

Taxonomic revision and cladistic analysis of *Diphyscium* (Family Diphysciaceae) of Taiwan

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Abstract. Six species of *Diphyscium*, with three new additions to the moss flora of Taiwan, are revised taxonomically, including *D. chiapense* Norris ssp. *unipapillosum* (Deguchi) T. Y. Chiang and S. H. Lin, stat. nov. Diagnosable keys are provided. In order to test Norris' and Deguchi et al.'s classifications, cladistic analyses were carried out on eleven morphological traits scored from nine Asiatic species of *Diphyscium*. Two equally parsimonious trees rooted at the *Theriotia* species were recovered by PAUP. The reconstructed phylogeny, which suggested a close relationship between the taxa with single papillose lamina cells and the species with pluripapillose lamina cells, invalidated Norris' hypothesis. The parsimony tree agrees with Deguchi et al.'s classification, in which three groups were classified based on cell-wall papillosity. Based on the inferred phylogeny, the "orifice" stomata may have evolved more than once in *Diphyscium*, while a single "secondary loss" event occurred in the group of *D. involutum*, *D. rupestre*, *D. mucronifolium* and *D. suzukii*.

Keywords: Cladistics; *Diphyscium*; *D. chiapense* ssp. *unipapillosum*; Orifice stomata; Papillosity; Phylogeny; Taiwan; Taxonomy.

Introduction

Diphyscium is a conspicuous moss characterized by its obliquely ovoid capsule with dorsiventral differentiation and a narrow mouth as well as strongly differential, bristled perichaetial leaves. *Diphyscium* and *Theriotia* constitute the Diphysciaceae. *Diphyscium* is distinguished from the latter by the well differentiated laminate portion of the leaves, waxy anticlinal walls in the dorsal side of the capsules, and the absence of chlorophylloids cells in the leaves (cf. Deguchi, 1984a). Phylogenetically, Diphysciaceae are closely related to the Buxbaumiaceae, sharing common structure and ontogeny of the capsules (Crum and Anderson, 1981). The reduced gametophytes and elongated setae in Buxbaumiaceae, however, suggest an independent lineage from the Diphysciaceae. Despite the remarkable differences of the sporophytic structure, the gametophytes of *Diphyscium* in some cases [e.g., *D. pocsii* (Bizot) Zand.] resemble the Pottiaceae. Deguchi (1975, 1984b) and Norris (1981) utilized the "collared" axillary hairs to differentiate the Diphysciaceae from the Pottiaceae.

About twenty-three species have been recognized, with a distribution ranging from the tropics to the temperate (van der Wijk et al., 1967; Crum and Anderson, 1981;

Crosby et al., 1992; Crosby and Magill, 1994; Deguchi et al., 1997). Deguchi et al. (1997) distinguished three groups of *Diphyscium* based on the papillosity of their leaf-cell surface: 1) species with smooth leaf cells (e.g., *D. involutum*), 2) species with unipapillose-mamillose leaf cells (e.g., *D. chiapense*), and 3) species with pluripapillose-mamillose leaf cells (e.g., *D. fulvifolium*). In contrast, Norris (1981) recognized two groups, with *D. foliosum* and *D. involutum* being representative. *Diphyscium chiapense* was regarded as a member of the *D. involutum* group according to his classification. Although Deguchi et al. (1997) treated *D. chiapense* and its relatives as a new group, the phylogenetic relationships among the three groups were not further discussed and therefore have remained unknown.

Interestingly, although the plants have discernible morphological characteristics, little research has been carried out on the east Asiatic (i.e. As 2; van der Wijk et al., 1967) taxa except for the Japanese species (Iwatsuki, 1976; Deguchi, 1983, 1984b; Noguchi, 1987; Deguchi et al., 1997). For example, the floristic survey of the Chinese *Diphyscium* has been poorly documented, with only four species and one variety known (cf. Redfearn et al., 1996). The tiny plants, with pottiaceous appearance when the sporophytes are absent, may have caused it to be overlooked by collectors.

The first record of this genus in Taiwan is from 1935, with the collections of *Diphyscium fulvifolium* and *D. formosicum* (= *D. involutum*) (Horikawa, 1935a, 1935b).

