeth of leaves, (6) predominantly angulate (vs. sphaeric) gemmae, and (7) occurrence of intermediate thickenings of basal leaf cells. All of these distinctions, however, may be explained as ecologically induced and genetically stabilized modifications of the character expressions. In fact, characters that distinguish *Macrodiplophyllum* from *Scapania* are not more significant than those of the subgenera *Plicicalyx* (Müll. Frib.) H. Buch emend. Potemkin (1999), *Ascapania* Grolle and *Scapania sensu* Potemkin 1998 of the genus *Scapania*

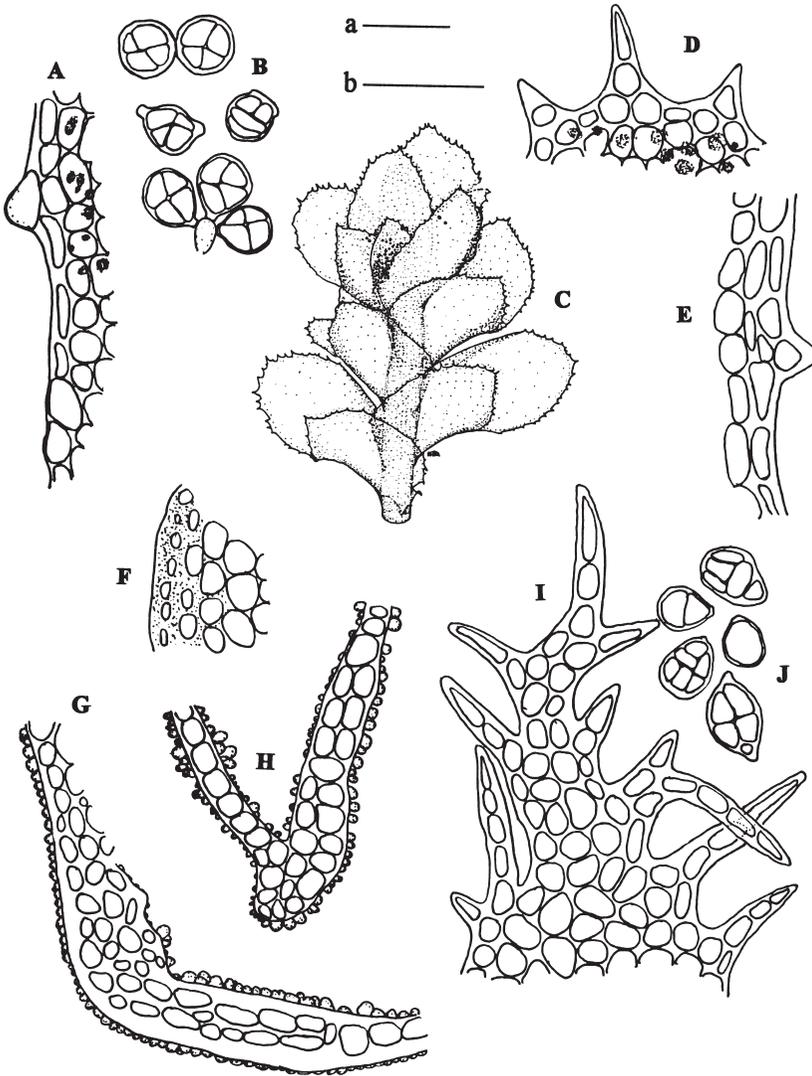


Fig. 1. *Scapania sphaerifera* H. Buch & Tuom. — A: Gemmiparous area along inner margin of ventral lobe. — B, J: Selected gemmae of different shapes. — C: Shoot sector, antical aspect. — D: Apex of ventral lobe with marked papillae. — E: Basal sector of ventral lobe margin. — F: Stem cross section, lateral sector. — G: Leaf base cross section. — H: Leaf keel section, distally. — I: Lobule of immature perianth mouth. — A–G, I drawn from 15.VIII.1989 Kazanovsky (LE); H, J from 9.VII.1998 Akimova (LE). — Scale bars: a = 800 μm (C); b = 50 μm (A, B, D–J).

pania.

The distinctions of *Macrodiplophyllum* and *Diplophyllum* appear to be considerably more significant than those of *Macrodiplophyllum* and *Scapania*. They are considered under *Diplophyllum*.

Diplophyllum s. str.

The morphology of *Diplophyllum* species is an expression of their adaptations to more xeric habitats in comparison with those of *Macrodiplophyllum* and most species of *Scapania*. *Diplophyllum* is primarily restricted to bare mineral soil and/or rocks (Amakawa & Hattori 1955, Schuster 1974,

Engel & Smith Merrill 1998). Occurrence of some species in different habitats appears to be secondary. So, *D. taxifolium* (Wahlenb.) Dumort. usually grows on bare mineral soil, but it behaves as a typical species of swampy tundras in the Seward Peninsula, Arctic Alaska (Potemkin, unpubl.). *Diplophyllum obtusifolium* (Hook.) Dumort. rarely grows on rotten wood (Smith 1990).