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Wang and Lin (1974a, 1974b) reported two new species, *D. macrophyllum* and *D. rotundatifolium*, which were later synonymized to *D. granulosum* and *D. fulvifolium*, respectively (Iwatsuki, 1976). Subsequently the above species have been revised in taxonomic treatments (Chuang, 1973) or described by floristic surveys (Lin, 1981, 1984; Lin and Tsai, 1984; Lai, 1986).

We studied the taxonomy of *Diphyscium* in Taiwan based on both our own collection and herbaria specimens. Six species, including three newly found taxa, are reported in this paper. We analyzed the phylogenetic relationships between the species belonging to the three groups of Deguchi et al.'s (1997) classification cladistically and tested the validity of Norris' (1981) hypothesis. Based on our reconstructed phylogeny, the morphological evolution of leaf-cell papillosity and stomata is discussed.

Materials and Methods

Materials were obtained both from field collection and loans from herbaria (HAST, HIRO, NMNS, TNS, TUNGH). Specimens were examined with stereo and light microscopes. Six species were identified and distinguished based on the diagnosable characters. In total, 11 characters were examined and scored to character states. Based on the previous taxonomy, *Theriotia lorifolia* and *T. kashmirensis* were chosen as outgroups and were used for character polarity (Deguchi, 1984a). In order to gain more insight into the phylogeny and morphological evolution, *D. suzukii* (a Japanese species), *D. mucronifolium* (a species of Java) and *D. chiapense* (a Mexican species) were also included in the analysis. The characters included in this analysis and the polarization of character states are as follows (Table 1):

1. Chlorophyllose cells in cross section of costa: present (0) and absent (1). The chlorophyllose cells are only present in *Theriolia*.
2. Thickness of lamina: multistratose (0) and bistratose (1). *Theriolia* species have multistratose lamina; while *Diphyscium* species have bistratose lamina (cf. Noguchi, 1987).

3. Waxy anticlinal walls in exothecial cells: absent (0) and present (1). The waxy anticlinal walls are differentiated on the dorsal side of the capsules of *Diphyscium* only.
4. Cell-wall papillosity: smooth (0), single-papillose (1), and pluri-papillose (2).
5. Stomata: differentiated at apophysis (0), differentiated at orifice (1), and absent (2). Most species, both ingroup and outgroup, have differentiated stomata either at apophysis (e.g., *D. foliosum*) or at orifice (e.g., *D. chiapense*). Stomata are absent in *D. involutum* and its relatives.
6. Subula of inner perichaetial leaves: smooth (0), and scabrous (1).
7. Upper portion of perichaetial leaves: entire (0), shallowly bifurcate (1), and deeply bifurcate (2). State 1 exists in *D. fulvifolium* only; state 2 exists in *D. foliosum* and *D. granulosum*.
8. Margins on inner perichaetial leaves: cilia (0), dissected (1), and entire (2). The appendages are differentiated in outgroups and most ingroup taxa except for *D. chiapense*.
9. Leaf-shape: linear with a short-ovate sheathing base (0), ovate-lanceolate (1), and linear without sheathing base (2). State 2 exists in most *Diphyscium*, except for *D. granulosum* (state 1).
10. Leaf apex: acute (0), apiculate (1), and obtuse (2).
11. Costa: excurrent (0), reaching apex (1), ending below apex (2).

Cladistic Analysis

Cladistic analyses of the morphological characters were carried out using the exhaustive searches of the PAUP computer software (Version, 3. 1. 1, Swofford, 1993). Most characters were treated as ordered, except for characters 5 and 10. All characters were unweighted.

Confidence of clades was tested using the complete-and-partial (CP) bootstrap technique to correct the bias (conservativeness) of the standard bootstrap approach (Li

Table 1. Distribution and polarization of characters and character states for *Diphyscium* and *Theriofia* in cladistic analysis.

Taxa\Characters	1	2	3	4	5	6	7	8	9	10	11
Outgroups:											
<i>Therlotia kashmirensis</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Therlotia lorifolia</i>	0	0	0	0	0	0	0	0	0	0	0
Ingroups:											
<i>Diphyscium suzukii</i>	1	1	1	0	2	0	0	0	2	1	2
<i>Diphyscium rupestre</i>	1	1	1	0	2	0	0	1	2	1	2
<i>Diphyscium mucronifolium</i>	1	1	1	0	2	0	0	1	2	1	0
<i>Diphyscium involutum</i>	1	1	1	0	2	0	0	1	2	0	1
<i>Diphyscium chiapense</i>	1	1	1	1	1	1	0	2	2	0	2
ssp. <i>unipapillosum</i>	1	1	1	1	1	0	0	2	2	0	2
<i>Diphyscium fulvifolium</i>	1	1	1	2	1	1	1	0	2	0	1
<i>Diphyscium foliosum</i>	1	1	1	2	0	1	2	0	2	2	2
<i>Diphyscium granulosum</i>	1	1	1	2	0	1	2	0	1	2	2

and Zharkikh, 1995). The fit of character data to phylogenetic hypotheses was evaluated using the consistency index (CI) (Kluge and Farris, 1969) and the retention index (RI) (Farris, 1989). The statistical significance of CI was determined according to Klassen et al. (1991).

Results and Discussion

Taxonomic Treatments

Six taxa of *Diphyscium* are revised, including three new additions to the moss flora of Taiwan. Diagnostic keys are provided.

Keys to the Species of *Diphyscium* in Taiwan

1. Laminal cells smooth 2
 2. Leaf apex apiculate *D. rupestre*
 2. Leaf apex acute *D. involutum*
1. Laminal cells mamilllose or papillose 3
 3. Laminal cells unipapillose *D. chiapense* ssp. *unipapillosum*
 3. Laminal cells pluri-papillose 4
 4. Upper portion of inner perichaetial leaves shallowly bifurcate, stomata distributing at orifice .. *D. fulvifolium*
 4. Upper portion of inner perichaetial leaves deeply bifurcate, stomata distributed at apophysis 5
 5. Leaves linear *D. foliosum*
 5. Leaves ovate-lanceolate *D. granulatum*

DIPHYSCIUM Mohr, 1803.

1. *Diphyscium chiapense* Norris ssp. *unipapillosum* (Deguchi) T. Y. Chiang and S. H. Lin, stat. nov.

Figure 1

Basionym. *Diphyscium unipapillosum* Deguchi, J. Jap. Bot. 59: 97, f. 1. 1984.—TYPE: Japan, Pref. Kochi: Kamiyashiki, Nakainura-shi; 380 m alt., *Deguchi 24901* (holotype in HIRO; isotype in TNS and Kochi University).

Syn. *Diphyscium buckii* Tan, Bryologist 93: 429, f. 1-5. 1990.

Taxonomic notes. This taxon was first described as *D. unipapillosum* (Deguchi, 1984b). Deguchi et al. (1997) synonymized both *D. unipapillosum* and *D. buckii*, a species described from the Philippines (Tan, 1990), with *Diphyscium chiapense* based on the uni-mamilllose-papillose (both dorsal and ventral sides) lamina cells. Nevertheless, they pointed out that *D. chiapense* has papillose subula of the perichaetial leaves, while the subulae of the two other taxa are smooth on the surface. They considered the papillosity of the subula as local expressions and summarized a conspecific relationship between the three taxa. Our own observation shows that materials collected in Taiwan also have smooth subula, as do *D. unipapillosum* and *D. buckii*. The smooth subula there-

fore appears to be stable in east Asian populations, from Japan to the Philippines, although few materials have been examined. From the view of phytogeography, the disjunct distribution between *D. chiapense* (Mexican populations) and *D. unipapillosum* (Asiatic populations) provides an opportunity for differentiation across geographical regions. Furthermore, the papillosity of subulae seems quite conserved in most *Diphyscium* species with no known polymorphism between populations. Based on the shared uni-mamilllose-papillose lamina cells, which suggest a common origin, as well as the differentiation of the papillosity of subulae, we recognize a subspecies status for *D. unipapillosum*.

Diagnosable characters. This taxon is characterized by uni-papillose laminal cells, differentiated stomata distributed at orifice of the capsules, smooth subula, and the absence of appendages on margins of inner perichaetial leaves.