Despite a considerable overlap of variability in many separate characters of *Diplophyllum*, *Scapania* and *Macrodiplophyllum*, the following features of *Diplophyllum*, when taken together, remain very distinctive: (1) transversely inserted leaves, (2) mostly \pm small leaf cells, (3) \pm evenly thick- to thin-walled cells without sharply defined

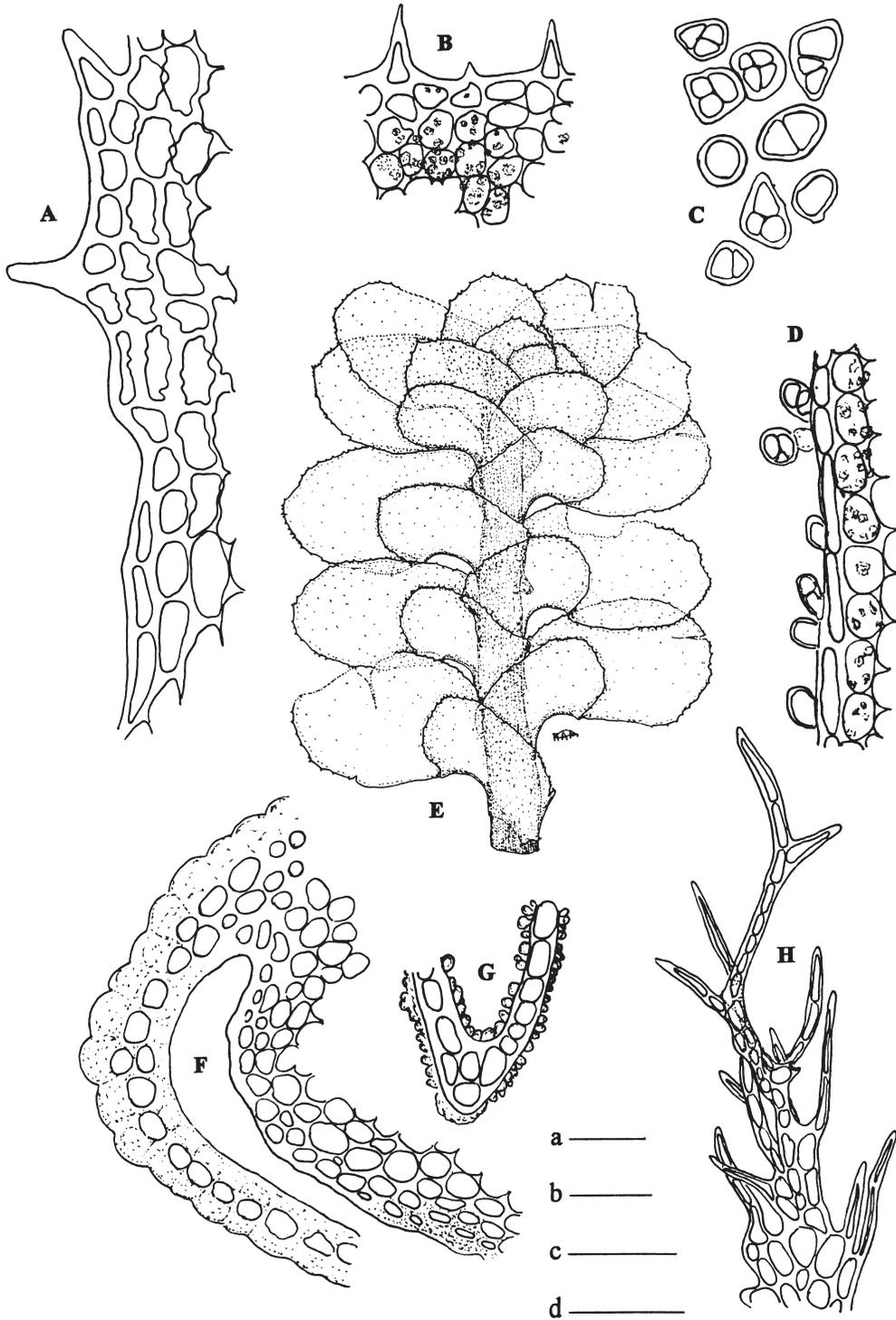


Fig. 2. *Macrodiplphyllum microdontum* (Mitt.) Pers. — A: Basal sector of ventral lobe margin. — B: Apex of ventral lobe with marked papillae. — C: Selected gemmae of different shapes. — D: Gemmiparous area along outer margin of ventral lobe with marked papillae. — E: Shoot sector, antical aspect. — F: Leaf base and stem cross section. — G: Leaf keel section, distally. — H: Lobule of immature perianth mouth. — All drawn from 8.VIII.1997 *Ignatov* (LE). — Scale bars: a = 50 μm (H); b = 800 μm (E); c = 50 μm (D); d = 50 μm (A–C, F, G).

trigones, (4) presence of a definite marginal border, (5) leaf margin chiefly finely densely crenulate to denticulate due to regularly projected walls of neighbor marginal cells, (6) with stronger developed projections to leaf bases (Fig. 3A, C, G, I and K), (7) development of strongly elongated basal leaf cells, (8) tending to form a vittate area (Fig. 3K), (9) small, polygonal (10) 1–2-celled gemmae with normally strongly projected and thickened angles (Fig. 3B), (11) predominantly monoicous sexual condition (17 of the 24 known species are monoicous), with (12) a frequent occurrence of autoicous condition, and (13) development of androecia in some taxa on specialized small-leaved branches restricted in growth.

Such an ensemble of characters, never recalling those of *Scapania* or *Macrodiplophyllum*, persuade me to consider *Diplophyllum* as a group of a different origin.

A different origin of *Diplophyllum* presumes designation of some basal group for evolution of the genus. Taking into account that the dioicous condition is characteristic of less advanced taxa, I consider that at the base of *Diplophyllum* evolution should be species with a dioicous or at most an unstable distribution of sex organs. The peculiarities of leaf dentition should be considered as derived. These two assumptions lead me to the only known dioicous species with entire to hardly crenulate leaves, *Diplophyllum nanum* Herzog (Fig. 3D–K). In addition to the characters mentioned above, this species is unique in having rather large leaf cells and rounded gemmae with low projections of the cell angles. Moreover, its perianth is slightly plicate and contracted to the mouth. Rhizoids, in material seen from Sumatra (*Wijk 1716*, L, LE), despite their rather scattered distribution, often originate from stem cells adjacent to the lowermost cells of the ventral lobe margin and may appear to be developed from it (Fig. 3D). All these features of *D. nanum* witness an absence of a stabilized diplophylloid morphology and confirm its rather close position to the base of evolution of the genus.

The other species, probably close to the base of the genus, is the only known dioicous representative of the subgenus *Austrodiplophyllum* R.M. Schust. of *Diplophyllum*, *D. recurvifolium* C. Massal. It requires further investigation.

Present data on distribution of *Diplophyllum*,

compiled by Engel and Smith Merrill (1998), show that in the Southern Hemisphere and sub-equatorial areas the genus has considerably more species than in the Northern Hemisphere (16 vs. 8 respectively), and these are chiefly very local endemics. Maximal level of endemism is known for the territory of New Zealand, Tasmania and South Australia (eight species, all endemics). The other endemics are known from southern South America (three species), Africa (Kenya, Rwanda, Tanzania) (one), Venezuela (one), Hawaii (one), Marion Is. (one). The most widespread species is *D. nanum* known from Papua New Guinea, Sumatra, Java, Borneo, Ceylon, and Bhutan.

My search for the ancestral group for *Diplophyllum* showed that *Diplophyllum* shares many characters with some Australasian species of *Anastrophyllum*, particularly *A. novazelandiae* R.M. Schust. (Schuster 1966: fig. 4) and *A. papillosum* J.J. Engel & Braggins (Engel & Braggins 1998: fig. 3). These include *inter alia* leaf insertion, shape and areolation; pattern of modification of marginal cell walls resulting in a \pm crenulate leaf margin; perianth and its mouth characteristics; gemma shape; oil-body characteristics. This suggests a Gondwanalandic, possibly Australasian origin of *Diplophyllum* from *Anastrophyllum*.

Douinia

The genus *Douinia* was established by Buch (1928). Among the generic criteria the following are noteworthy: non-keeled, loosely folded entire leaves with usually non-sheathing bases and narrowly lanceolate lobes; peculiarly copiously ciliate perianth mouth having branched cilia with \pm curved ends; 1-spiral elaters; and absence of gemma production. Schuster (1979: 74, 1984: 67) suggested the new subfamily of Scapaniaceae, Douinioideae, broadly accepted by other hepaticologists (Grolle 1983, Smith 1990, and others).

Douinia resembles *Diplophyllum* in general appearance, frequently incurved leaves and shape of perianth. Occasionally, the plants may develop \pm lingulate diplophylloid ventral lobes (Fig. 4A and C). It is also characteristic for *Douinia* to form a \pm thick-walled and often bleached marginal border with \pm distinct regular projections of walls of neighbor cells. The projections are stronger de-