Illustrations. Deguchi (1984): f. 1-2 (as *D. unipapillosum*); Tan (1990): f. 1-5 (as *D. buckii*); Deguchi et al. (1997): f. 1.

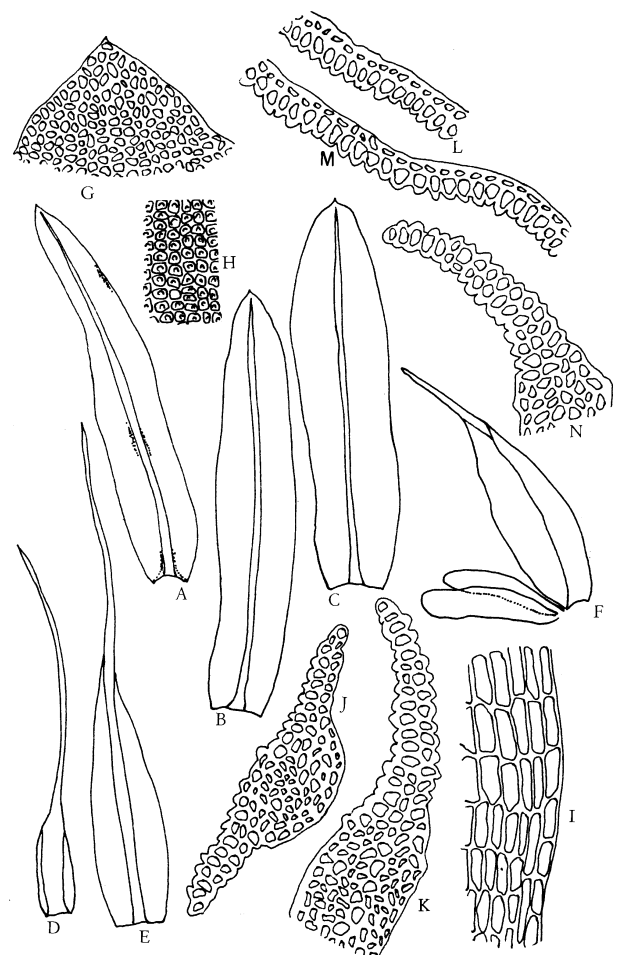


Figure 1. *Diphyscium chiapense* Norris ssp. *unipapillosum* (Deguchi) T. Y. Chiang and S. H. Lin (drawn from Chiang 25316). A-C, Leaves ($\times 32$); D-E, Perichaetial leaves ($\times 32$); F, Antheridia ($\times 71$); G, Apical cells of leaf ($\times 303$); H, Median laminal cells ($\times 303$); I, Cells from basal part of leaf ($\times 303$); J-N, Parts of cross-sections of leaf ($\times 303$).

Specimen examined. NANTOU HSIEN: Mt. Lu-lin, 2, 600 m alt., *Chiang 25316* (MO).

Distribution. Japan, Philippines and Taiwan (new record).

2. *Diphyscium foliosum* (Hedw.) Mohr, Ind. Mus. Pl. Crypt.: 3. 1803. Figure 2

Taxonomic notes. *Diphyscium foliosum* is closely related to *D. granulosum*, sharing pluripapillose leaf cells and a bifurcate apex of perichaetial leaves. The lingulate leaves distinguish *D. foliosum* from the latter species, which has ovate-lanceolate leaves. *Diphyscium foliosum* is a new addition to the moss flora of Taiwan.

Diagnosable characters. Leaves are strongly curled and contorted when dry, and are erect-spreading when moist. This species is characterized by the lingulate leaves, scabrous subula, deeply bifurcate upper portion of the perichaetial leaves, and pluri-papillose lamina cells.