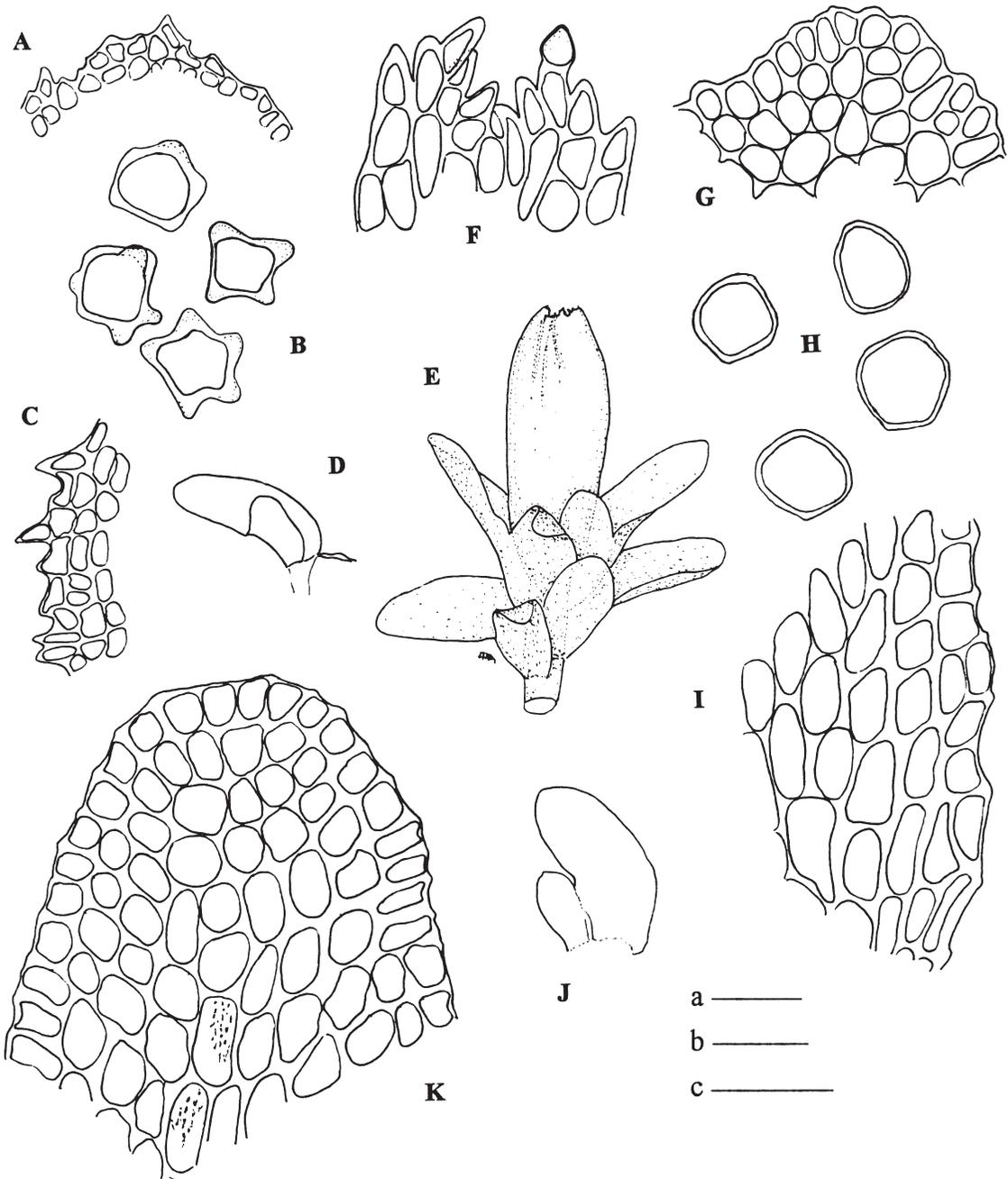


Fig. 3. *Diplophyllum taxifolium* (Wahlenb.) Dumort. (A–C) and *Diplophyllum nanum* Herzog (D–K). — A, G: Ventral lobes of leaves, apical sectors. — B, H: Gemmae. — C, I: Basal sectors of ventral lobe margins. — D: Leaf with rhizoids near ventral lobe base. — E: Sector of shoot with perianth, antical aspect. — F: Sector of perianth mouth. — J: Leaf. — K: Distal part of ventral lobe with elongated lower median cells with shown papillae. — A–C drawn from 8.VIII.1997 *Ignatov* (LE); D–K from *Wijk 1716* (L, LE). — Scale bars: a = 400 μ m (D, E, J); b = 50 μ m (A, C, F, G, K, I); c = 20 μ m (B, H).

fined to the leaf base (Fig. 4J, K and N).

On the other hand, *Douinia* demonstrates a

number of features which make its position within Scapaniaceae obscure. The characters of primary

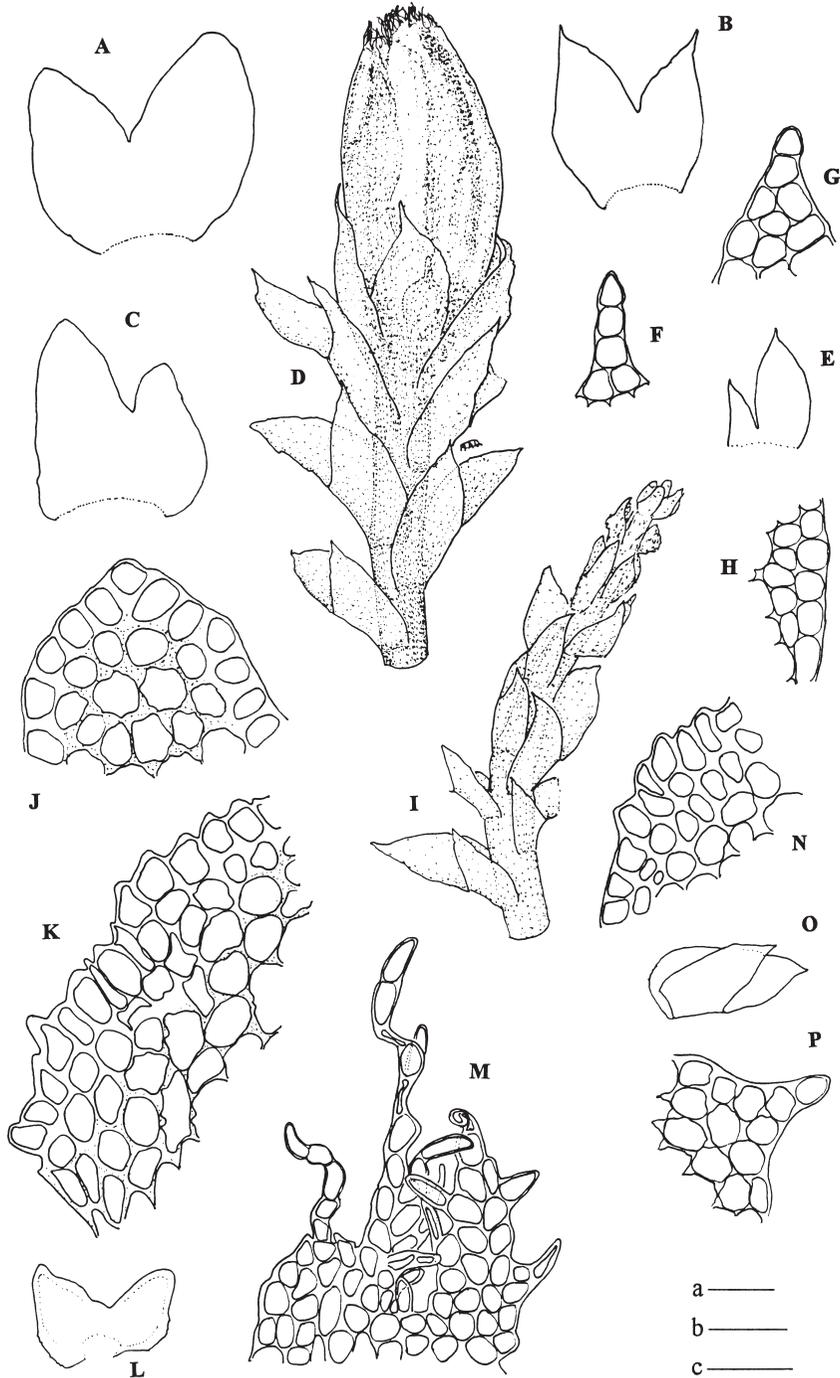


Fig. 4. *Douinia ovata* (Dicks.) H. Buch — A–C: Subfloral leaves. — D: Sector of shoot with perianth, antical aspect. — E: Leaf, mod. *mesoderma-viridis*. — F: Dorsal lobe apex of leaf from E. — G: Ventral lobe apex of leaf from E. — H: Ventral lobe margin of leaf from E, basal sector. — I: Sector of presumably gemmiparous shoot without gemmae, antical aspect. — J: Ventral lobe apex of male bract from L. — K: Ventral lobe margin of male bract from L, basal sector. — L: Male bract with marked bleached marginal sector, mod. *pachyderma-fusca*. — M: Sector of perianth mouth. — N: Ventral lobe margin of leaf from O, basal sector. — O: Leaf, mod. *mesoderma-fusca*. — P: Ventral lobe apex of leaf from O. — All drawn from 21.VII.1885 Kies (LE). — Scale bars: a = 50 μm (M); b = 400 μm (A–E, I, L, O); c = 50 μm (F–H, J, K, N, P).

importance are densely spiny papillose spores, 1-spiral elaters, absence of gemmae, and long-ciliate perianth mouth developing on plants with ± entire leaves.

In the process of evaluating the above criteria from the position of the evolutionary ecology and morphology, their origin from a diplophylloid progenitor becomes clear. Distinctions of *Douinia* from *Diplophyllum* are apparently related to evolution of the former to exploit “non-diplophylloid” habitats. *Douinia* probably evolved as an epiphytic hepatic of oceanic humid areas (the presence of *Douinia* on other substrates — rocks, rotten wood — may be secondary). In humid epiphytic conditions many water-preserving diplophylloid adaptations became “unnecessary” and were subjected to gradual modification resulting in larger and thin-walled cells, slightly defined marginal border, non-sheathing leaf bases, and hardly developed marginal serration. It is remarkable that diplophylloid features of *Douinia* developed distinctly in plants of mod. *densifolia-colorata* (xeric forms) and mostly not developed in plants of mod. *laxifolia-viridis* (forms of wet habitats). Growth in principally different niches led to a transformation of reproductive strategies expressed in suppression of gemma formation (gemmae are uncommon in epiphytic hepatics), enlargement of spore papillosity, and formation of 1-spiral elaters (capsules with very rare 2-spiral elaters occur sporadically as Schuster’s (1988: fig. 14, 5) and my own observations show). It is noteworthy that development of a long ciliate perianth mouth associated with slightly dentate to entire leaves is characteristic also for *Macrodiplrophyllum* (cf. Figs. 2H and 4M). It is pertinent to mention that small-leafed upper shoot sectors, resembling those of gemmiparous plants of *Diplophyllum*, were found in *Douinia* during this study (Fig. 4I).