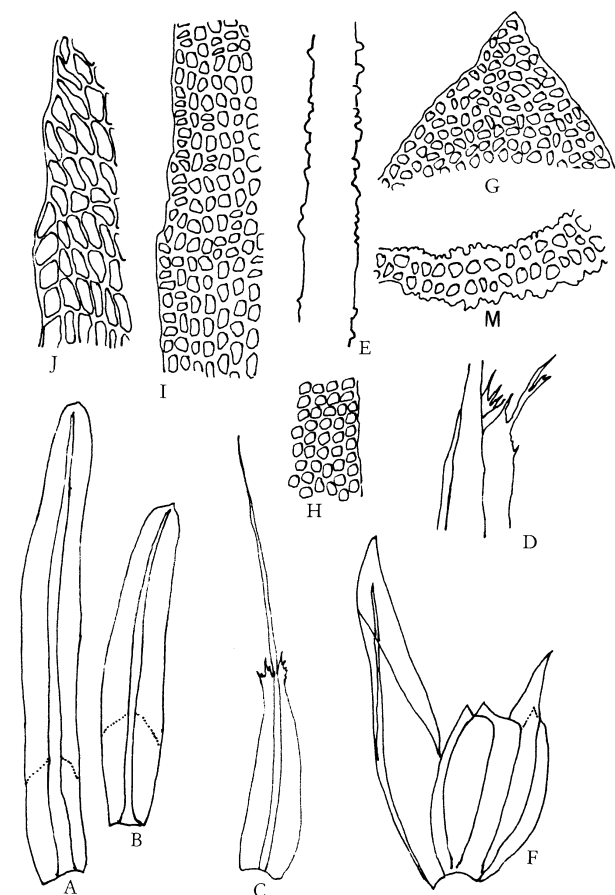


Figure 2. *Diphyscium foliosum* (Hedw.) Mohr (drawn from *Chiang 11465*). A-B, Leaves ($\times 32$); C, Perichaetial leaf ($\times 32$); D, Shoulder part of perichaetial leaf ($\times 71$); E, Surface of subula ($\times 71$); F, Antheridia ($\times 71$); G, Apical cells of leaf ($\times 303$); H-I, Marginal cells of leaf ($\times 303$); J, Cells of basal part of leaf ($\times 303$); K, Part of Cross-section of leaf ($\times 303$).

Illustrations. Iwatsuki & Mizutani (1972) f. 32; Noguchi (1976): f. 14h; Crum and Anderson (1981): f. 615; Noguchi (1987): f. 5A.

Specimen examined. KAOHSIUNG HSIEN: Mt. Chitou, ca. 2,700 m, *Chiang 11465* (HAST)

Distribution. N. and C. America, Europe, Africa, Japan and Taiwan (new record).

3. *Diphyscium fulvifolium* Mtt., Trans. Linn. Soc. Bot. 2, 3: 143. 1891. Syn. *Diphyscium rotundatifolium* Wang & Lin, Ann. Missouri Bot. Gard. 61: 526. 1974.—TYPE: Taiwan. Nantou Hsien, Luku Hsiang, Chitou, 1,150-1,750 m alt., 12 Nov 1971, *Lin s. n.* (holotype, TUNGH no. 1267!).

Taxonomic notes. *Diphyscium fulvifolium* is one of the most common species of this genus in Taiwan and is also highly polymorphic in leaf shape. Wang and Lin (1974b) reported *D. rotundatifolium* based on the obtuse to rounded leaf apices and uni-mamillose leaf cells. However, the description of the mamillosity of the leaf-cell surface was later found to be erroneous and was corrected to pluri-papillose (Iwatsuki, 1976). Iwatsuki (1976) further showed the variation in range of the leaf apices in both *D. fulvifolium* and *D. rotundatifolium* and reached the conspecificity conclusion. This species is generally distributed in the middle elevations of mountains in Taiwan.

Diphyscium fulvifolium is closely related to both *D. foliosum* and *D. granulosum*, sharing the pluri-papillose leaf cells. The shallowly bifurcate upper portion of the perichaetial leaves distinguishes it from the latter two species, in which the perichaetial leaves are deeply bifurcate.

Diagnosable characters. *Diphyscium fulvifolium* is characterized by pluri-papillose lamina cells, scabrous subulae, and shallowly bifurcate upper portion of the perichaetial leaves.

Illustrations. Iwatsuki & Mizutani (1972): Pl. 2, 23; Noguchi (1976): f. 14f; Wang and Lin (1974b): f. 1-34 (as *D. rotundatifolium*); Iwatsuki (1976): f. VI; Noguchi (1987): f. 4.

Specimens examined. TAICHUNG HSIEN: Anmashan, ca. 1,650 m, *Lin 4020*, *Wang 0042* (identified as *D. perminutum*) (TNM).