Such an analysis reveals a possibility of ecologically induced transformation of *Diplophyllum* in *Douinia* and persuades me to consider *Douinia* as a close relative of *Diplophyllum*, not meriting a subfamilial segregation.

Delavayella

Buch (1928: 9, 10) pointed out the unclear family position of *Delavayella*. Schuster (1961) estab-

lished the family Delavayellaceae on the basis of (1) the ability of the leaves to develop a postical, saccate, gibbous lobule which is so situated as to be somewhat appressed to the stem when the plant is dry, (2) the dorsal lobe tends to be larger than the ventral, although the lobes are often subequal, (3) the distal part of the leaf is explanate and flattened, and the lobes are non-conducuplicate, and (4) the gemmae are globose and unicellular and appear to be fundamentally different from the fasciculate, catenulate-produced gemmae of the Scapaniaceae.

My study of *Delavayella* revealed the following reasons to distinguish it as a separate family (Fig. 5): (1) leaves absolutely non-keeled and (2) succubous, obliquely inserted, (3) strongly broadened basally, (4) divided by a very shallow sinus (ca. 0.15–0.25 the leaf length) into two very narrow lobes, (5) of which the dorsal is always definitely larger than ventral, (6) female bracts similar to sterile leaves, differing in the deeper sinuses and absence of sacs and showing no parallels with the bracts of the other genera of Scapaniaceae, (7) perianth narrow, long exerted and compressed in distal half only, being subcylindric proximally (such the compression is probably not highly specialized as well as the perianth mouth, which is similar to leaf lobes), (8) branching pattern (terminal, pseudodichotomous and lateral intercalary), (9) sporadic occurrence of rhizoids with branched ends, (10) abrupt development of almost naked or small-leafed flagella associated with asexual reproduction.

The pattern of asexual reproduction remains unclear to me. Despite a careful study of materials with flagellae, no gemmae were found. They are apparently weakly attached to gemmiparous vestiges. According to the original description by Stephani (1894: 4) accomplished in Stephani (1910: 119), the gemmae are hyaline, globose, 1-celled, on small scales appressed to the flagella (“*propagula in squamulis minutis appressis, hyalina, globosa, unicellularia*”).

Blepharidophyllum and *Blepharidophyllaceae*

Schuster (1983: 541), validating the family status of Blepharidophyllaceae (*Blepharidophyllum*, *Clandarium* (Grolle) R.M. Schust., *Krunodiplo-*

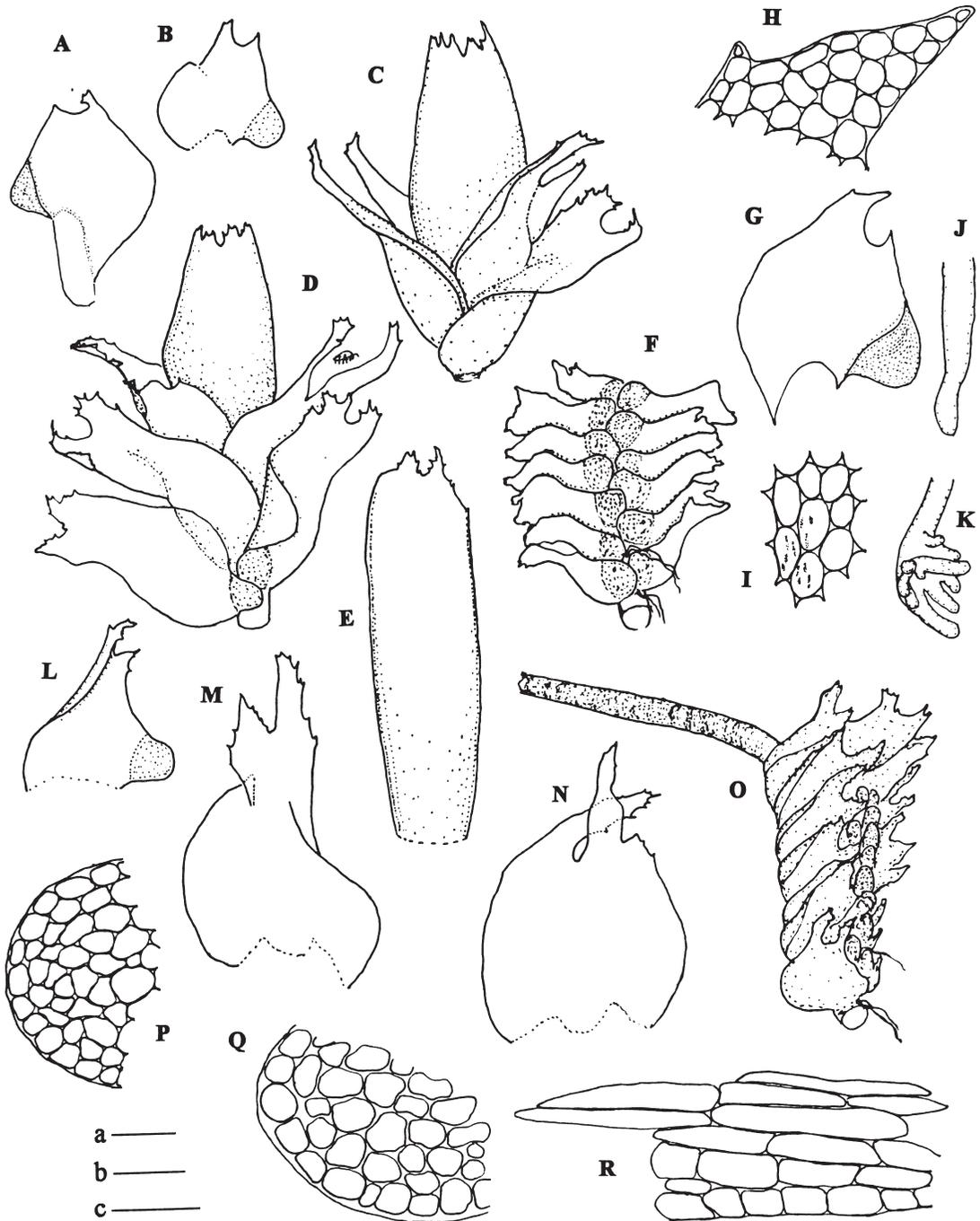


Fig. 5. *Delavayella serrata* Steph. — A, B, G, L: Leaves (A — of mod. *laxifolia*, with small sac and sector of stem). — C: Sector of shoot with perianth, antical aspect. — D: Same shoot sector, postical aspect. — E: Perianth. — F: Shoot sector, postical aspect. — H: Dorsal lobe of leaf from G. — I: Basal leaf cells medially (lower left with papillae). — J: End of normal rhizoid. — K: End of branched rhizoid. — M, N: Female bracts. — O: Shoot sector with gemmiparous flagellum, ventro-lateral aspect. — P: Lateral sector of stem cross section of mod. *laxifolia*. — Q: Ventro-lateral sector of stem cross section of mod. *densifolia*. — R: Sector of longitudinal section of stem. — A, B, F–L, and O–R drawn from *Tagawa & Kitagawa T3109* (NICH); C–E, M, N from 19.XII.1965 *Tagawa & Kitagawa* (NICH). — Scale bars: a = 500 μm (B–F, L–O); b = 50 μm (H–K, P–R); c = 400 μm (A, G).

phyllum Grolle), stated they have “a different phylogenetic” history, and are “at best remotely allied to the basically Laurasian family Scapaniaceae”. Engel and Smith Merrill (1998) showed the position of the single *Krunodiplophyllum* species within *Diplophyllum* subgen. *Austrodiplophyllum* R.M. Schust., and retained *Clandarium* as a subgenus of *Blepharidophyllum*. They (Engel & Smith Merrill 1998) noted that the species of the subgenus *Austrodiplophyllum* of *Diplophyllum* show evidence of relationship to both *Blepharidophyllum* and *Diplophyllum*.

I consider that leaf areolation of the species in subgenus *Austrodiplophyllum* indicates a close relationship with the subgenus *Diplophyllum*. The 4-ranked appearance, almost equally bilobed leaves, and strongly squarrose-recurved leaf lobes of the *Austrodiplophyllum* species may represent ecologically induced parallelism with *Blepharidophyllum*. Occurrence of rhizoids in fascicles in *Diplophyllum* (*Austrodiplophyllum*) *gemmaiparum* J.J. Engel & G.L. Sm., which is also characteristic for species of *Blepharidophyllum*, does not correlate with the other characters and appears to show no close relationships of both groups. Bifid dorsal lobes, sporadically occurring in *Diplophyllum* *incrassatum* J.J. Engel & G.L. Sm. (Engel & Smith Merrill 1998: 267, fig. 6: 8), are very different from the bisbifid leaves of *Blepharidophyllum*.

The facts above confirm Schuster's (1979, 1983:541) segregation of Blepharidophyllaceae from the other representatives of Scapaniaceae *s. lato*. It seems natural primarily because of the bisbifid leaves, which are uncharacteristic of *Diplophyllum* but are observed in some other Gondwanalandic groups (e.g., superficially similar to Balantiopsaceae H. Buch), and also because of the leaf areolation, which is principally different from *Diplophyllum*. Absence of any intermediate taxa between *Blepharidophyllum* and *Diplophyllum* supports this idea.

CONCLUSIONS

Macrodipllophyllum and *Diplophyllum* represent different groups from morphological and phylogenetic points of view.