Distribution. Japan, Korea, China, Taiwan, and the Philippines.

4. *Diphyscium granulosum* Chen, Rep. Spec. Nov. Regn. Veg. 58: 34. 7. 1955. Syn. *Diphyscium macrophyllum* Wang & Lin, Hikobia 7: 21-24. 1974.—TYPE: Ilan Co., Tatung Hsiang, Mt. Taiping, ca. 2,000 m alt., 7 Jul 1972, *Lin s. n.* (holotype, TUNGH, no. 2804!).

Taxonomic notes. *Diphyscium granulosum* is phylogenetically related to *D. foliosum* in sharing the scabrous subulae and pluri-papillose lamina cells. Ovate-lanceolate leaves distinguish *D. granulosum* from the latter. This species is distributed in the middle elevations of mountain areas in Taiwan.

Diagnosable characters. *Diphyscium granulolum* is characterized by incurved leaves, both when dry and moist. Leaves are broadest at the base, tapering to an acute apex.

Illustrations. Wang and Lin (1974a): f. 1-25; Iwatsuki (1976): f. V.

Specimens examined. ILAN HSIEN: Mt. Taiping, ca. 2,200 m alt., *Lin 2804b* (TNM); KAOHSIUNG HSIEN: Hsiangyang, ca. 2,500 m alt., *Lin 1133* (TNM).

Distribution. China and Taiwan.

5. *Diphyscium involutum* Mitt., J. Linn. Soc. Bot. Suppi. 1: 149. 1859. Syn. *Diphyscium formosicum* Horikawa, Bot. Mag. Tokyo 49: 677. 1935.

Taxonomic notes. *Diphyscium involutum* is closely related to *D. suzukii* and *D. rupestre*, sharing the smooth lamina cells and subulae, and the absence of stomata. Narrowly-spathulate leaves and acute apices distinguish it from the latter two species. This species also shares dissected appendages on perichaetial leaves with *D. rupestre*.

Diagnosable characters. *Diphyscium involutum* is characterized by spatulate leaves with costa reaching to the apex.

Illustrations. Horikawa (1935): f. 31 (as *D. formosicum*); Bartram (1939): Pl. 28, f. 491; Iwatsuki and Mizutani (1972): f. 32; Noguchi (1987): f. 6.

Specimens examined. NANTOU HSIEN: Funghuangku, *Lin 11* (TNM). YUNLIN HSIEN: Kukeng, 1,400 m alt., 21 Feb 1991, *Lin s. n.* (TNM); KAOHSIUNG HSIEN: Mt. Nanfeng, *Wang 1098* (TNM).

Distribution. Japan, Taiwan, the Philippines, India, Sri Lanka.

6. *Diphyscium rupestre* Doz. et Molck., Pl. Jungh. 3: 340. 1854. Figure 3

Taxonomic notes. *Diphyscium rupestre* was described only from tropical Asia. This species is related to *D. mucronifolium* Mtt. and *D. suzukii* Iwats. phylogenetically. The three species, belonging to the group with smooth lamina cells, also share the apiculate leaf apices that distinguish them from *D. involutum*. The cilia appendages on the perichaetial leaves distinguish *D. suzukii* from the other two species, which in contrast have dissected apices on the appendages. The excurrent costa distinguishes *D. mucronifolium* from *D. rupestre*. *Diphyscium rupestre* is reported for the first time in Taiwan and in the As2 area as well.

Diagnosable characters. *Diphyscium rupestre* is characterized by its three-celled margins, smooth lamina cells, and apiculate leaf apices.

Illustrations. Fleischer (1922): f. 248; Bartram (1939): pl. 28, f. 492.

Specimens examined. TAINAN HSIEN: Mt. Taddon, ca. 600 m alt., *Chiang 5547*, *Lin 5547* (TNM; MO).

Distribution. Philippines, Malesia, and Taiwan (new record).