Distinctions of *Macrodipllophyllum* from *Scapania*

are comparable with those of the subgenera of *Scapania*, not forming a generic hiatus and may be considered as gradually ecologically induced and genetically stabilized modifications of the character expressions.

Macrodipllophyllum is recognized as a subgenus of *Scapania*:

Scapania subgen. *Macrodipllophyllum* (H. Buch) Potemkin, *comb. nov.* — Basionym: *Diplophyllum* subgen. *Macrodipllophyllum* H. Buch, Soc. Sci. Fenn. Comm. Biol. 3(1): 29. 1928.

Species: *Scapania imbricata* M. Howe; *S. microdonta* (Mitt.) Müll. Frib.; *S. plicata* (Lindb.) Potemkin, *comb. nov.* — Basionym: *Diplophyllum plicatum* Lindb., Acta Soc. Sci. Fenn. 10: 235. 1872.

Diplophyllum is recognized as separate from *Scapania* and Scapaniaceae and placed in a separate family.

Diplophyllaceae Potemkin, *fam. nov.*

Familiae Scapaniaceae similis, sed origine differt, quae ex characteribus sequentibus recognoscitur: (1) dispositio primigenis basalis dentium marginalium foliorum, (2) dentes projecturis parietum cellularum contiguarum formantur, (3) plantae generaliter minores, ut plurimum monoeciae, saepe autoeciae, (4) cellulae foliorum minores, (5) margines foliorum limbo e cellulis parietibus crassis, (6) gemmae polygonales e 1–2 cellulis, (7) perianthium distaliter pluriplicate, saepe plus minusque ad orem constrictum.

Type: *Diplophyllum* (Dumort.) Dumort.

Similar to Scapaniaceae, but differing in the following complex of characters: (1) ± bordered small-celled leaves with (2) primarily basal tooth distribution and (3) tooth formation due to regular projecting of walls of neighbor marginal cells, (4) ± sheathing and rounded leaf bases, (5) ± falcate ventral lobes, (6) small 1–2-celled polygonal gemmae with ± projected thick-walled angles, (7) predominantly monoicous sex distribution, (8) with frequent formation of androecia on separate intercalary ± specialized branches, and (9) development of pluriplicate, mostly ± contracted to the mouth lophozoid perianth.

Douinia is distinguished as a genus of Diplophyllaceae derived from *Diplophyllum* and not

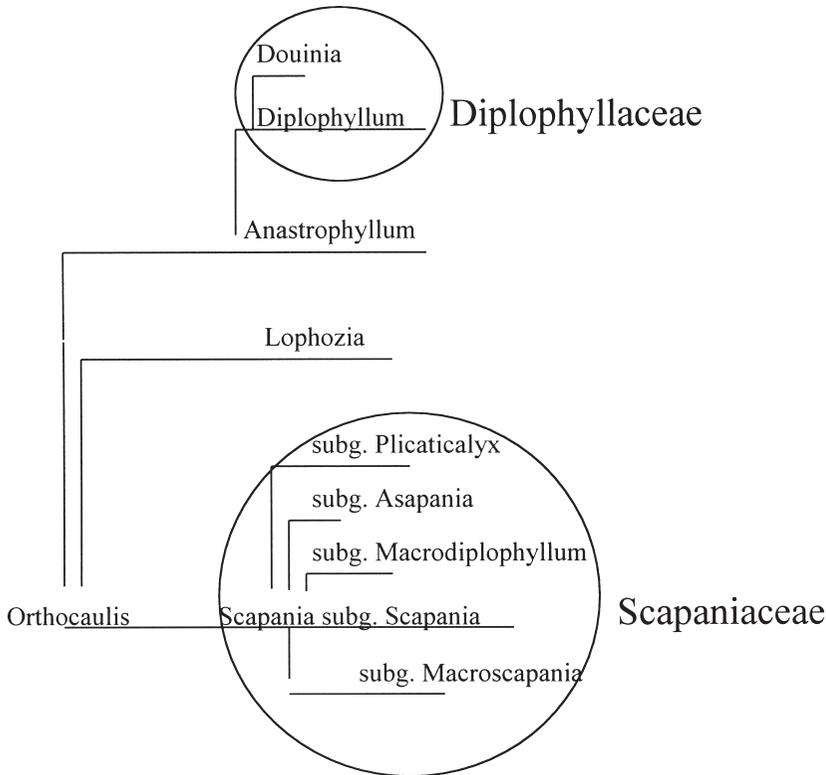


Fig. 6. Hypothesized phylogenetic relationships of *Scapania*.

deserving the subfamilial rank.

Delavayellaceae and Blepharidophyllaceae are independent families separate from Scapaniaceae.

The Scapaniaceae contains only the genus *Scapania*. The hypothesized phylogenetic relationships of *Scapania* are shown in Fig. 6.

The family Scapaniaceae is an example of how progressive and repeated study gradually narrowed our concept of it to the point where a more homogenous taxon resulted (Schuster 1961: 202).

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