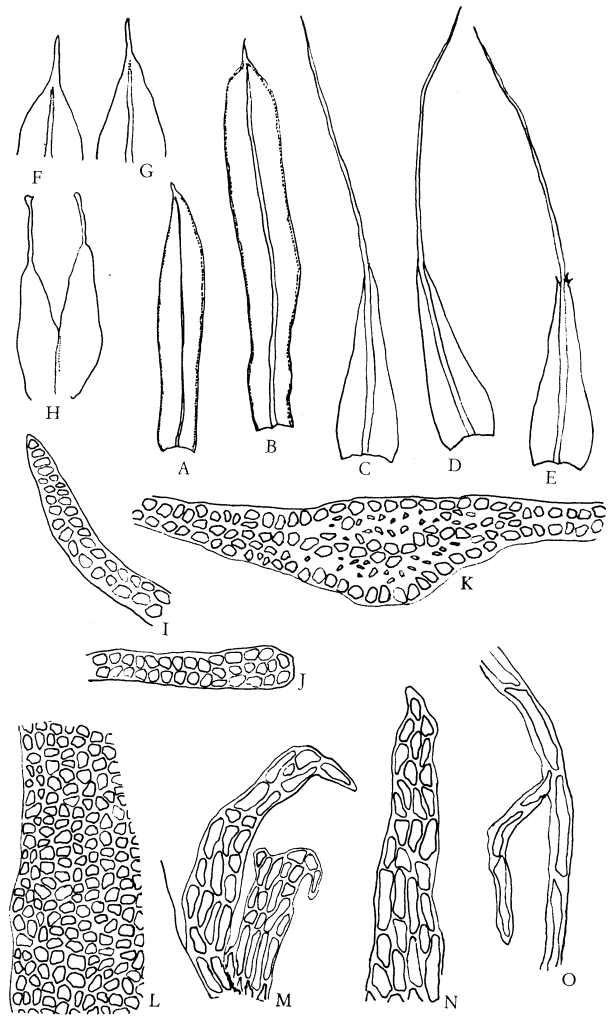


Figure 3. *Diphyscium rupestre* Doz. & Molck. (drawn from Chiang 5547). A-B, Leaves ($\times 32$); C-E, Perichaetial leaves ($\times 32$); F-G, Leaf apices ($\times 72$); H, Archegonia ($\times 72$); I-J, Cross-sections of leaf margin ($\times 303$); K, Cross-section of costa ($\times 303$); L, Marginal cells of leaf ($\times 303$); M, Appendages of pedchaetial leaf ($\times 303$); N, Cells of basal part of leaf ($\times 303$); O, Rhizoid ($\times 303$).

Phylogeny Reconstruction

In order to test Norris' (1981) classification, cladistic analysis was conducted on the morphological characters based on the parsimony assumption using PAUP. Two equally parsimonious trees (Figure 4) were recovered with 22 steps, a consistency index (CI) of 0.818 ($p < 0.05$), and a retention index (RI) of 0.840, rooted at *Theriotia kashimirensis* and *T. lorifolia*. *Diphyscium* is differentiated from *Theriotia* by four morphological characters (1-3, 11). The monophyly of *Diphyscium* is significantly supported, with a bootstrap value of 100%. Three groups can be identified: the group with smooth lamina cells [*D. involutum*, (*D. mucronifolium*, (*D. rupestre*, *D. suzukii*))], the group with pluripapillose lamina cells [*D. fulvifolium*, (*D. granulolum*, *D. foliosum*)] and the group with single-

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台灣產短頸蘚屬植物的分類訂正及親緣分析研究

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本研究針對台灣產六種短頸蘚植物進行分類訂正，其中包含單疣短頸蘚（新位階），並提供一檢索表，為測試 Norris 及 Deguchi et al. 的分類假說，本研究針對九種分布於亞洲的短頸蘚根據十一個形態特徵進行親緣分析。以厚葉蘚為外群，PAUP 鑑定出兩個等簡約的親緣樹，由重建的親緣顯現葉細胞具單疣及多疣的分類群最為近緣，而不支持 Norris 的假說，相對地，Deguchi et al. 依據細胞壁的特性所提出的三分類群被顯著的支持。依據重建的親緣，分布於胞蒴口緣的氣孔在本屬為多次演化，而在卷葉短頸蘚及其近緣種中則為單一的二次消失事件。

關鍵詞：分岐分類學；短頸蘚；單疣短頸蘚；口緣氣孔；疣；親緣；台灣；分類。